Integrating human and species habitat preferences in conservation in heterogeneous urban settings

Heather A Sander ⓘ, Cody B Hodson and Brandon M Macdougall

Department of Geographical and Sustainability Sciences, University of Iowa, Iowa City, IA 52242, USA

Summary

Cities are becoming increasingly important to biodiversity conservation, conservation that could also benefit urban people given the importance of nature to human well-being. Urban conservation is challenging, however, given cities' primary role as human habitats and the need to simultaneously support heterogeneous human and wild species communities in similarly heterogeneous environments. We demonstrate a framework for identifying conservation zones within cities and human and species habitat preferences within them, thereby identifying habitat attributes that management could target to support human well-being and conservation objectives. The framework first categorizes conservation zones within a city, then develops species indicator communities for each zone. Habitat preferences are identified for each indicator community using richness modelling, and human habitat preferences within zones are identified using one of several approaches. Lastly, habitat preferences are compared to identify commonalities and differences within zones. We demonstrate our framework in Iowa City (IA, USA) using songbirds, identifying similarities in human and bird habitat preferences within conservation zones that management could target to support human well-being and species conservation and differences in preferences that could be proactively managed to reduce conflict. This framework can thus identify key habitat attributes and approaches to inform conservation planning targeted to specific settings within cities.

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Introduction

Cities are becoming increasingly important sites of biodiversity conservation (Ellis 2013). While urban species assemblages are generally depauperate (Aronson et al. 2014), cities provide enhanced habitats for some species (Shochat et al. 2010, Bateman & Fleming 2012). Given unique urban biotic communities (Aronson et al. 2016) and the proportion of species cities support, urban conservation could enhance biodiversity. Urban conservation, by increasing urban biodiversity and human–nature interactions, could also benefit humans given the benefits to human health and well-being associated with biodiversity exposure (Luck et al. 2011, Bell et al. 2018, Liddicoat et al. 2018) and the potential to mitigate extinction of experience with nature whereby limited opportunities to interact with nature lead to disconnection from it, reduced quality of life and loss of understanding and concern for nature (Miller 2005, Soga & Gaston 2016). Enhancing urban biodiversity could also build support for conservation given that frequent nature interaction is linked to higher likelihood of participation in conservation efforts (Prévot et al. 2018). Despite this potential to benefit both humans and biodiversity, urban areas remain underexplored as conservation sites, making urban conservation an area of research need (Aronson et al. 2017).

Urban conservation must consider the requirements and preferences of diverse urban species and human residents (Aronson et al. 2017, Turo & Gardiner 2020) across similarly diverse urban environments. Urban humans are highly heterogeneous in their environmental preferences (Cho et al. 2008, 2009, Sander & Zhao 2015) and respond differently to various conservation actions (Turo & Gardiner 2020). Urban species' habitat requirements are also heterogeneous, leading to the assembly of different communities in different urban settings (Aronson et al. 2016). The high spatial heterogeneity of urban landscapes (Pickett et al. 2001) also complicates urban conservation, making management actions that are suitable for some urban settings inappropriate in others. Failure to recognize this heterogeneity could produce management that fails to support humans, biodiversity or both. Additionally, the importance of engaging local residents throughout conservation activities is well-established (Turo & Gardiner 2020) but requires researchers and policymakers to come to the table with knowledge of both human preferences and conservation requirements to ensure the productivity of stakeholder activities, information that is often lacking early in conservation planning.

How, then, can urban environmental management be structured and informed to support biodiversity conservation and human quality of life, recognizing environmental variation within

cities and diversity in their human and non-human inhabitants? Past work suggests efforts should target particular species in different urban 'habitat zones' (Goddard et al. 2010, 2017). The spatial locations of these habitat zones could be clearly delineated within cities (e.g., based on land cover). The resulting zones could then be used as formal 'conservation zones' to which conservation objectives, targets and management activities appropriate for the habitats and limitations of specific urban settings could be designed and applied. Urban humans, in making choices regarding housing, select living environments based on their preferences in a way that resembles species habitat selection, balancing their preferences with the costs associated with particular housing attributes, including local environmental attributes, to select residences that represent their perceptions of human habitat quality. Conservation zones might thus be extended to represent not just urban species habitat types and preferences, but also human habitat types and preferences in different urban settings.

We present a framework for informing urban conservation planning in existing urbanized settings that identifies urban conservation zones and corresponding species targets and assesses and integrates human and species habitat preferences in these zones using techniques from ecology, geography and economics. We hypothesize that human and wild species habitat preferences will vary among zones, reflecting key attributes of these settings for both groups given that species assemblages vary within cities based on habitat requirements and that humans select different neighbourhood settings based on their preferences. In so doing, we recognize that the habitat preferences identified using this framework will not accurately reflect the requirements of species that humans actively and successfully seek to maintain or exclude (e.g., garden plants, invertebrate pests), but will be more accurate for species that experience less direct human management. We further hypothesize that humans and species occupying a given zone will have similar habitat preferences. We demonstrate our approach in Iowa City (IA, USA) and discuss how zone-specific comparisons in human and species habitat preferences could inform conservation planning efforts within cities to simultaneously support biodiversity and human well-being.

Methods

Framework overview

Our framework (Fig. 1) begins with conservation-zone delineation. This process could be subjective (e.g., based on neighbourhood boundaries or input from local planners) or could identify environments based on attributes such as land cover using techniques such as *k*-means (MacQueen 1967), hierarchical (Rokach & Maimon 2005) or spatially constrained multivariate (Duque et al. 2007) clustering. Clustering approaches could delineate zones that better represent environmental conditions while subjective approaches could produce zones that are easier to administer in practice. Approach selection should be based on social–ecological conditions or conservation programme objectives. The resulting conservation zones should reflect particular habitat conditions and will be the focus of tailored management efforts focused on local conservation objectives.

Our second framework step identifies indicator communities for each zone while our third framework step identifies their habitat requirements. Indicator communities are multi-species conservation surrogates that consist of species with close links to zones whose habitat requirements indicate zone attributes that affect their biotic communities. Conservation surrogates are often required when time and funding limitations constrain projects (Caro et al. 2010), and different surrogates are typically needed for different conservation zones (Goddard et al. 2010). We suggest that indicator communities, rather than single indicator species, may better represent broader communities and support their conservation (Roberge & Angelstam 2004). The focus of these communities (e.g., taxonomic, rare species, common species) should reflect conservation programme objectives and should be selected in collaboration with local experts and stakeholders to ensure their fit with those objectives. As noted above, human-maintained species such as garden plants and pest species against which humans mount active control measures should be avoided in constructing indicator communities as their abundance may reflect human management more than local habitat conditions.

Indicator-community development uses georeferenced, species abundance data for a taxon or multiple taxa, depending on conservation goals. Data could be collected by experts or citizen-scientists via field surveys or from existing sources (e.g., Sullivan et al. 2014). Observations are classified by zone, and species closely associated with a zone are identified using indicator-community analysis (e.g., Dufrêne & Legendre 1997) and comprise its indicator community. Community abundance or richness modelling techniques are then employed to assess each indicator community's relationships with habitat attributes. Coefficients for covariates from these models identify key habitat attributes and relationships for each management in a conservation zone.

Our fourth framework step identifies human habitat preferences within conservation zones. Surveys, participatory mapping or focus groups could be used to identify preferences for the habitat attributes used in indicator-community habitat modelling. Preference assessment could also use revealed-preference economic valuation techniques (e.g., contingent valuation, hedonic pricing) that identify habitat preferences based on surveys or the values of marketed goods to which they contribute (Freeman 2003).

The final framework step identifies similarities and differences between indicator-community and human habitat preferences by comparing human and indicator-community habitat preferences by conservation zone. Attributes with similar relationships for humans and indicator communities could be managed to support both species conservation and human well-being in each zone. Management of attributes with different relationships could cause conflict. Management should avoid these attributes if possible or proactively address potential conflict prior to implementation. Conservation zones and their identified human and species habitat relationships could thus provide preliminary data to guide conservation planning activities including stakeholder discussions and management plan development, providing a foundation for conservation planning.

Case study

We demonstrate our framework in Iowa City, a city of 75,000 residents, which consists predominantly of suburban environments over an area of 65 km^2 (US Census 2018) and includes grass (43%), impervious (27%), forest (17%), agriculture (10%) and water and wetland (3%) cover. Most wetland and contiguous forest cover occurs in parks. Surrounding landscapes consist largely of corn and soybean agriculture (IDNR 2012). Iowa City encourages urban infill and most new construction within the city occurs on urban renewal sites and agricultural land (City of Iowa City, 2013), while most development in the surrounding area occurs on

A. Step 1: Conservation zone delineation

1. **Goal**: Identify conservation zones in a study area landscape
2. **Case Study**
   a. Identified land-cover attributes
      i. Overlayed land-cover raster with 50-m grid in GIS
      ii. Calculated % tree canopy, grass, and impervious cover for each cell
   b. K-means clustering
      i. Inputs: Grid cell % cover of tree canopy, grass, and impervious cover
      ii. Constructed and compared schemes of 4-12 conservation zones
3. **Output**: Grid of study area with cells classified into conservation zones

B. Step 2: Indicator community development

1. **Goal**: Identify indicator community for each conservation zone from (A)
2. **Case Study**
   a. Identified 50-m survey plots in each zone from (A) using stratified, random sampling the grid from (A)
   b. Conducted point-count surveys on identified plots
   c. Predicted true abundance of each species using binomial N-mixture models
   d. Identified indicator species for each conservation zone using Dufrene-Legendre indicator species analysis
3. **Output**: Indicator communities (groups of indicator species) for each

C. Step 3: Indicator community habitat preference identification

1. **Goal**: Identify habitat preferences of indicator communities for each zone from (B)
2. **Case Study**
   a. Identified indicator community species richness for each visit to each plot
   b. Calculated habitat covariates for each plot and neighbourhood (250-m buffer)
      i. GIS: Land-cover and vegetation covariates (Table S1)
      ii. Fragstats: Landscape metrics (Table S1)
   c. Construct binomial N-mixture models for richness of each indicator community
3. **Output**: Habitat preferences of each indicator community

D. Step 4: Human habitat preference identification

1. **Goal**: Identify habitat preferences of human residents of each zone
2. **Case Study**
   a. Assemble dataset:
      i. Identified sample: Single-family residences (parcels) sold 2011-2015
      ii. Identified structure and neighbourhood attributes for each parcel
      iii. Calculated habitat covariates for each parcel and neighbourhood as in (C.2.b)
   b. Hedonic price modelling using geographically weighted regression (GWR)
      i. Ran GWR with data from (2a) to identify relationships between sale price and structural, neighbourhood, and habitat attributes
      ii. Calculated mean coefficient value for covariate in each conservation zone
3. **Output**: Habitat preferences of human residents of each conservation zone

E. Step 5: Comparison of human and bird habitat preferences

1. **Goal**: Identify similarities and differences in human and bird habitat preferences in each zone
2. **Case Study Output**: Comparison of coefficients for each conservation zone from (C) and (D) to identify similarities and differences

Fig. 1. Flowchart that depicts the five framework steps, their goals and the steps used in their implementation in the case study example.

agricultural land (Johnson County, 2020). We identified conservation zones, human habitat preferences and indicator communities and their habitat requirements for this study area to illustrate our framework (Fig. 1).

In the first step in our framework, we used *k*-means clustering to identify conservation zones (Fig. 1a). This process began by overlaying a 50-m grid on the study area, then identifying proportional built (e.g., pavement, buildings), canopy and grass cover in each grid cell using 1-m resolution 2009 High-Resolution Land Cover (HRLC; IDNR 2012) updated to represent development since 2009 (see Zhao & Sander 2018) and a lidar-derived urban forest dataset (Zhao & Sander 2018) in *ArcGIS* v10.6 (ESRI 2018). We then used the resulting dataset to implement *k*-means clustering in the *R* v3.4.1 ('Single Candle') package *stats* (R Core Team 2017) to delineate different conservation zone classification schemes for our study area based on proportional built, canopy and grass cover in each 50-m grid cell. We constructed and examined a series of classification schemes that grouped grid cells into 4–12 zones and selected the scheme that produced conservation zones that were neither too general (i.e., covering large areas of heterogeneous landscapes) nor too specific (i.e., covering small, fragmented areas

or including very few grid cells); in this case, this meant selecting a scheme that included five zones. Each grid cell in our 50-m grid was thus classified into one of five conservation zones.

In our second framework step (Fig. 1b), we used point-count data to construct songbird indicator communities for conservation zones. Using stratified random sampling, we selected 259 survey plots (hereafter, 'plots') to represent the proportional occurrence of each conservation zone type in the study area. To do so, we used conservation zones as strata and sampled a number of grid cells proportionate to the occurrence of each zone type in the landscape. We used the centroid of each selected grid cell as the centre of a 50-m radius survey plot. Two experienced birders conducted 10-min point-count surveys (Reynolds et al. 1980) on these plots from June to mid-July (the peak breeding season in eastern Iowa) during 2014–2016 on dry days without strong winds within 4 h of sunrise (Bibby et al. 2000), visiting each plot four times in total (Sander & McCurdy 2021). Half of these plots were visited twice in 2014 and twice in 2015, 40% were visited twice in 2015 and twice in 2016 and 10% were visited once in 2014 and three times in 2015 due to flooding that restricted access to these plots in late June and early July of 2014.

We next constructed binomial *N*-mixture models – hierarchical models that use repeated counts to predict true abundance adjusting for imperfect detection probability (Kéry et al. 2005) using the *R* package *unmarked* (Fiske & Chandler 2011) for species detected on 5% or more of plots given the lower effectiveness of this approach for less commonly detected species. Excluding these species assumes that the conservation of more common species is the focus of this application; in cases where conservation targets rarer species, alternative modelling approaches such as multispecies beta *N*-mixture modelling (Gomez et al. 2018) or approaches that use rarefaction could be employed. These models include detection (i.e., likelihood of observing a species that is present) and abundance (i.e., true abundance given imperfect detection) sub-models. We included minutes since sunrise, plot forest cover from the HRLC and categorical covariates for survey year and surveyor in our detection sub-model and agricultural, grass and built cover from the HRLC and canopy cover from an urban forest dataset as abundance covariates (Supplementary Table S1, available online). We first fitted detection models with all abundance covariates using all combinations of detection covariates and Poisson distributions and selected the best-fitting model based on the minimum Akaike information criterion (AIC), then we fit abundance sub-models in the same manner. We refitted top models with zero-inflated Poisson and negative-binomial distributions, selecting models that minimized AIC, and calculated goodness-of-fit statistics following MacKenzie and Bailey (2004). We assessed residual spatial autocorrelation for each model using Moran's *I* statistic and, when results were significant, calculated spatial autocovariates in the *R* package *spdep* (Bivand & Yu 2022) using the *autocov_dist* function and added them to the top models to address this autocorrelation. We used the resulting models to predict the true abundance of each species on each plot, then we used the *multipatt* function of the *R* package *indicspecies* (De Cáceres & Legendre 2009) to implement Dufrêne–Legendre indicator species analysis to identify species with significant, positive relationships between abundance and each conservation zone. These species comprised the indicator community for that zone.

In our next framework step, we modelled relationships between indicator-community species richness and habitat attributes to identify indicator-community habitat attributes (Fig. 1c). We first pooled counts of species in each indicator community to create indicator-community richness datasets for each visit to each plot. We calculated habitat covariates for plots and 250-m radius areas

surrounding them (hereafter, 'neighbourhoods') from the above datasets (Table S1) in *ArcGIS* to identify habitat attributes on and surrounding each plot including built, agricultural, grass, wetland and water cover; mean canopy cover and tree height; and vertical structure and tree height standard deviation (Table S1). We calculated attributes at both local (plot) and neighbourhood (250-m) levels given that birds respond to their environments at local and landscape levels in choosing breeding sites (Pennington & Blair 2011, Rega-Brodsky & Nilon 2017), suggesting that habitat management should focus on both extents. Other applications of this approach could include variables measured over either one or both of these extents to match with the extents over which conservation actions will be targeted. Lastly, to measure landscape structure on and surrounding each plot, we calculated landscape metrics, including the patch cohesion index (a metric that identifies the degree to which patches of the same land-cover type are aggregated such that values of 0 indicate isolation while increasing values indicate increasing aggregation; i.e., spatial connectivity) to indicate forest, built and grass connectivity and Simpson's diversity index to identify land-cover heterogeneity using *Fragstats* v4 (McGarigal et al. 2012) and the HRLC. We used this dataset and the detection covariates employed in species abundance modelling to construct binomial *N*-mixture models in order to identify the relationships between the species richness of each indicator community (i.e., count of species observed on a site) and mean-centred and scaled habitat covariates using the process outlined above. We used coefficients for habitat covariates from the final richness models for each indicator community to identify habitat relationships for its conservation zone.

In our next framework step, we identified human habitat preferences using a local hedonic pricing model (HPM), an economic valuation technique that can utilize readily available tax-assessor data (Fig. 1d). HPM is a statistical modelling approach under which the sale price, P, of a marketed good (e.g., residential parcel), i, is seen as a function of its structural (S_i), neighbourhood (N_i) and environmental (habitat) attributes (Q_i; Freeman 2003), such that:

$$P_i = \beta_0 + \beta_1 S_i + \beta_2 N_i + \beta_3 Q_i + \varepsilon_i \qquad (1)$$

Estimated coefficients identify the direction and magnitude of the relationships between parcel price and covariates, and, under assumptions that the geographical area in question represents a single, perfectly competitive market in equilibrium and that buyers are well-informed, the covariates also identify how much homeowners are willing to pay for those attributes (Freeman 2003), thereby indicating homeowner preferences for those attributes, including preferences for habitat attributes. While HPMs typically use global regression, fitting one regression equation for a study area with one coefficient for each covariate, they can be implemented using a local regression technique, such as geographically weighted regression (GWR). GWR can capture variation in homeowner preferences by estimating coefficients for each covariate for each parcel in a sample, such that:

$$P_{ij} = \beta_{j0} + \beta_1 S_{ij} + \beta_2 N_{ij} + \beta_3 Q_{ij} + \varepsilon_{ij} \qquad (2)$$

where j represents specific parcels (Fotheringham et al. 2002). We used GWR to estimate HPMs using the attributes of 2316 single-family residences and the land (i.e., cadastral parcel) associated with them (hereafter, 'parcels') that sold in the area during 2011–2015 identified from data from the Iowa City Tax Assessor. The single-family parcels used in this case study occurred

solely in existing residential areas (i.e., they were not in newly developed locations) within the City of Iowa City's municipal boundary, which is in alignment with the intent of the framework to support conservation in existing urbanized settings and not to identify or plan building in undeveloped locations. In implementing GWR, we used the natural logarithm of the sale price in 2015 US\$ as our dependent variable and included structural covariates from tax-assessor data (lot area in acres; building and garage area in ft^2; numbers of rooms, bathrooms and fireplaces; age in years; presence of air conditioning; location in a flood zone) and binary covariates for the presences of a neighbourhood elementary school to indicate neighbourhood attributes. We calculated habitat covariates for parcels (all land within the ownership boundary for each parcel) and surrounding neighbourhoods (Table S1) as described above for bird modelling. We utilized a spatially adaptive kernel and followed a cross-validation approach that used predicted values to minimize the residual sum of squares and an adaptive bandwidth of *c.* 85 neighbours in implementing GWR. We identified parcels with significant relationships between each covariate and sale price in each zone, then we calculated the mean coefficient for that covariate for those parcels and used the resulting values to identify human habitat preferences in each zone.

In our last framework step, we compared mean coefficients for each zone with indicator-community habitat relationships to identify commonalities and differences in the habitat preferences of humans and indicator communities within conservation zones (Fig. 1e).

Case study results

The *k*-means analysis from our first framework step (Fig. 1a) identified five conservation zones in the study area (Fig. S1). Zones included a higher-intensity (HI) zone with high built and minimal grass and canopy cover and a moderate-intensity grass (MIG) zone with moderate built and grass cover and low canopy cover. Lower-intensity zones with low built cover included a mixed vegetation (LIM) zone with similar canopy and grass cover; a grass-dominated (LIG) zone with high grass and low canopy cover; and a canopy zone (LIC) with high mean canopy and minimal grass cover. Our sample of parcels included 119 HI, 636 MIG, 798 LIM, 346 LIG and 417 LIC parcels, while our songbird survey plots included 60 HI, 37 MIG, 65 LIM, 35 LIG and 62 LIC plots.

In the point-count surveys from our second framework step (Fig. 1b), surveyors recorded 65 bird species with highest richness on LIM plots (mean = 12.06, S D= 3.75) and lowest richness (mean = 6.73, SD = 2.79) on HI plots. We constructed abundance models for 40 species detected on 5% or more of plots given that binomial *N*-mixture models are less effective for less commonly observed species (Fig. 1b & c). Two models failed to converge, resulting in 38 models with which we predicted true species abundance for use in Dufrêne–Legendre indicator species analysis. Based on this analysis, we identified indicator communities that included 6–11 species with predicted abundances that were positively correlated with each conservation zone (Box 1). The LIC indicator community included 11 predominantly cavity- and tree-nesting, forest and open woodland species. The LIG indicator community included nine tree- and cavity-nesting species, approximately half of them typical of scrub or grassland and approximately half of them typical of forest or open woodland, suggesting edge habitat with mixed vegetation. The LIM indicator community included six mainly open-woodland species: three shrub, two tree and one secondary cavity-nesting species. The

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Box 1. Bird species included as indicator communities for each conservation zone as identified using Dufrêne–Legendre indicator species analysis.

High-intensity (HI)
Common grackle (*Quiscalus quiscul*)
European starling (*Sturnus vulgari*)
House finch (*Haemorhous mexicanus*)
House sparrow (*Passer domesticus*)
Song sparrow (*Melospiza melodia*)
Rock pigeon (*Columba livia*)

Moderate-intensity grass (MIG)
American crow (*Corvus brachyrhynchos*)
American robin (*Turdus migratorius*)
Brown-headed cowbird (*Molothrus ater*)
Black-capped chickadee (*Poecile atricapillus*)
Cedar waxwing (*Bombycilla cedrorum*)
Chipping sparrow (*Spizella passerina*)

Low-intensity mixed vegetation (LIM)
American redstart (*Setophaga ruticilla*)
Baltimore oriole (*Icterus galbula*)
Gray catbird (*Dumetella carolinensis*)
House wren (*Troglodytes aedon*)
Indigo bunting (*Passerina cyanea*)
Northern cardinal (*Cardinalis cardinalis*)

Low-intensity grass (LIG)
American goldfinch (*Spinus tristis*)
Cerulean warbler (*Setophaga cerulean*)
Common yellowthroat (*Geothlypis trichas*)
Eastern towhee (*Pipilo erythrophthalmus*)
Eastern wood-peewee (*Contopus virens*)
Mourning dove (*Zenaida macroura*)
Rose-breasted grossbeak (*Pheucticus ludovicianus*)
Red-bellied woodpecker (*Melanerpes carolinus*)
Red-winged blackbird (*Agelaius phoeniceus*)

Low-intensity canopy (LIC)
Blue jay (*Cyanocitta cristata*)
Carolina wren (*Thryothorus ludovicianus*)
Downy woodpecker (*Picoides pubescens*)
Eastern bluebird (*Sialia sialis*)
Eastern phoebe (*Sayornis phoebe*)
Great-crested flycatcher (*Myiarchus crinitus*)
Hairy woodpecker (*Picoides villosus*)
Red-eyed vireo (*Vireo olivaceus*)
Ruby-throated hummingbird (*Archilochus colubris*)
Tufted titmouse (*Baeolophus bicolor*)
White-breasted nuthatch (*Sitta carolinensis*)

MIG indicator community included six largely open-woodland, tree-nesting species typical of suburban yards and parks. Four out of six HI indicator-community species were exotics common in intensely urban settings.

Best-fitting richness models from our third framework step (Fig. 1c) used a Poisson distribution and goodness-of-fit tests indicated reasonable fit. Two models (HI, MIG) exhibited significant residual spatial autocorrelation ($p < 0.05$). We estimated and added spatial autocovariates to these models, reducing spatial autocorrelation. Models included two to three detection covariates (Table S4). Abundance sub-model covariates and coefficient signs and magnitudes varied among zones (Fig. 2 & Table S4). HI indicator community richness exhibited a weak negative relationship with plot agricultural cover, stronger negative relationships with plot grass cover, cohesive forest and neighbourhood canopy cover and variation in tree height and positive relationships with plot grass cohesion and tree height. MIG indicator community richness was negatively related to plot grass, built, wetland and water cover and neighbourhood built, agricultural and water cover and tree height, with strong relationships for built and grass cover and weaker relationships for water cover. MIG richness was positively related to plot built cohesion and plot and neighbourhood Simpson's land-cover diversity. LIM indicator-community richness increased with decreasing neighbourhood water, grass and built cover, plot-level agricultural cover and neighbourhood tree height. LIM indicator-community richness also increased with increasing plot water and neighbourhood canopy cover and plot and neighbourhood land-cover diversity, with the strongest relationship being with neighbourhood built cover. LIG indicator-community richness increased with decreasing variation in tree height and built cohesion at the plot level and with decreasing built cover and increasing grass cohesion in neighbourhoods. LIC indicator-community richness exhibited strong negative relationships with plot grass and built cover, moderate negative relationships

with plot water, wetland and agricultural cover and neighbourhood variation in tree height, moderate positive relationships with neighbourhood canopy cover, tree height and grass cohesion and a strong positive relationship with neighbourhood forest cohesion. These diverse relationships between indicator-community richness and covariates among zones support the need to tailor approaches to bird conservation among urban settings.

Our results from our fourth framework step (Fig. 1d) indicate some similarities and many differences in human habitat preferences among zones (Figs 3–5 & Tables S2 & S3). The mean coefficients for many parcel-level covariates were in the same direction but of different magnitudes across zones (Figs 3 & 4 & Table S3). Parcel grass cover exhibited negative, weak mean relationships with parcel sale price across zones (Fig. 3). Parcel-level built cover exhibited positive relationships with sale price in all zones, with the strongest positive relationships being in the HI zone and the weakest relationships being in the LIC zone (Fig. 3). Water cover on parcels was negatively related to sale price across zones, with strong negative relationships on HI, LIM and LIC parcels and weak relationships and high variation on LIG and MIG parcels (Fig. 3). Relationships with parcel wetland cover were negative in HI, LIG and MIG zones and positive in LIM and LIC zones, with high within-zone variation in HI and LIM zones (Fig. 3). Parcel-level canopy cover and mean tree height exhibited weak, positive relationships with sale price across zones (Fig. 3). Parcel-level variation in tree height was negatively and similarly related to sale price across zones, with a slightly stronger relationship on LIG parcels (Fig. 4b). Negative relationships of equal magnitude occurred between parcel price and parcel-level grass cohesion across conservation zones (Fig. 3). Relationships between parcel-level built cohesion and parcel price varied, with mean negative relationships on LIG and MIG parcels and mean positive relationships on LIM, HI and LIC parcels (Fig. 3). Parcel-level forest cohesion exhibited similar, weak negative mean relationships with sale price across
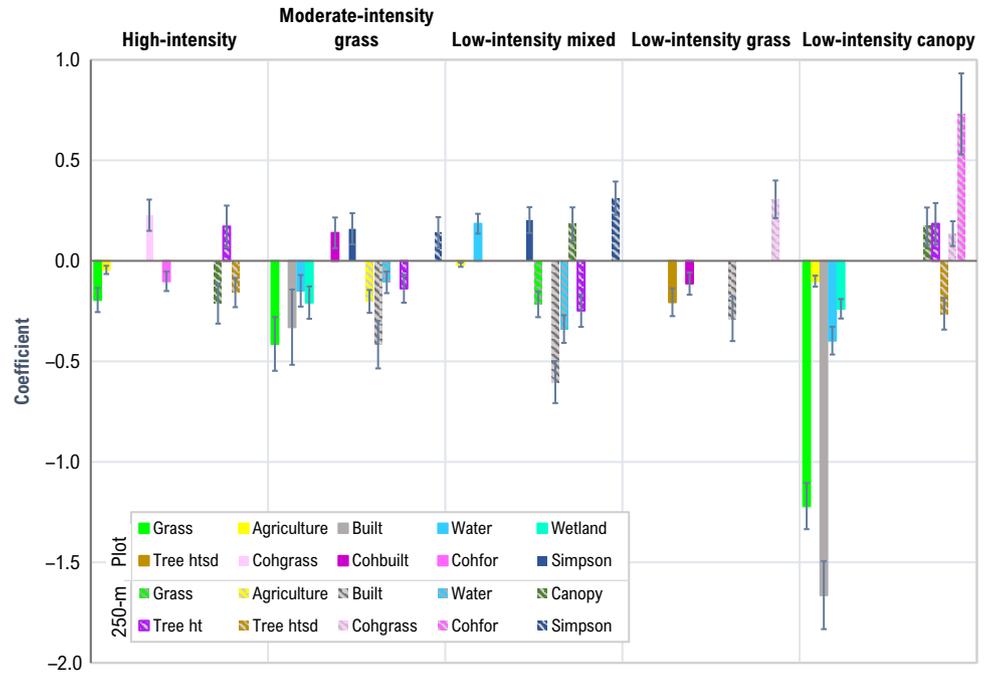
Fig. 2. Coefficients for survey plot and neighbourhood (250-m) covariates included in the top models of indicator-community richness. Positive coefficients indicate a positive relationship between a given covariate and indicator-community species richness, while negative coefficients indicate a negative relationship. Error bars are standard deviations. For covariate definitions, see Table S1. (Full models are given in Table S4.)

zones (Fig. 3). Lastly, parcel-level Simpson's land-cover diversity exhibited mean positive relationships with sale price across zones, with the strongest relationships being on LIM, LIG and HI parcels and weakest relationships being on MIG parcels (Fig. 4a).

Human preferences for neighbourhood covariates also varied among zones (Figs 4 & 5 & Table S3). Neighbourhood agricultural cover exhibited a weak negative relationship with sale price in the LIM zone and weak positive relationships in the HI, MIG, LIG and LIC zones, with high within-zone variation (Fig. 5). Neighbourhood grass cover was negatively related to sale price in the HI, LIM and LIC zones but positively related to sale price in the MIG and LIG zones, again with weak relationships and high within-zone variation (Fig. 5). Relationships with built cover were positive but weaker than parcel-level relationships (Fig. 5). Neighbourhood water cover was negatively related to sale price across zones, with the strongest relationship being in the LIM zone and weakest relationship being in the LIG zone (Fig. 5). Relationships with neighbourhood wetland cover were positive, with a strong relationship in the LIC zone, a weak relationship in the LIG zone and high within-zone variation in the LIG, MIG and LIM zones (Fig. 5). Mean relationships with neighbourhood urban forest attributes exhibited similarities and differences with parcel-level relationships (Fig. 4b). As at the parcel level, mean relationships between sale price and neighbourhood canopy cover were positive and similar across zones (Fig. 5). Mean relationships with neighbourhood tree height were negative in the MIG, LIG and LIM zones and positive in the HI and LIC zones but exhibited high within-zone variation (Fig. 4b). Neighbourhood tree height variation differed in its mean relationship with sale price among zones, with positive relationships in the HI, MIG and LIG zones and negative relationships in the LIM and LIC zones, as well as high variation in all zones except the LIC zone (Fig. 4b). Neighbourhood grass and built cohesion were negatively related to sale price on average, with much stronger relationships for built cover and moderate to high within-zone variation (Fig. 5). The LIG zone exhibited the strongest mean negative relationship with neighbourhood
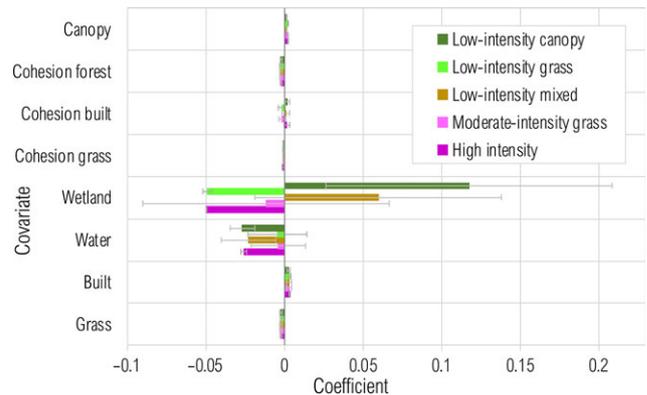
Fig. 3. Mean significant coefficients for parcel-level land cover and cohesion from the local hedonic pricing model by zone. Positive coefficients indicate a positive relationship between a given covariate and home sale price, while negative coefficients indicate a negative relationship. Error bars are standard deviations. For covariate definitions, see Table S1. (Full model specification is given in Table S2; mean coefficient values by zone are given in Table S3.)

grass cohesion with low variation, while the HI zone exhibited the weakest relationship with neighbourhood grass cohesion with high variation (Fig. 5). Relationships with neighbourhood forest cohesion were positive for the MIG and LIG zones and negative for the HI, LIM and LIC zones, with high variation within zones (Fig. 5). Neighbourhood Simpson's land-cover diversity exhibited strong, positive relationships with sale price across zones, with the strongest relationship being in the LIM zones and the weakest relationship being in MIG zones (Fig. 4a).

Commonalities and differences existed in urban bird and human habitat preferences within conservation zones (Fig. 6). While the directions of many relationships were similar, the magnitudes were usually different, especially for stronger relationships. HI birds and humans exhibited similar preferences for plot-level grass and forest cohesion and neighbourhood tree height but
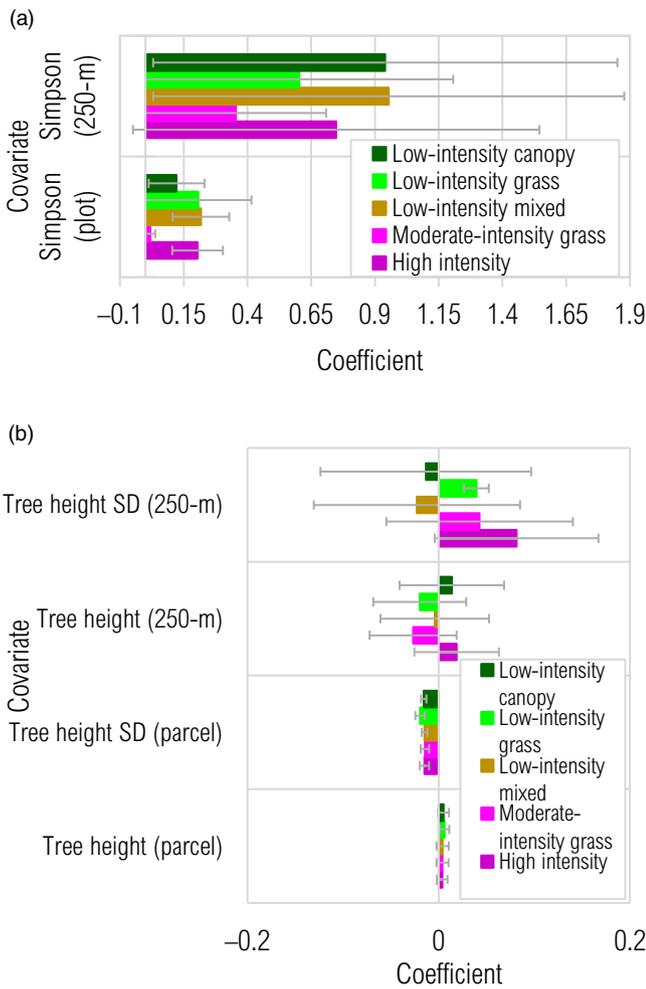
Fig. 4. Mean significant coefficients for parcel and neighbourhood-level (250-m) (a) Simpson's land-cover diversity and (b) tree height and tree height standard deviation (SD) from the local hedonic pricing model by zone. Covariate ranges are: (a) height 0–30, height SD 0–18; and (b) 0–1. Positive coefficients indicate a positive relationship between a given covariate and home sale price, while negative coefficients indicate a negative relationship. Error bars are standard deviations. For covariate definitions, see Table S1. (Full model specification is given in Table S2; mean coefficient values by zone are given in Table S3.)
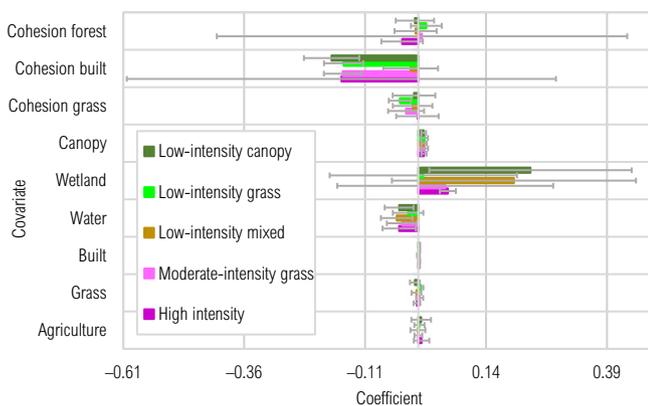
Fig. 5. Mean significant coefficients for neighbourhood (250-m) land-cover and cohesion covariates from the local hedonic pricing model by zone. Positive coefficients indicate a positive relationship between a given covariate and home sale price, while negative coefficients indicate a negative relationship. For covariate definitions, see Table S1. (Full model specification is given in Table S2; mean coefficient values by zone are given in Table S3.)

Variable	HI Home owner	HI Ind. comm.	MIG Home owner	MIG Ind. comm.	LIM Home owner	LIM Ind. comm.	LIG Home owner	LIG Ind. comm.	LIC Home owner	LIC Ind. comm.
Parcel/plot										
Grass	-0.002	-0.195	-0.002	-0.413					-0.002	-1.220
Built			0.003	-0.330					0.003	-1.663
Water	-0.026		-0.004	-0.149	-0.023	0.184			-0.027	-0.397
Wetland	-0.050		-0.012	-0.208					0.117	-0.239
Cohesion grass	-0.001	0.227								
Cohesion built			-0.001	0.139			-0.002	-0.113		
Cohesion forest	-0.002	-0.102								
Tree height sd							-0.004	-0.206		
Simpson			1.9E-4	0.159	0.002	0.203				
Neighbourhood										
Agriculture			1.0E-4	-0.202						
Grass					-0.004	-0.217				
Built			0.002	-0.417	2.0E-4	-0.603	0.002	-0.289		
Water			-0.034	-0.107	-0.045	-0.339				
Wetland										
Cohesion grass							-0.038	0.306	-0.009	0.135
Cohesionbuilt										
Cohesion forest									-0.007	0.731
Canopy	0.012	-0.213			0.012	0.184			0.011	0.172
Tree height	1.7E-4	0.171	-2.4E-4	-0.138	-4.0E-5	-0.248			1.2E-4	0.184
Tree height sd	0.015	-0.158							-0.002	-0.263
Simpson			0.004	0.141	0.010	0.312				

Fig. 6. Human and indicator-community (Ind. comm.) habitat preferences by conservation zone. Red boxes (solids in greyscale) indicate positive relationships between bird species richness or home sale price and a given covariate, while blue boxes (hashed in greyscale) indicate negative relationships. Values are coefficients. Darker shading indicates increasing preference magnitude. Only covariates included in indicator-community models are shown. For covariate definitions, see Table S1. HI = high-intensity; LIC = low-intensity canopy; LIG = low-intensity grass; LIM = low-intensity mixed vegetation; MIG = moderate-intensity grass.

differed strongly in their preferences for plot grass cohesion, neighbourhood canopy cover and variation in tree height, with negative relationships for the bird indicator communities and positive relationships for homeowners. The MIG zone exhibited seven preference commonalities and four disagreements, indicating common preferences for low grass, water and wetland cover and high land-cover diversity at the parcel/plot level and low water cover, smaller trees and high land-cover diversity in surrounding neighbourhoods. MIG birds preferred plots with little and less cohesive built cover and low neighbourhood agricultural and built cover, while humans preferred the opposite.

Low-intensity zones varied in the degree to which human and bird preferences coincided. The LIM zone exhibited high agreement with six commonalities (higher parcel/plot and neighbourhood land-cover diversity and lower neighbourhood grass and water cover, smaller trees and higher canopy cover) and two differences, with birds preferring high plot water and low neighbourhood built cover, but with humans exhibiting opposite preferences. LIG zone homeowners and birds both preferred low plot/parcel tree height variation and built cohesion, but homeowners preferred high neighbourhood built cover and low neighbourhood grass cohesion, while birds preferred the reverse. LIC indicator communities and human residents exhibited similarities for five covariates (low plot/parcel grass and water cover, high neighbourhood canopy cover and tall neighbourhood trees with little variation in height) and differences for three covariates: plot/parcel built and wetland cover, with humans preferring more and birds preferring less, and neighbourhood forest and grass cohesion, with human preferring lower levels and birds preferring higher levels.

Discussion

The goal of integrating the needs of heterogeneous human and non-human communities challenges urban conservation (Aronson et al. 2017, Turo & Gardiner 2020), as does urban environmental heterogeneity. The framework we designed and demonstrated could help address these challenges by identifying commonalities and differences in the habitat preferences of humans and biotic communities in specific urban settings. We found that humans and birds in similar urban environments exhibited at least some common habitat preferences that could inform management to support both human well-being and conservation, but we also found differences that could complicate management. Such information could particularly support conservation planning during its preliminary stages.

In accordance with past studies and our hypotheses, we found that human environmental preferences (Cho et al. 2008, 2009, Sander & Zhao 2015) and species habitat requirements (Aronson et al. 2016) varied among urban environments. Our case study identified few habitat attributes that could be managed to support conservation and human well-being city-wide, and most attributes varied in their relationships with parcel price, indicator-community richness or both among zones, supporting the need to target urban conservation to specific settings identified by past research (Goddard et al. 2010). Our framework extends this idea by producing a means for identifying conservation zones, indicator communities for them and habitat preferences for both their indicator communities and human residents.

Our case study demonstrated the ability of our framework to identify zone-specific human and bird habitat preferences that conservation planners could target. For example, common preferences of human and indicator communities suggest that both groups would benefit from policies that reduce lawn cover and provide tall trees and high canopy cover in the LIC zone and that minimize parcel/plot grass cover and provide patchy tree cover and tall neighbourhood trees in the HI zone. Such management acknowledges species and human habitat preferences and would provide for both in specific urban settings. Human residents may also be more receptive to conservation efforts that explicitly consider human preferences in this way but require further exploration through stakeholder-centred activities (e.g., focus groups, community forums).

Our approach identifies dissimilarities in human preferences and species–habitat relationships in conservation zones. LIG and HI homeowner and indicator-community habitat preferences differed in direction for half of the significant covariates from the bird models, suggesting that conservation will be more challenging in these zones than others. Conflict may be particularly great when human preferences for a key habitat attribute are strong. Awareness of such differences could help managers design and implement stakeholder engagement and management activities to avoid attributes of high disagreement or provide outreach to build understanding regarding the reasons behind actions that residents are unlikely to support. For example, LIG residents preferred neighbourhoods with low built cover and high grass cohesion, but indicator-community richness exhibited strong, opposite relationships with these attributes. Conducting public forums and educational programmes before undertaking management aimed at reducing built cover and increasing grass cohesion could build understanding regarding the benefits of such management and so bolster public support. Our comparison of human and bird indicator-community preferences also identified zones where

concurrently supporting species conservation and human well-being is likely to be easier (e.g., LIC) or more challenging (e.g., LIG), helping identify ways in which conservation planning may need to differ among settings.

The HI indicator community contained largely exotic species. Management to support them could prove contentious, particularly given the knowledge gap that exists in our understanding of exotic and novel urban assemblages (Aronson et al. 2017), but such management would ensure the presence of some biodiversity in these often hostile environments. Additionally, commonalities between human and indicator-community preferences in less intense zones could inform management to enhance native biodiversity in HI settings. For example, HI homeowners and MIG indicator communities preferred high neighbourhood land-cover diversity. Land-cover diversity was not significantly related to HI indicator-community richness, suggesting that increasing HI-zone land-cover diversity could support human well-being and bring in MIG species without impacting HI species, although interactions among these species require consideration.

Wild species and humans exhibit common preferences for some attributes that cannot or should not be managed to reflect identified preferences. For example, several human and bird communities preferred low plot or neighbourhood water or wetland cover. These features are difficult or illegal to alter and species not represented in indicator communities rely on them. The reasons for such negative preferences should be explored and addressed when possible. Additionally, indicator-community development could be improved by considering a broadly representative species pool (e.g., including upland and wetland species or explicitly including wetland and aquatic conservation zones) and could also focus on rare species or species of particular concern based on the objectives of an urban conservation programme.

Our framework could support conservation planning in many metropolitan areas. Tax assessor and land-cover datasets are broadly available in cities, and data to support indicator-community development and habitat modelling are available for some taxa (e.g., via eBird); citizen-scientists could also collect relevant data. Some analyses from our case study require expertise but could be implemented more simply using software that includes a graphical user interface (e.g., the GWR tool in *ArcGIS*). Species habitat modelling might benefit from collaboration with local universities, government agencies or consultants. Conservation planners could use our framework at the onset of conservation planning to highlight preliminary conservation zones and targets and provide understanding of human and species habitat preferences. This information could be used to construct initial management plans and facilitate focus groups and stakeholder meetings to identify the reasons behind relationships and preferences missed by the framework and to refine conservation plans. Importantly, this framework is meant to provide guidance for conservation planning focused on existing urban environments and should not be used in designing or identifying locations for new development.

Additional research and implementation in practice would refine our framework. Firstly, we did not use a spatial constraint in delineating conservation zones, allowing zones to be discontinuous. Spatially constrained multivariate clustering (e.g., via *ArcGIS*) would create contiguous zones. Secondly, our case study omitted non-linear relationships from HPM and richness modelling – relationships that warrant exploration. Additionally, our example focused on songbirds, particularly more common songbirds. Future studies should develop indicator communities with broader suites of species to provide representative species pools or using

rarer or particularly sensitive species to identify the habitat attributes of species of particular concern. Similarly, HPM focused on single-family homes fails to represent the values of many urban residents, including renters. HPM is also based on actual sales transactions and thus estimated values are probably a function of ability to pay and may thus miss the values of those less able to pay. Implementing models with rental datasets or using stated-preference techniques with broader stakeholder groups could extend representation in preference identification, increase stakeholder involvement and provide educational and consensus-building opportunities that could enhance support for conservation actions. Additionally, while conservation strategies focused on the habitat characteristics of indicator species in specific zones could act to maintain heterogeneous communities city-wide, they could lead to homogenization within zones. This potential should be carefully assessed (e.g., by modelling the effects of proposed management on communities within zones or through frequent monitoring of these communities as management occurs). Lastly, data quality could affect all framework analyses, making rigorous data selection and processing key to ensuring the reliability of identified relationships.

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