Rain Birds: Green Stormwater Infrastructure as Avian Migratory Habitat

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Abstract

Background, Question and Methods

Cities are often located on migratory flyways, and the urban stopover site may be a critical bottleneck in the lives of migratory species. These stopover sites can be composed of novel anthropogenic land cover types and configurations, with built elements as well as open space types. Green stormwater infrastructure (GSI) elements, including constructed wetlands, detention/retention ponds, bioswales, and rain gardens are designed for stormwater function, but may support resident or transitory wildlife. Research into the habitat value of rain gardens is scarce, but previous work on bird diversity in rural and urban contexts has supported the importance of patch area, vegetation structure, and plant diversity and origin. Some have found landscape-scale characteristics can also be predictive. Remotely-sensed data and GIS have become ubiquitous tools to replace labor-intensive methods of measuring habitat characteristics. What are important predictors of bird occurrence in urban GSI sites during spring migration?

During spring 2018, standardized area searches were performed for bird species in Ann Arbor, MI, USA, on GSI sites (n=37). Discrete-return LiDAR data was used to measure vegetation structure (including Foliage Height Diversity via the Shannon-Weaver Diversity index for 0.5′ return height bins) and classification of 4-band ortho-imagery to measure land cover within multiple scales around each site. Generalized linear models using Bayesian methods were built to analyze predictors of bird species richness, abundance, and abundance weighted by conservation value.

Results and Conclusions

3407 birds were recorded using the GSI sites, comprising 97 total species, including 22 of moderate or high conservation concern according to the Partners in Flight. The best model for landbird species richness included three positive significant explanatory variables (with mean-standardized parameter estimates: Site Area (0.175), % Shrub Cover (0.09), and Foliage Height Diversity (0.335), while the effect of Plant Species Richness was inconclusive. These results support that classic theories regarding bird occurrence in response to habitat structure prevail in novel ecosystems within urban settings. The explanatory power of foliage height diversity is a confirmation of vertical vegetation structure as an important determinant in bird diversity, as well as the utility of multiple-return LiDAR as a method to measure FHD. This is an important point in the urban context, where simplification of structure is a common practice, and shows that novel habitat types formed by GSI can support biodiversity close to where people live.

CONTENTS

INTRODUCTION

As global human population continues to grow—now above 7.6 billion, and projected to be 9.4-10.2 billion by 2050 (United Nations 2017)—the vast majority of that growth will be in urban areas (United Nations 2015). In the United States, 80.7% of people lives in cities and suburbs (US Census Bureau 2010). Areas classified as urban covered 3.1% of US land area in 2000 and are projected to cover 8.1% in 2050 (USDA 2015, Nowak 2005). This will result in 118,300 km^2 of forested lands being subsumed by urban growth, with most of that forest cover being removed but up to 20% retained within cities. Urbanization implies an almost complete alteration to remnant ecosystems, including changes in composition, structure and function (Faeth 2005, Aronson 2014). This results in both reduced species richness and evenness for most biotic communities including wild birds (McKinney 2006, Grimm et al. 2008, but see Saari 2016) as well as novel arrangements of biodiversity (McKinney 2002). Regardless of these changes and simplifications, the ecosystems that do persist in human-dominated landscapes still carry out important functions, e.g., regulation of atmospheric conditions, interception of air pollutants, recreation, aesthetics welfare (MEA 2005). Moreover, the design, development and management of human landscapes can shape the various ecosystem services provided by these urban areas.

Among the ecosystem services affected by urbanization, development restricts the ability of land surfaces to filter and infiltrate stormwater, which can exacerbate flooding and reduce downstream water quality. Traditional approaches to stormwater treatment in cities focus on piped solutions, moving excess volumes of water away from buildings and roads as quickly and efficiently as possible, subjecting receiving waters to concentrations of contaminants (Walsh 2005). Green stormwater infrastructure (GSI) involves treating stormwater closer to its source, by mimicking or exceeding the capacity of undeveloped areas to absorb, infiltrate, and clean stormwater (EPA 2014). At broader scales, green infrastructure is a landscape planning approach that envisions an interconnected network of natural areas and infrastructure that mimics natural function that are designed to support ecosystem services for a community (Benedict and McMahon 2006). Therefore, the implementation of GSI in a community can have benefits beyond stormwater treatment, including benefits to public health via reduced exposure to water and air pollutants, ameliorating extreme heat, recreation and social activity (EPA 2017). Furthermore, plant-based GSI that increases local floristic and faunal diversity could support organisms with conservation value, provided that they function as habitat in a similar way to remnant and restored habitats.

Like a growing number of communities, Washtenaw County, in southeast Michigan, USA, has recognized the benefits of GSI. The Washtenaw County Water Resources Commissioner's Office (WCWRC) has regulatory authority over stormwater management and provides to developers a set of stringent design standards directly addressing flood control and water quality (Washtenaw County Resources Commissioner, 2016). These rules for low-impact development are driven by the need for the county to comply with the Clean Water Act of 1972 and its subsequent amendments. The city of Ann Arbor has taken the uncommon step of operating a stormwater utility, which collects fees from ratepayers based on impervious surface on their property, and helps encourage infiltration. Low-impact development is complemented by a land-based publicly owned GSI system consisting of 124 units in 34 locations, including rain gardens, detention basins and constructed wetlands. The system is managed comprehensively to support multiple functions, including water quality, acceptance by the public, and support for floristic and faunal diversity. Consequently, sites are planted with native and climate-adaptive species and efforts are made to control invasive weeds that may inhibit these functions. A broad assumption about this approach is that sites will provide some wildlife habitat value, above and beyond their function for treating stormwater.

Birds are often considered an indicator of environmental change and habitat quality (Butler 2012), and have been used to inform urban planning (Stagoll 2010). Bird populations are also demonstrably under threat, with as many as one third of North American bird species needing urgent conservation action (NABCI 2016). Survival of migratory Nearctic landbirds may be particularly affected by events away from their breeding grounds, i.e. during migration and on wintering grounds. Migration places extraordinary energetic demands on birds and the provisioning of food resources during stopover is important to successful migration. Combined with other stressors, the conditions during migration, both at stopover sites and in-flight, may limit populations (Newton 2006). While research on stressors on wintering grounds of Nearctic migrants has begun to catch up with research addressing conditions in the breeding season, stopover ecology of migrants is still understudied.

Although urban avian ecology has concentrated on breeding populations, with some notable exceptions (Craves 2009, Pennington 2008, Rodewald 2008, Rodewald 2005), cities function as seasonal habitat for migratory species. Many cities are located in migratory flyways and in resource-rich parts of a landscape such as along major rivers and coastlines. In addition, migrating birds may occur at higher densities in urban habitat patches than in surrounding rural areas (Buler and Dawson 2014, Bonter et al 2008). These populations may also be affected by urban light pollution (Van Doren 2017) or novel food resources (such as exotic flower and fruit trees and/or birdfeeders) in the urban/suburban landscape (Galbraith 2015). Regardless of whether or not migrating birds preferentially select patches in urban sites or are drawn there as a "last resort," the abundance and diversity of birds in urban areas during spring and fall migration are higher than in any other season (eBird 2019).

While cities generally do not provide as wide a diversity of self-sustaining populations of native plants and animals, the urban stopover site may be a critical bottleneck in the lives of migratory species (Sillett 2002). At stopover sites, birds are exposed to a variety of hazards (e.g., glass and automobile strikes, threats from domestic and anthropophilic meso-predators) and lack of resources (food and protection from predators) which affect their survival in route. Still, little is known about what makes an urban stopover suitable for migratory birds. Urban environments are characteristically lacking in natural cover, and often a large proportion of what pervious land cover exists in cities is made up of exotic plant species, particularly turfgrass lawns. During the spring, most migratory songbirds are insectivorous, and are particularly reliant on lepidoptera larvae, which have been shown to be strongly associated with native host plant species (Burghardt et al 2009).

Some research has indicated that the abundance and diversity of urban birds can be predicted by characteristics intrinsic to a site, especially area (see meta-analysis in Beninde

2015), as well as planted species richness, vegetation structure (both vertical and horizontal), and edge to area ratio (Kohut 2009). Vegetation height heterogeneity has classically been seen as a strong predictor of bird species richness (MacArthur 1961), and several recent studies has confirmed this using LiDAR as a means of measuring height heterogeneity (Goetz 2007, Weisberg 2014, Clawges 2008, Flaspohler 2010). Others have found landscape-scale characteristics, including the amount or proportion of land cover classes such as native tree canopy cover (Pennington 2008) found within a certain radius, or distance to large natural areas or open water (Canedoli 2018), add significantly to the likelihood of bird presence (Melles 2003). Advances in acquiring remotely-sensed data is making geospatial data increasingly useful in measuring habitat characteristics, especially heterogeneity, at various scales (Bergen 2009).

In urban areas such as Ann Arbor, where conservation is valued, the benefit of native landscaping to wildlife is widely advertised; however, while there are indications that other types of green stormwater infrastructure such as green roofs do support urban biodiversity (Tonietto 2011, Baumann 2006), the use of rain gardens by birds per se has not been studied. New research in this area could help designers and decision makers in any community that values biodiversity.

RESEARCH QUESTIONS

This study aims at addressing the following research questions:

1) Do small, urban green infrastructure sites support significant avian diversity during the spring migratory period?

2) What are the influences of the following site characteristics on bird species richness, abundance and abundance weighted by species conservation value?
   - area
   - plant diversity
   - heterogeneity of vegetation structure,
   - distance from large patches of natural land cover
   - distance to open water, and
   - percent land cover classes within buffers ranging from 100m-1000m.

Answering these questions will provide information for shaping the design, planning, and maintenance of similar sites to enhance migratory bird communities, and more generally inform the extent to which green infrastructure in urban areas can provide habitat and support biodiversity.

METHODS

Study area

Study sites were drawn from the land-based GSI network in Ann Arbor, Washtenaw County, Michigan, USA. The city occupies a land area of 72.27 km^2, with a population estimated in 2017 to be 121,477 (US Census Bureau, 2017) and a population density of 1681 people per km^2. Ann Arbor is located in the watershed of the Huron River, a state-designated Scenic Natural River, and the city contains over 485.6 hectares of preserved or restored natural areas including woodlands, wetlands, and prairies (NAP 2019). This system of preserves is managed by the city of Ann Arbor Natural Areas Preservation program, private and state land owners such as the University of Michigan, and is supported by easement properties in the Greenbelt, which, in collaboration with township and county land conservation programs, has protected over 5000 acres of farmland and open space surrounding the city. Two major bird migratory corridors (the Atlantic and Mississippi flyways) overlap in Washtenaw County, where 302 bird species have been observed since 1902 (eBird 2012) and 104 species are confirmed to be breeding in city Natural Areas during 2018 (Juliet Berger, personal communication).

The present study was designed to examine bird occurrence on the 124 units in 34 locations that make up the land-based public GSI network (City of Ann Arbor, 2018). The land area of the system is 8.65 hectares in a city of 72.27km^2; in other words, for every 1000m^2 of land within the city, 1m^2 is on public lands dedicated to green stormwater treatment (City of Ann

Arbor, 2017). For the purposes of maintaining independence of observations, units whose boundaries were located within 100m of each other were considered to be one site, while locations with restricted access were not surveyed. An additional 7 sites managed by other entities, including under public and private ownership, were added, totaling 37 sites that generally represent the range of site characteristics, including area (.01-5.75 hectares), contiguity to natural landcover, and context, ranging from the urban core to peripheral low-density neighborhoods. Two sites were later removed from the analysis because planned management activities resulted in the wholesale removal of vegetation during the season.

Field Methods: Birds

For this multi-site study, a broad scale survey technique was thought to be limiting (Siegel 2009), but a standardized search with results-based stopping rules (following Watson 2003) was considered an appropriate technique because of the small size, well-delineated edges, and generally open sight-lines of this study's sites. Each site was surveyed once during each of five 10-day periods from April 9 through May 28, covering major spring migratory peak periods for the region (eBird 2012), between sunrise and 5 hours after sunrise. Surveys were also conducted under conditions of minimal wind and precipitation. Observers were experienced and trained in the protocol, and randomly assigned to survey periods to minimize any observer effect. Area searches were broken into ten-minute segments; each survey consisted of a minimum of two segments and continued until a segment passed during which no new bird species were detected. All birds detected by sight or sound were identified to species or lowest possible taxon; any flyovers (with the exception of insectivorous aerial predators and birds of prey exhibiting localized hunting behavior) and detections made outside of unit boundaries were removed from analysis. Although all species were recorded, only those that do not require open water as primary habitat were included in the analysis, in order to make more informative inferences about site characteristics.

Total number of species and individuals detected across all visits were used to define (land-bird) species richness (*SR*) and relative abundance (*RA*) for each site. Because urban habitats often support a high abundance of anthropophilic bird species that contribute little to global conservation efforts, a conservation-weighted relative abundance (*CA*), was also calculated (following Nuttle 2003) based on the Partners in Flight Avian Conservation Assessment Database (Partners in Flight 2019 and Panjabi 2017).

Field Methods: Plant species richness

Plant species inventories were updated by WCWRC personnel for those sites under their maintenance responsibility during the 2019 growing season. Vegetation assessments were conducted in the field by walking around the perimeter and through the interior of each site. Plant species from existing lists were marked as present or absent, additional field-identifiable species added, and samples (particularly flowering stalks and flowers) from unknown species were refrigerated overnight and identified within 24-48 hours. Multiple sources were used for field identification, and verified against the Michigan Flora lists (UM Herbarium, 2019) and Lady Bird Johnson Wildflower Center (NPIN, 2013). Surveys recorded herbaceous and woody plant species, including those that were planted and those have established spontaneously. Some early-season species may not have been detected.

Remote sensing and geospatial analysis

Site and landscape-scale metrics were calculated in ESRI's ArcGIS Desktop 10.6.1, using recently acquired remotely sensed data and publicly available feature data. Site boundaries were drawn based on Green Infrastructure Maintenance Manual (City of Ann Arbor 2017) and delineation via satellite imagery. Distance was measured from the nearest edge of these polygons to habitat "strongholds" and distance to water, both defined by a combination of feature data provided by Ann Arbor Natural Areas Preservation (NAP 2012) and the Protected Areas Database of the US (Conservation Biology Institute 2016).

Four-band (capturing the visible spectrum (RGB) as well as near infrared) leaf-off ortho-imagery flown in April 2018 for the city of Ann Arbor, along with a feature set for buildings, pavement and water derived by the imagery contractor and surface models derived from LiDAR point clouds acquired in 2009 were the main source of landcover classification. Ten defined and one undefined landcover classes (broadleaf canopy, evergreen canopy, shrubs, herbaceous, turfgrass, bare ground, mulch, water, buildings, pavement, and other/unknown) were produced, using the stratified ortho-imagery raster, maximum likelihood classification with ground-truthed training samples, and the addition of a "first-return" digital surface model derived from LiDAR data. Multiple iterations of distinct spectral signatures within each class were performed in order to maximize confidence levels. The "mulch" class is composed of broad areas of woodchips, mulch, and fallen leaves. The “other/unknown” class is mostly composed of shadowed areas that yielded inadequate data. Within multiple nested buffers (100m, 200m, 500m, 1000m) around each site, each 1ft^2 cell was classified discretely into one class, except where tree canopy of either type was detected above known building, pavement or water, in which case that cell could effectively permit two overlapping classes.

In order to measure structural habitat heterogeneity, multiple discrete-return LiDAR point cloud data acquired in mid-April, 2018, and published by Southeast Michigan Council of Governments (SEMCOG) were analyzed using LASTools toolbox in ArcGIS Desktop. Using the LASCanopy tool, point elevation values were subtracted from a ground surface interpolated from points designated as such by the vendor, in order to estimate canopy height and vertical vegetation profiles. Vegetation point heights were binned into 2ft intervals on a 4ft^2 raster grid, and for each site we calculated a Shannon diversity index, which has been found to correspond well with foliage height diversity (Lesak 2011, Weisberg 2014). Horizontal heterogeneity of the canopy height was measured as the highest returns of each grid cell. Percent cover was measured for each site by canopy (first returns > 3m), and shrub (first returns >1m, <3m).

Modeling bird diversity and abundance

A series of models were built to explore the explanatory effect of site characteristics and landscape metrics on response variables species richness (*SR*), relative abundance (*RA*), and conservation value-weighed abundance (*CA*). Because response variables were based on over-dispersed count data, a quasi-Poisson distribution with an extra error term for over-dispersion was used. Models were explored incorporating 15 different explanatory variables (see Table 1) comprised of site scale characteristics, landscape distance to potentially important landscape features, and percent “natural” land cover (a combined metric comprised of woodland, shrub and herbaceous cover but not turfgrass) within four different distance buffers. Because directly measured plant species richness was only available for 24 out of 35 sites, *psr* was included as a latent variable with those missing values estimated as part of the model (Lee 2007). Model selection was guided by DIC (Deviance Information Criterion), which balances the fit of the model against penalties for the number of variables. Generalized linear models were programmed in BUGS language using OpenBugs and analyzed using a Bayesian approach with Markov chain Monte Carlo methods.

RESULTS

Bird diversity in the study area

We recorded 3407 birds on the GSI sites, comprising 97 total species (see Appendix B), 78 of which were landbirds included in the statistical analysis. The four most common species by abundance (and by number of observations) were Red-winged Blackbird (19.8% by abundance), American Robin (13.4%), House Sparrow (8.9%) and Song Sparrow (8.2%). There were 50 neotropical or temperate migratory species, 28 of which (33.5% by abundance) are known to breed within the city (eBird 2019, Natural Areas Preservation 2019b) and 22 species (0.7%) that are transient. Another 32 species (63.9% by abundance) were year-round, breeding residents, and 11 more (1.8%) that are winter residents that migrate elsewhere during the breeding season. By habitat guild, there were 26 interior forest species, 23 woodland species, 16 freshwater species, 8 shrubland species, 7 wetland species, 6 grassland species, and 6 anthropophilic species associated with towns. We recorded 22 species of moderate or high conservation concern according to the Partners in Flight Conservation Value ranking discussed above, including Marsh Wren, a Michigan Species of Concern, and two non-native, anthropophilic species. Of the three main response variables considered in the analysis, landbird species richness (*SR*) ranged between sites from 3 to 32 (13.7 ± 8; mean ± SD), relative abundance (*RA*) from 8 to 410 (84.9 ± 89.1), and abundance weighted by PIF CV (*CA*) from 14 to 822 (143 ± 168.3).

Table 1: Explanatory variables

Variable	Min	Max	Mean	SD	Description
hect	0.011	5.752	0.502	0.993	Site area (hectares)
perimratio	38	1450	405	339	Ratio of site perimeter to site area
psr	7	63	25.4	13.8	Surveyed plant species richness
treeprc	0.0%	82.5%	19.0%	22.6%	% tree canopy cover (derived from LiDAR)
shrubprc	0.0%	35.4%	6.2%	7.9%	% shrub cover (derived from LiDAR)
fhd	0.001	3.239	1.391	0.979	Foliage height diversity
maxtop	1.893	31.420	16.791	7.855	Site max. height of vegetation (m)
meantop	0.026	12.831	2.719	3.153	Site mean height of highest vegetation (m)
sdtop	0.062	9.823	3.541	2.863	Site standard deviation of highest veg. (m)
strongdist	0	1160	430	415	Distance to habitat stronghold (m)
waterdist	0	1454	304	370	Distance to open water (m)
nat100	15.1%	77%	42.3%	19.3%	% Natural cover within 100m buffer
nat200	20%	83.7%	44.7%	17.6%	% Natural cover within 200m buffer
nat500	16.6%	88.4%	47.2%	47.8%	% Natural cover within 500m buffer
nat1000	26.4%	67.3%	47.8%	11.1%	% Natural cover within 1000m buffer

Model selection

As expected, site area (*hect*) was an important explanatory variable in all models (Table 2). The latent variable plant species richness (*psr*) was included regardless of its relative contribution because of its interest to designers and managers of such systems. All other variables in the model were included via forward selection, wherein parameters were added to the base model one at a time and retained if they reduced DIC by ≥2. Finally, two additional random effects were tested: spatial correlation among the data via the addition of a conditional auto-regressive (CAR) parameter, and a term to account for over-dispersed data in the response variables.

Table 2: Species richness model comparison

Model	Components	Dbar	Dhat	pD	**DIC**	**Pred/obs R^2**
1a	*Hect*	274.9	272.9	1.99	276.9	0.246
1c	$Hect^{z}$	248.2	246.1	2.159	250.4	0.412
1e	$Hect^{0.2984}$	247.1	245.9	1.22	248.3	0.422
1f	**log(*Hect*)**	238.1	236.1	1.989	**240.1**	0.465
1g	log(*Hect*) + *PerimRatio*	236.1	233.3	2.817	238.9	0.473
2f	log(*Hect*) + *NatPSR*	221.6	215	6.541	228.1	0.618
2h	**log(*Hect*) + *PSR***	221.3	214.9	6.439	**227.8**	0.642
3i	log(Hect)+ *PSR* + *TreePerc*	216.4	213.6	2.750	219.1	0.668
3j	log(Hect)+ *PSR* + *ShrubPerc*	208.1	204	4.146	**212.3**	0.726
4h	**log(*Hect*) + *PSR* + *ShrubPerc* + *FHD***	196.3	191.7	4.540	**200.8**	0.790
4i	log(*Hect*) + *PSR* + *ShrubPerc* + *SDTop*	199.1	194.7	4.412	203.5	0.756
9f	log(*Hect*) + *PSR* + *ShrubPerc* + *FHD* + *%Nat100*	195.2	189.9	5.336	200.60	0.791
10f	log(*Hect*) + *PSR* + *ShrubPerc* + *FHD* + *%Nat200*	195.4	190	5.353	200.70	0.792
11f	log(*Hect*) + *PSR* + *ShrubPerc* + *FHD* + *%Nat500*	196.8	191.3	5.516	202.30	0.790
12f	log(*Hect*) + *PSR* + *ShrubPerc* + *FHD* + *%Nat1000*	196.1	190.7	5.369	201.5	0.789
7m	**log(*Hect*) + *PSR* + *ShrubPerc* + *FHD* + *Spatial CAR***	193.1	192.4	0.748	**193.9**	0.828
7n	log(*Hect*) + *PSR* + *ShrubPerc* + *FHD* + *OT*	192.6	184.4	8.219	200.8	0.833
7o	log(*Hect*) + *PSR* + *ShrubPerc* + *FHD* + *Spatial CAR* + *OT*	190.4	182.7	7.644	198	0.861

Because of small sample size, some explanatory variables that may have predictive power were excluded from the model. The model (7m, above) that best explained species richness without over-fitting the data takes the form:

$$SR_i \sim Poisson(\lambda_i)$$

$$\lambda_i = e^{\alpha_1+\alpha_1\times\ Hect_i+\alpha_2\times\ PSR_i+\alpha_3\times\ ShrubPrc_i+\alpha_4\times\ FHD_i}$$

The model includes three significant parameters (in bold, Table 3): *Hect*, *ShrubPrc*, and *FHD*. When standardized by the mean of the variable for the sake of comparison (Figure 1), foliage height diversity (*FHD*) has the strongest positive effect, followed by site area (*Hect*) on a logarithmic curve, and shrub cover (*ShrubPrc*), in order of effect size. Plant Species Richness (*PSR*), although significant and positive in simpler models, had no significant effect on bird diversity. A slight improvement in model fit indicates that spatial correlation was present.

Site area (*hect*) contributed best fit when included in the form C*log(*hect*[i]) where C was a coefficient estimated by the model. According to comparison of DIC scores (Table 2), this form improved the model over its inclusion as a simple geometric parameter (C**hect*[i]) or as a parameter with the form C**hect*[i]^{z}. Two forms of modeling z were attempted: either a constant (in this case, 0.2866) calculated directly from the data (Gleason 1922) or as an additional random variable coefficient estimated by the model.

Table 3: Model Parameter Estimates

Parameter	Mean	SD	95% Credible Interval
Intercept	**2.673**	0.182	2.317 - 3.04
Hect	**0.348**	0.055	0.243 - 0.459
PSR	-0.002	0.005	-0.012 - 0.007
ShrubPrc	**1.454**	0.624	0.212 - 2.680
FHD	**0.241**	0.066	0.113 - 0.371

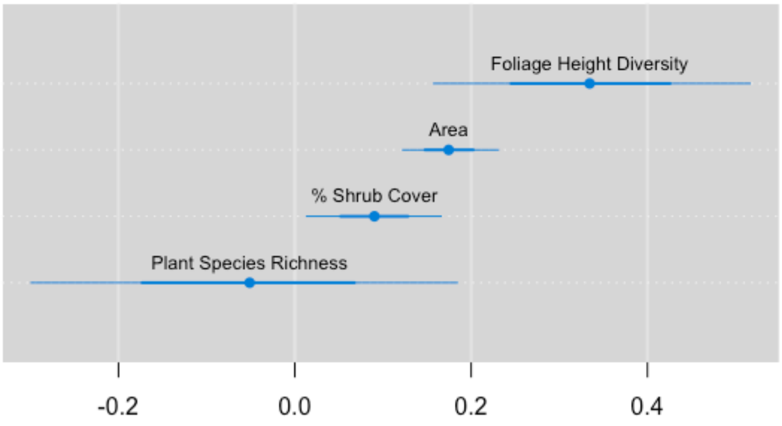

Figure 1: Mean-standardized model parameter estimates

DISCUSSION

Our research suggests this guiding principle for GSI design: the provision of a diverse palette of structurally complex plants in large-enough patches is likely to have real habitat value, regardless of where it is implemented in the urban matrix. These results support that classic theories regarding bird occurrence in response to habitat structure prevail in novel ecosystems within urban settings. The explanatory power of foliage height diversity is a confirmation of vertical vegetation structure as an important determinant in bird diversity, as well as the utility of multiple-return LiDAR as a method to measure FHD. This is an important point in the urban context, where simplification of structure is a common practice.

The process of model selection also illuminated how well different forms of some explanatory variables performed. The substitution of native plant species richness (*natpsr*) as in model 2f, did not perform better than overall plant species richness (*psr*), perhaps suggesting that exotic and/or invasive species, at the levels at which they occur in this system, are not strongly associated with reduced bird occurrence. However, the occurrence of exotic plant species in this system is comparatively low, and it may be that a threshold at which bird diversity would be impacted has not been reached. Likewise, none of the landscape-scale metrics, distance to water, distance to preserved habitat strongholds, and surrounding landcover at different scales, had enough explanatory power to be included. This may suggest that site characteristics have a dominant role in maintaining wildlife diversity regardless of the position of a site in the urban landscape, at least for taxa that, like birds, are highly mobile and capable of crossing barriers to dispersal.

The aesthetic of well-maintained public and private natural spaces in cities is synonymous with open, “park-like” settings with well-pruned trees and little to no understory or herbaceous layers. These preferences, driven by perceptions of safety, real estate value, and convention, must be weighed against support for biodiversity. One of the other dilemmas here is that many historical descriptions of the Ann Arbor area indicate open park-like woods and oak openings, managed by fire, and likely located in a broader matrix of structurally complex forest and shrubland. For restoration practitioners, there is a tension between restoring past ecological patterns and maintaining more structurally complex landscapes in a fragmented urban setting. A well-articulated set of objectives for restoration and design of green spaces should not rely on a single indicator such as bird species richness, and a mosaic of community types should be a preferred reference condition at the landscape scale.

The greater influence of patch characteristics over matrix quality in this case supports the efforts of urban habitat managers in the implementation of biodiversity-driven design in fragmented and isolated patches. However, the potential of these sites to represent ecological traps (Chalfoun et al. 2002, Leston 2006) is real and can only be explored via research that measures productivity of resident birds and/or physiological condition of migrants. As cities become more extensive and as global extinction rates continue their rapid increase, it is imperative that ecologists, designers, and managers collaborate across disciplines in support of shared conservation goals.

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Appendix 1: Site variables

Site code	Site	BMP type	Bird species richness	Total bird abundance	CV-weighted abundance	Land area (m2)	Perimeter to area ratio	Distance to stronghold (m)	Distance to nearest other site (m)	Distance to water body (m)	Natural cover within 100m (hect)	Natural cover within 200m (hect)	Natural cover within 500m (hect)	Natural cover within 1000m (hect)
AO	Arbor Oaks	Rain Garden	15	101	162.0	3084	791	354	978	338	32.379	89.157	448.8546	1886.8312
AP	Argo Park	Rain Garden	17	53	94.0	345	70	77	1002	14	31.428	116.3277	541.6966	1900.2692
BEP	Bandemere Nature Area	Rain Garden	14	66	121.0	1434	225	0	1643	0	39.861	128.6289	699.3037	2439.0167
BEP	Belize Park	Rain Garden	7	11	26.0	106	38	430	1300	600	18.151	39.3852	397.0439	1663.0519
BH	Bird Hills Nature Area	Rain Garden	5	8	16.0	82	68	0	3707	275	29.523	103.8145	534.086	2294.3515
BLNA	Bluffs Nature Area	Rain Garden	24	57	113.0	2233	251	1	871	121	33.814	107.9844	594.702	2006.7165
BR	Briarcliff	Rain Garden	8	31	50.0	485	101	977	6346	65	15.987	65.0181	344.1483	1361.9323
BRP1	Buhr Park 1: Children's Wet Meadow 1, Children's Wet Meadow Annex, etc.	Rain Garden	18	70	115.0	5846	959	288	302	457	37.440	110.6302	599.388	2210.2181
BRP2	Buhr Park 2: Children's Wet Meadow 2, South Parking Lot, Tennis Court	Rain Garden	19	70	76.0	4411	542	289	302	326	30.370	70.8331	499.983	1984.6835
BRP3	Buhr Park 3: Children's Wet Meadow 3	Rain Garden	16	73	81.0	4608	392	272	384	618	11.097	46.0049	480.3686	1905.3989
BSP	Burns Park Tennis Court	Rain Garden	13	39	59.0	1068	336	1160	3912	1169	26.566	90.918	121.0236	1746.3306
CFP1	County Farm Park Malletts Creek	Dry Detention Basin	16	124	238.0	15272	563	0	636	733	73.356	186.7404	747.2162	2150.6287
CFP2	County Farm Parking Area	Wet Detention Basin, Dry Detention Basin	14	66	113.0	2631	387	73	636	515	37.044	105.4867	590.7593	1992.7754
EP	Earhart Park	Wet Detention Basin	34	136	229.0	1408	242	161	5630	0	34.858	97.9021	511.679	2098.3965
FC	Fuller Road	Wet Detention Basin	16	43	77.0	1522	183	0	1216	0	42.474	152.5807	717.7944	2354.7776
FNA	Furstenberg Nature Area	Rain Garden	6	19	20.0	2158	295	25	1216	57	38.912	126.8705	445.3417	2518.2434
HP	Hunt Park	Rain Garden	3	8	14.0	135	43	100	871	197	13.146	75.4673	492.2007	1960.1378
HH	Huron Hills Golf Course	Dry Detention Basin	14	74	146.0	5964	469	235	5287	21	29.166	117.641	751.5188	2574.8061
MBD	Mary Beth Doyle Park	Wet Detention Basin, Dry Detention Basin, Constructed Wetland	40	605	1074.0	31758	1450	0	1053	0	86.454	210.7609	745.8124	2169.0482
MNA	Miller Nature Area	Rain Garden	8	15	22.0	773	110	1114	2718	712	32.850	108.1091	488.1993	1689.4419
NC	North Campus	Wet Detention Basin	25	270	441.0	12452	749	228	1717	0	22.462	65.2346	532.5909	2471.2673
OP	Olson Park	Bioswale, Constructed Wetland, Rain	23	252	486.0	9544	1067	0	4071	0	69.753	183.9459	767.2892	2767.2765
RS	Rudolf Steiner High School	Dry Detention Basin	7	25	38.0	1214	146	14	3899	408	30.810	95.8768	594.3409	2308.7655
SI	South Industrial	Rain Garden	7	38	28.0	1093	292	684	3912	154	10.120	46.7254	311.9045	1304.0825
SM	South Main St.	Rain Garden	3	13	16.0	466	187	1042	2888	1454	9.288	40.9232	277.4039	993.9452
SSR1	Stone School Road North	Rain Garden	9	34	55.0	1844	372	588	732	16	30.238	96.1118	465.7141	1548.4834
SSR2	Stone School Road South	Rain Garden	5	20	16.0	2703	850	571	732	151	21.495	76.6595	448.193	1709.519
VMP2	Veterans Memorial Park 2: Skatepark	Rain Garden	6	57	68.0	812	235	1098	291	111	14.872	36.7462	322.3909	1529.179
VMP3	Veterans Memorial Park 3: Ice Arena and Fire Station	Rain Garden	10	56	43.0	365	107	958	470	484	11.088	50.512	228.1898	1376.9405
VMP4	Veterans Memorial Park 4: Zamboni	Rain Garden	14	58	74.0	1033	253	810	470	355	19.595	64.958	323.6854	1531.4261
WAY	Waymarket Park	Wet Detention Basin	28	151	227.0	1341	195	835	6817	0	13.238	51.7791	299.3693	1148.614
WP1	West Park 1: Northwest and Bandshell	Constructed Wetland	20	202	310.0	8205	999	913	215	73	43.312	117.8412	506.5792	1685.0027
WP2	West Park 2: SW Wetland, Central Pond, SE Wetland and East Parking Lot	Constructed Wetland, Wet Detention Pond, Bioswale	30	283	451.0	6367	609	788	215	0	68.893	148.2935	545.8836	1730.3409
YMCA	YMCA	Dry Detention Basin	8	45	72.0	2627	250	967	455	1093	12.214	50.9923	303.8226	1285.0248
ZLC	Zion Lutheran Church	Dry Detention Basin	24	125	190.0	5699	340	0	3565	131	36.973	123.5652	562.9696	1644.8125

Appendix 2: Bird species occurrence (in order of abundance)

AOU code	Common name	Resident (r), migrant (w), winter resident (w)	Breeding (b), non-breeding (nb)	Conservation Value rank	Conservation Concern	Habitat guild	Total abundance	Total density (% of all individuals)	Total observations	% of all observations	# of site visits observed	% of site visits observed
RWBL	Red-winged Blackbird	m	b	2	Low	Wetland	674	19.8%	209	12.2%	61	33.0%
AMRO	American Robin	r	b	2	Low	Woodland	455	13.4%	270	15.8%	90	48.6%
HOSP	House Sparrow	r	b	0	Low	Town	304	8.9%	133	7.8%	60	32.4%
SOSP	Song Sparrow	r	b	2	Low	Woodland	278	8.2%	202	11.8%	69	37.3%
MALL	Mallard	r	b	1	Low	Freshwater	236	6.9%	62	3.6%	27	14.6%
AMGO	American Goldfinch	r	b	2	Low	Woodland	226	6.6%	120	7.0%	61	33.0%
EUST	European Starling	r	b	0	Low	Town	199	5.8%	75	4.4%	45	24.3%
NOCA	Northern Cardinal	r	b	2	Low	Woodland	98	2.9%	76	4.4%	46	24.9%
COGR	Common Grackle	m	b	2	Moderate	Woodland	77	2.3%	36	2.1%	20	10.8%
CANG	Canada Goose	r	b	2	Low	Wetland	69	2.0%	20	1.2%	9	4.9%
HOFI	House Finch	r	b	2	Low	Town	63	1.8%	32	1.9%	25	13.5%
CHSP	Chipping Sparrow	m	b	2	Low	Woodland	62	1.8%	32	1.9%	22	11.9%
BARS	Barn Swallow	m	b	2	Low	Town	47	1.4%	21	1.2%	16	8.6%
MODO	Mourning Dove	r	b	2	Low	Woodland	46	1.3%	36	2.1%	26	14.1%
BHCO	Brown-headed Cowbird	m	b	0	Low	Grassland	41	1.2%	30	1.8%	22	11.9%
BCCH	Black-capped Chickadee	r	b	2	Low	Forest	38	1.1%	30	1.8%	26	14.1%
NRWS	Northern Rough-winged Swallow	m	b	2	Moderate	Freshwater	31	0.9%	13	0.8%	9	4.9%
BLJA	Blue Jay	r	b	2	Low	Forest	29	0.9%	24	1.4%	17	9.2%
DEJU	Dark-eyed Junco	w	nb	1	Low	Forest	28	0.8%	14	0.8%	13	7.0%
YEWA	Yellow Warbler	m	b	2	Low	Woodland	27	0.8%	23	1.3%	17	9.2%
CHSW	Chimney Swift	m	b	4	Moderate	Town	23	0.7%	9	0.5%	8	4.3%
DOWO	Downy Woodpecker	r	b	2	Low	Forest	22	0.6%	16	0.9%	14	7.6%
KILL	Killdeer	m	b	3	Moderate	Grassland	22	0.6%	16	0.9%	8	4.3%
TRES	Tree Swallow	m	b	2	Moderate	Freshwater	22	0.6%	14	0.8%	10	5.4%
CEDW	Cedar Waxwing	r	b	2	Low	Woodland	19	0.6%	4	0.2%	4	2.2%
GRCA	Gray Catbird	m	b	2	Low	Woodland	16	0.5%	12	0.7%	13	7.0%
AMCR	American Crow	r	b	2	Low	Town	15	0.4%	10	0.6%	8	4.3%
NOFL	Northern Flicker	r	b	2	Moderate	Woodland	14	0.4%	14	0.8%	12	6.5%
AMRE	American Redstart	m	b	2	Moderate	Forest	11	0.3%	4	0.2%	3	1.6%
RTHA	Red-tailed Hawk	r	b	2	Low	Woodland	10	0.3%	8	0.5%	7	3.8%
WBNU	White-breasted Nuthatch	r	b	2	Low	Forest	10	0.3%	8	0.5%	8	4.3%
WODU	Wood Duck	r	b	1	Low	Freshwater	10	0.3%	4	0.2%	3	1.6%
BAOR	Baltimore Oriole	m	b	2	Moderate	Woodland	8	0.2%	6	0.4%	6	3.2%
EAPH	Eastern Phoebe	m	b	2	Low	Woodland	8	0.2%	7	0.4%	5	2.7%
SPSA	Spotted Sandpiper	m	b	3	Moderate	Freshwater	8	0.2%	5	0.3%	3	1.6%
CSWA	Chestnut-sided Warbler	m	b	3	Moderate	Woodland	7	0.2%	2	0.1%	2	1.1%
FOSP	Fox Sparrow	w	nb	1	Low	Shrubland	7	0.2%	3	0.2%	3	1.6%
RCKI	Red-bellied Woodpecker	r	b	1	Low	Forest	7	0.2%	4	0.2%	3	1.6%
SAVS	Savannah Sparrow	m	b	2	Low	Grassland	7	0.2%	3	0.2%	3	1.6%
CAWR	Carolina Wren	r	b	1	Low	Woodland	6	0.2%	4	0.2%	3	1.6%
COGO	Common Goldeneye	w	nb	3	Moderate	Freshwater	6	0.2%	2	0.1%	2	1.1%

AOU code	Common name	Resident (r), migrant (w), winter resident (w)	Breeding (b), non-breeding (nb)	Conservation Value rank	Conservation Concern	Habitat guild	Total abundance	Total density (% of all individuals)	Total observations	% of all observations	# of site visits observed	% of site visits observed
REVI	Ruby-crowned Kinglet	m	nb	2	Low	Forest	6	0.2%	1	0.1%	1	0.5%
WAVI	Warbling Vireo	m	b	2	Moderate	Woodland	6	0.2%	6	0.4%	5	2.7%
CLSW	Cliff Swallow	m	b	2	Low	Freshwater	5	0.1%	3	0.2%	3	1.6%
EABL	Eastern Bluebird	r	b	2	Low	Grassland	5	0.1%	5	0.3%	3	1.6%
FISP	Field Sparrow	m	b	3	Moderate	Shrubland	5	0.1%	4	0.2%	4	2.2%
LISP	Lincoln's Sparrow	m	nb	1	Moderate	Shrubland	5	0.1%	2	0.1%	2	1.1%
TUVU	Turkey Vulture	m	b	1	Low	Woodland	5	0.1%	3	0.2%	2	1.1%
WTSP	White-throated Sparrow	w	nb	1	Moderate	Forest	5	0.1%	4	0.2%	4	2.2%
BGGN	Blue-gray Gnatcatcher	m	b	1	Low	Forest	4	0.1%	4	0.2%	3	1.6%
HOME	Hooded Merganser	r	b	2	Moderate	Freshwater	4	0.1%	1	0.1%	1	0.5%
PISI	Pine Siskin	w	nb	1	Moderate	Woodland	4	0.1%	2	0.1%	2	1.1%
RTHU	Ruby-throated Hummingbird	m	b	2	Low	Woodland	4	0.1%	3	0.2%	3	1.6%
WIWR	Winter Wren	w	nb	1	Low	Forest	4	0.1%	1	0.1%	1	0.5%
SWTH	Swainson's Thrush	m	nb	3	Moderate	Forest	3	0.1%	2	0.1%	1	0.5%
WCSP	White-crowned Sparrow	w	nb	1	Low	Shrubland	3	0.1%	3	0.2%	3	1.6%
YRWA	Yellow-rumped Warbler	m	nb	1	Low	Forest	3	0.1%	3	0.2%	3	1.6%
BEKI	Belted Kingfisher	r	b	3	Moderate	Freshwater	2	0.1%	2	0.1%	2	1.1%
BWHA	Broad-winged Hawk	m	b	2	Low	Forest	2	0.1%	1	0.1%	1	0.5%
BWTE	Blue-winged Teal	m	nb	1	Low	Freshwater	2	0.1%	1	0.1%	1	0.5%
COYE	Common Yellowthroat	m	b	2	Moderate	Shrubland	2	0.1%	2	0.1%	2	1.1%
HOWR	House Wren	m	b	2	Low	Woodland	2	0.1%	2	0.1%	2	1.1%
INBU	Indigo Bunting	m	b	2	Moderate	Woodland	2	0.1%	2	0.1%	2	1.1%
PBGR	Pied-billed Grebe	r	b	2	Moderate	Freshwater	2	0.1%	1	0.1%	1	0.5%
RBGR	Rose-breasted Grosbeak	m	b	3	Moderate	Forest	2	0.1%	2	0.1%	2	1.1%
RBWO	Ring-billed Gull	r	b	2	Low	Forest	2	0.1%	7	0.4%	6	3.2%
RIGU	Red-eyed Vireo	m	b	2	Low	Freshwater	2	0.1%	1	0.1%	1	0.5%
TUTI	Tufted Titmouse	r	b	2	Low	Forest	2	0.1%	2	0.1%	2	1.1%
VESP	Vesper Sparrow	m	nb	3	Moderate	Grassland	2	0.1%	2	0.1%	2	1.1%
AGWT	American Green-winged Teal	w	nb	2	Low	Freshwater	1	0.0%	1	0.1%	1	0.5%
ALFL	Alder Flycatcher	m	b	1	Moderate	Shrubland	1	0.0%	1	0.1%	1	0.5%
AMWI	American Wigeon	w	nb	2	Moderate	Freshwater	1	0.0%	1	0.1%	1	0.5%
AMWO	American Woodcock	m	b	3	High	Forest	1	0.0%	1	0.1%	1	0.5%
ATSP	American Tree Sparrow	w	nb	1	Moderate	Shrubland	1	0.0%	1	0.1%	1	0.5%
BRCR	Brown Creeper	r	b	1	Low	Forest	1	0.0%	1	0.1%	1	0.5%
CMWA	Cape May Warbler	m	nb	3	High	Forest	1	0.0%	1	0.1%	1	0.5%
EAKI	Eastern Kingbird	m	b	3	Moderate	Grassland	1	0.0%	1	0.1%	1	0.5%
GCKI	Golden-crowned Kinglet	w	nb	1	Low	Forest	1	0.0%	1	0.1%	1	0.5%
GREG	Great Egret	m	b	2	Low	Wetland	1	0.0%	1	0.1%	1	0.5%
GRHE	Green Heron	m	b	3	Moderate	Wetland	1	0.0%	1	0.1%	1	0.5%
HAWO	Hairy Woodpecker	r	b	2	Low	Forest	1	0.0%	1	0.1%	1	0.5%
HEGU	Herring Gull	r	b	3	Moderate	Freshwater	1	0.0%	1	0.1%	0	0.0%

AOU code	Common name	Resident (r), migrant (w), winter resident (w)	Breeding (b), non-breeding (nb)	Conservation Value rank	Conservation Concern	Habitat guild	Total abundance	Total density (% of all individuals)	Total observations	% of all observations	# of site visits observed	% of site visits observed
LEFL	Least Flycatcher	m	b	3	Moderate	Forest	1	0.0%	1	0.1%	1	0.5%
MAWR	Marsh Wren	m	b	2	Low	Wetland	1	0.0%	1	0.1%	1	0.5%
MUSW	Mute Swan	r	b	0	Low	Freshwater	1	0.0%	1	0.1%	0	0.0%
NAWA	Nashville Warbler	m	nb	1	Moderate	Forest	1	0.0%	2	0.1%	2	1.1%
OSFL	Olive-sided Flycatcher	m	nb	4	High	Woodland	1	0.0%	1	0.1%	1	0.5%
PUMA	Purple Martin	m	b	3	Moderate	Freshwater	1	0.0%	1	0.1%	1	0.5%
SWSP	Swamp Sparrow	r	b	2	Low	Wetland	1	0.0%	1	0.1%	1	0.5%
UNBU	[Unidentified buteo]			NA	NA	NA	1	0.0%	1	0.1%	1	0.5%
UNFL	[Unidentified flycatcher]			NA	NA	NA	1	0.0%	1	0.1%	1	0.5%
UNWA	[Unidentified warbler]			NA	NA	NA	1	0.0%	1	0.1%	1	0.5%
VEER	Veery	m	nb	4	Moderate	Forest	1	0.0%	1	0.1%	1	0.5%
WIFL	Willow Flycatcher	m	b	4	Moderate	Wetland	1	0.0%	1	0.1%	1	0.5%
WIWA	Wilson's Warbler	m	nb	3	Moderate	Shrubland	1	0.0%	1	0.1%	1	0.5%
YBCU	Yellow-billed Cuckoo	m	b	3	Moderate	Forest	1	0.0%	1	0.1%	1	0.5%