Contents lists available at ScienceDirect

Landscape and Urban Planning

Research Paper

A functional trait approach reveals the effects of landscape context on ecosystem services provided by urban birds

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HIGHLIGHTS

- Bird communities responded to landscape-scale context of urban green spaces.
- Community-scale effect trait composition also varied with landscape context.
- Thus, cultural and regulating service supply is affected by landscape context.
- Landscape-scale management is needed to impact bird-mediated ecosystem service supply.

ARTICLE INFO

ABSTRACT

Land use intensification in urban areas can have profound effects on biological communities that provide valuable ecosystem services to urban residents. We used a response-and-effect functional trait approach to determine how bird species' responses to local and landscape-scale habitat of urban green spaces affects the supply of cultural and regulating ecosystem services. We sampled bird communities and habitat variables in urban green spaces that varied in local- and landscape-scale habitat composition and compiled a dataset of species' response and effect traits related to nesting, foraging, diet, and visual and acoustic aesthetic appeal. Overall, the landscape-scale context of a green space had a stronger influence on species' abundances than local-scale habitat. Landscape-scale impervious surface surrounding our study sites interacted with response traits related to nesting in human-built structures, clutch size, wing length, canopy foraging, and consumption of seeds and invertebrates to drive bird species' abundances. Because correlations between response and effect traits can influence the effect traits available to provide ecosystem services at a site, we explored the correlation of these three response traits to a suite of effect traits. We determined that the response traits were correlated with several effect traits related to diet and regulating services but correlated with few of the plumage and acoustic traits that produce cultural services. Finally, we found that effect traits associated with cultural and regulating ecosystem services varied strongly along the landscape-scale gradient of urbanization. Sites with high impervious surface cover are expected to have low levels of invertebrate pest control and visual appeal but high levels of acoustic appeal, diet evenness (generalism), and granivory. Overall, our study highlights the key role of landscape-scale habitat in driving bird-mediated ecosystem services and underscores the importance of regional urban planning to create healthy and livable cities.

1. Introduction

By 2030, 60 % of the Earth's human population is expected to live in cities (United Nations, 2018) and global urban land area will have tripled from its 2000 baseline (Seto et al., 2011; Seto et al., 2012). In this context, it is increasingly important that urban green spaces – the natural, semi-natural, and artificial ecosystems within and around a city

(after Cilliers et al., 2013) – provide a wide range of high-quality ecosystem services to urban residents (Aronson et al., 2017; Dickinson & Hobbs, 2017; Young, 2010). As such, understanding how the species within urban green spaces generate ecosystem services has become a research priority (Schwarz et al., 2017; Ziter, 2016).

Species' functional traits are a promising tool for addressing this environmental challenge. Functional traits include any measurable

characteristic of a species and can be physical, biochemical, behavioral, temporal, or phenological (Cadotte et al., 2011). While functional traits have long been studied in the context of ecosystem functioning and resilience (de Bello et al., 2021), they are more recently being studied in the context of urban ecosystem services (Behm et al., 2022). Theoretically, the contribution of a particular species to an ecosystem service can be predicted by its functional "effect traits", which are attributes like a species' diet, growth form, or coloration that influence its contribution to an ecosystem service (Lavorel & Garnier, 2002; Suding et al., 2008). When the relationships between effect traits and ecosystem services are well-established, green spaces can be managed to provide particular ecosystem services by selecting species with optimal effect traits.

Functional trait approaches have shown promise for urban green space and ecosystem service management. Plants are typically the focus of this research because strategic plantings can directly increase the abundance of species with optimal effect traits (e.g., Anderson et al., 2020; Goodness et al., 2016; Kleyer, 2021; Tran et al., 2020). However, application of this approach to other organisms, like animals, which also provide numerous ecosystem services (e.g., Ghanem & Voigt, 2012; Valencia-Aguilar et al., 2013; Whelan et al., 2008), poses distinct challenges since they cannot easily be introduced directly into urban green spaces. Rather, ecosystem services provided by animals depend on whether habitat characteristics within and around the green space attract and support species that contribute to the service. As a result, functional "response traits", like a species' breeding habitat, morphology, or reproductive output, which affect its tolerance of environmental conditions (Lavorel & Garnier, 2002; Luck et al., 2012; Suding et al., 2008), must also be considered.

Species with response traits suited to habitat conditions are expected to be more abundant in a particular locality (e.g., Cane et al., 2006; Luck et al., 2013; Pardo et al., 2018). In urban areas, habitat conditions can be affected by social and environmental factors that act at multiple scales to shape biological communities (Aronson et al., 2016). Both local-scale habitat within a green space as well as a green space's landscape-scale context (i.e., the habitat surrounding it) are important for explaining community composition (Aronson et al., 2017; Lerman et al., 2021). Local habitat suitability can depend on attributes like vegetation structure and composition that relate to how green spaces are managed (Aronson et al., 2017). The extent of suitable habitat in the landscape surrounding a green space can also have a marked effect on species abundances within a green space (e.g., Blair, 1996; Litteral & Shochat, 2017). From a management perspective, it is particularly important to determine the relative influence of local- versus landscape-scale habitat variables on the species in a green space (Threlfall et al., 2017; Villa-señor et al., 2021). If species respond more strongly to the landscape-scale variables that are beyond a green space manager's jurisdiction, coordinated urban planning at a regional scale may be necessary to augment biodiversity and the services it provides.

The provisioning of ecosystem services in urban green spaces by animal species is a result of correlations between species' response and effect traits. Species with the optimal effect traits that provide desired ecosystem services will be abundant in a green space only if they have response traits that allow them to tolerate the site's habitat conditions (Lavorel & Garnier, 2002). Relationships between response and effect traits will drive variation in effect trait distributions across an urban landscape along gradients in the habitat variables to which species are responding. As a result, due to their habitat conditions, green spaces may vary significantly in the amount of ecosystem services they provide (Aronson et al., 2017; Gardiner et al., 2013). While relationships between response and effect traits are predicted (Stachowicz et al., 2021; Suding et al., 2008), explorations of these relationships and their influence on effect trait variation in the context of ecosystem service provisioning in urban landscapes are scant. Further, it is unknown how these response-effect trait relationships vary for different types of ecosystem service.

Two important groups of ecosystem services in urban areas that involve animals are regulating and cultural ecosystem services (Millennium Ecosystem Assessment, 2005). Regulating services, like seed dispersal and biological control of pests, tend to depend on effect traits related to trophic position, foraging strategy, and morphology (Luck et al., 2012). Animals also provide numerous cultural ecosystem services (Millennium Ecosystem Assessment, 2005), which encompass the diverse range of non-material benefits people derive from nature, like spiritual (De Lacy and Shackleton, 2017), psychological (Cox et al., 2017; Dayer et al., 2019; White et al., 2023), or recreation benefits (Liu et al., 2019; Vallecillo et al., 2019). Effect traits underlying cultural services include those that influence how humans perceive or interact with species (Echeverri et al., 2019a; Goodness et al., 2016), such as traits relating to behavior and aesthetic appeal. Cultural services can be particularly important in cities due to limited opportunities for human-nature connections (Dickinson & Hobbs, 2017; Goodness et al., 2016) and cannot always be easily replaced by socio-economic means if lost (Plieninger et al., 2013; Szücs et al., 2015).

Here we use response and effect functional traits to examine how habitat conditions impact regulating and cultural ecosystem services provided by bird communities in urban green spaces. Birds readily occupy habitats throughout the urban landscape (Blair, 1996; Callaghan et al., 2020) and are sufficiently well-studied that detailed trait data can be obtained across a broad suite of response and effect traits (e.g., Wilman et al., 2014), from diet and foraging behavior to plumage coloration and song characteristics. In turn, these traits link them to a wide range of regulating and cultural ecosystem services (Cameron et al., 2020; Echeverri et al., 2019a; Sekercioglu, 2006; Whelan et al., 2008). In addition, there is a deep literature describing how urbanization shapes urban bird communities (reviewed by Chace & Walsh, 2006) and how avian response traits like diet, foraging, and nesting behavior affect species responses to urban habitat conditions (Evans et al., 2011).

We hypothesized that response traits explain how bird species abundances vary in relation to habitat variables. Specifically, we expected that response traits such as morphology, diet, foraging, and nesting behavior would explain species abundances in relation to local-scale habitat, including vegetation within green space boundaries, and landscape-scale habitat, like cover of trees or impervious surfaces surrounding a green space. We then tested whether there were correlations between response and effect traits that could explain how community-scale composition of effect traits varies with local and landscape habitat. We expected that response-effect trait correlations would scale up to influence the composition of effect traits at a community scale. Finally, we estimated how the bird-mediated supply of cultural and regulating ecosystem services may vary across urban green spaces due to these habitat and trait relationships. Together, these analyses create an integrative approach exploring how urban landscapes and green spaces can be managed for bird-mediated ecosystem services.

2. Methods

2.1. Study region

We studied public urban green spaces in Philadelphia County, Pennsylvania, USA. As the sixth most populous city in the United States (U.S. Census Bureau, 2019), Philadelphia's green spaces service a population of 1.58 million people. These green spaces consist of about 4,100 ha of public parks including plazas, playgrounds, sports fields, and forest preserves (Philadelphia Parks & Recreation, 2021) as well as about 1000 ha of approximately 40,000 vacant lots (City of Philadelphia, 2020; Pearsall, 2017). The Pennsylvania Horticultural Society has renovated 12,000 of these vacant lots (South et al., 2018), which now supplement conventional green spaces in many neighborhoods (Heckert & Kondo, 2018).

2.2. Study site selection

We measured bird communities and habitat at 60 sites in green spaces across the urban landscape of Philadelphia (Table S1, Fig. S1). We selected study sites to be distributed across two gradients representing the availability of suitable habitat at the local and landscape scales (after Cox et al., 2018): 1) *local scale tree canopy cover* within the site boundaries and 2) *landscape scale cover of impervious surfaces,* which includes roads, sidewalks, and buildings within a 500 m radius from the site centroid. The 500 m buffer corresponds to the scale at which most species in our study respond to land cover in urban landscapes (Pennington & Blair, 2011). Both gradients were derived from a high-resolution land cover raster (3 m resolution; City of Philadelphia, 2018) using ArcGIS Pro 3.0 (ESRI, Redlands, California, USA). Selected study sites were located ≥ 250 m from each other (after Ralph et al., 1995). The selected study sites were located within green spaces ranging from small vacant lots (0.05 ha) to large forest preserves (e.g., Wissahickon valley park, 826 ha; Table S2).

2.3. Avian point counts

We sampled bird communities in each site to generate an estimate of the average number of individuals of each species that could be expected to be present and providing services in each site on a given day during the breeding season. We conducted our sampling using 5-minute, 50 m radius point counts at each site. All birds seen or heard were counted and identified and their distance from the observer was recorded with a laser range finder (Impact 850, Vortex Optics, Barneveld, WI). Counts were conducted at the center of small sites (<100 m across) or at a random point ≥50 m from the edge of larger sites. Sites were sampled during the breeding season of resident birds (May 21–July 29, 2019) to avoid including migrant species in our counts, maximize detectability, and measure bird communities during the period when park visitation and ecosystem service demand are highest. We sought to reduce bias caused by factors that influence the detectability of birds (Buckland et al., 1993) by ensuring that all counts at all sites were conducted by a single observer (TMS) from 6:00 AM to 10:30 AM, when bird activity and detectability are highest (Rega-Brodsky & Nilon, 2017), and that no counts took place during periods of precipitation or high wind. We sampled each site at two-week intervals and varied the daily sampling order of sites. Each site was visited at least four times, with 55 of the 60 sites being visited 5 times. We calculated site-level species abundances as the mean number of individuals per species seen or heard across all sampling visits rounded up to the nearest integer to accommodate use of 'fourth corner' analyses (see below). We excluded all individuals flying over or through the site and also excluded raptors, which have home ranges much larger than the studied sites, as these individuals would be minimally affected by the habitat in the site (after Lerman et al., 2021).

2.4. Landscape context and local habitat variables

We measured landscape- and local-scale variables for each site to determine how they were related to bird response and effect traits. At the landscape scale, we measured landscape context based on proportion of impervious surface cover (3 m resolution; City of Philadelphia, 2018) and tree canopy cover (3 m resolution raster generated from the 2018 Philadelphia Tree Canopy Assessment; see O'Neil-Dunne, 2019) within a 500 m buffer radius of the avian sampling point in ArcMap (Table 1). Other measures of landscape composition and configuration surrounding the sites calculated with the R package *landscapemetrics* (Hesselbarth et al., 2019) were considered for inclusion in the analysis but were highly correlated with the proportion of impervious surface cover and were therefore excluded.

At the local scale, we assessed local habitat using field surveys of herbaceous and woody vegetation composition and structure (Table 1) at each site. We modified the Breeding Biology Research and Monitoring Database protocol (BBIRD; Martin et al., 1997) to measure woody vegetation and used Daubenmire (Daubenmire, 1959) methods to measure herbaceous vegetation (Fig. S2). There was substantial variation across sites in terms of the density and distribution of woody vegetation (trees and shrubs), so we used two sampling methods. A "complete census" method was used for sites (N = 33) with sparse enough vegetation that all trees and shrubs could be censused within a 100 m radius from the bird point count location or within the site boundaries for sites smaller than 100 m in radius. For sites with higher woody plant density (N = 27) we used a "census plot" method based on the BBIRD field protocol, which is designed for assessing relatively homogenous habitats (Martin et al., 1997). For this method, woody vegetation was assessed in four circular plots, with one plot centered on the point count location and three located 10–30 m (depending on the size of the site) from the center point and evenly arranged at 120° angles. The radius of the census plot was adjusted based on vegetation density to ensure sampling efficiency (reduced from 10 m radius to 5 m radius in very dense shrubs; after Martin et al., 1997). For both the complete census and census plot method, we recorded the identity of all woody species, counted shrub stems, and measured the diameter at breast height (DBH) of all trees >1 cm DBH within the whole site (complete census) or circular plot (census plot). We used counts of stems and tree DBH to calculate stem densities and basal area to use in subsequent analyses.

Herbaceous vegetation (forbs and grasses) was sampled using a set of eight paired 0.5 m² quadrats. A pair of quadrats was located within each of the four BBIRD plots in census plot sites or their approximate location for complete census sites. In each quadrat, we visually estimated the percent cover of grass (Daubenmire, 1959) and recorded the height of the tallest stem of herbaceous vegetation. The eight quadrat values were averaged for a site-level measurement for each variable. Within each

Table 1
Habitat variables assessed for each study site.

Scale	Variable	Description	Mean[1]	Minimum	Maximum	SD
Landscape Context	Impervious surface cover	Percent cover of impervious surfaces within 500 m of bird count point	52.15	1.31	87.48	21.17
	Tree cover	Percent cover of trees within 500 m of bird point count	23.93	2.22	84.49	18.15
Local Habitat	Site canopy	Percent cover of tree canopy within site measured by spherical densiometer	49.49	0.00	100.00	38.11
	Shrub stems	Density of all shrub stems per m²	0.19	0.00	1.40	0.32
	Tree basal area	Basal area of trees, scaled to site size	0.25	0.00	3.82	0.54
	Woody species richness	Species richness of woody plants (trees and shrubs)	9.82	2.00	25.00	5.21
	Grasses cover	Average percent cover of grasses measured by Daubenmire class	40.07	0.00	92.81	27.63
	Vines cover	Average percent cover of vines measured by Daubenmire class	5.86	0.00	69.06	12.91
	Bare ground cover	Average percent cover of bare ground measured by Daubenmire class	11.55	0.00	58.75	13.37
	Forb cover	Average percent cover of forbs measured by Daubenmire class	30.30	0.00	76.56	20.63
	Vegetation height	Average height of tallest non-woody vegetation present across all sampling quadrats	20.17	0.00	98.38	17.61
	Log area	Log-transformed area of the green space in m²	3.98	2.72	6.92	1.20

[1] Mean values were standardized to have a mean of zero and unit variance prior to analyses.

plot we also estimated tree canopy cover using a spherical densiometer (Lemmon, 1956) and averaged these four measurements for a site-level canopy cover value.

2.5. Response and effect traits acquisition

We synthesized information from multiple sources to identify response traits related to how birds respond to environmental conditions (Callaghan et al., 2019; Leveau, 2013; Luck et al., 2012) and effect traits related to regulating and cultural ecosystem services (Echeverri et al., 2019a; Goodness et al., 2016; Lišková & Frynta, 2013; Luck et al., 2012). We compiled a dataset of 16 response traits and 14 effect traits for which data were available or could be acquired (Table 2). We included response traits related to morphology (body size and shape), diet composition, foraging stratum, and reproduction (nest location and clutch size). For effect traits contributing to cultural services, we used acoustic traits related to song complexity or variability, as well as bird size, shape, and plumage color. For effect traits contributing to regulating services, we used diet traits.

For all response and effect traits apart from acoustic traits, we obtained trait values from the literature (sources detailed in Table 2). Due

to the absence of published acoustic trait data, we measured acoustic traits related to song variability and complexity in Raven Pro (v. 1.6.1, The Cornell Lab of Ornithology, Ithaca, NY). Following Echeverri et al. (2019a), we selected a single representative recording for each species from the Xeno-Canto database (https://www.xeno-canto.org). We selected recordings with low background noise, consisting of the primary song, and recorded from southeastern Pennsylvania or the surrounding region, where possible (Echeverri et al., 2019a). A call was used for species lacking song-type vocalizations (N = 12). The full list of recordings used is available in Table S3. For species with very large song repertoires (e.g., Northern Mockingbird [*Mimus polyglottus*]), measurements were confined to a representative 30 s clip. Two song characteristics were measured: number of syllables and total song frequency range (Table 2). Research explicitly linking acoustic traits to human perception of bird song aesthetics is scarce (Goodness et al., 2016), so we measured traits that capture the variability and diversity of the pitch and syllables, which may reflect how acoustically interesting and pleasant the songs are to human listeners (Echeverri et al., 2019a).

Table 2

Descriptions and data sources for bird response and effect functional traits used to explain how local habitat and landscape context shape bird communities and ecosystem services in urban green spaces.

Trait Family	Trait Name	Variable Type	Description	Data Source	Response Trait	Effect Trait*
Reproduction	Clutch Size	Numerical, Integer	Number of eggs in a clutch	1	✓	
	Structure nests	Binary	Whether the species nests in human-built structures	1,5	✓	
	Cavity nests	Binary	Whether the species nests in cavities (natural or human-created)	1,5	✓	
	Parental care	Numerical, integer	Number of days over which parents provide care to eggs and nestlings	1	✓	
Morphology	Body size	Numerical, continuous	Body mass (g)	2	✓	C
	Wing length	Numerical, continuous	Wing length relative to body length (tip-to-tail [mm])	Calculated from data in 3,4,5	✓	
	Bill length	Numerical, continuous	Ratio of the bill length (length of culmen from the tip of the upper mandible to the front of the skull [mm]) to body length (tip-to-tail [mm])	Calculated from data in 3,4,5	✓	C
	Tail length	Numerical, continuous	Ratio of tail length (length of the tail from the base of the feathers in the center of the tail to the tip of the longest rectrix [mm]) to body length (tip-to-tail [mm])	Calculated from data in 3,4,5		C
	Crest	Binary	Presence of crest	6		C
Foraging Stratum	Ground foraging	Numerical, percentage	Proportion of foraging time spent on ground	2	✓	
	Mid-high foraging	Numerical, percentage	Proportion of foraging time spent <2 m	2	✓	
	Understory foraging	Numerical, percentage	Proportion of foraging time spent 2 m to canopy	2	✓	
	Canopy foraging	Numerical, percentage	Proportion of foraging time spent in canopy	2	✓	
Diet Preference	Diet generality	Numerical, continuous	Shannon evenness of diet across all diet categories	Calculated from data in 2	✓	R
	Invertebrates	Numerical, percentage	Proportion of diet consisting of invertebrates	2	✓	R
	Seeds	Numerical, percentage	Proportion of diet consisting of seeds	2	✓	R
	Fruits	Numerical, percentage	Proportion of diet consisting of fruits	2	✓	R
	Plants	Numerical, percentage	Proportion of diet consisting of plant material other than seeds or fruit	2	✓	
Acoustic	Syllable count	Numerical, integer	Number of unique syllables in a typical song or call	6		C
	Delta frequency	Numerical, continuous	Mean difference in Hz between the highest and lowest frequency of each syllable in the song	6		C
Plumage	Cool plumage	Binary	Blue, purple, or green hues are predominant colors (>50 % of body surface area)	6		C
	Warm plumage	Binary	Red, yellow, or orange are predominant colors	6		C
	Dull plumage	Binary	Gray, brown, tan, or beige are predominant colors	6		C
	Black plumage	Binary	Black is predominant color	6		C

[1]Ehrlich et al. (1988) [2]Wilman et al., 2014 [3]Pyle (1997) [4]Ricklefs (2017) [5]Birds of North America (2020) [6]Collected for this study; *C = Cultural ecosystem service, R = Regulating ecosystem service.

2.6. Statistical analyses

We performed a series of analyses to link habitat and ecosystem services with response and effect traits of bird species in urban green spaces (Fig. S3). We first identified response traits and local and landscape habitat variables driving the abundances of bird species across our study sites. We then determined whether any of these response traits were correlated with effect traits that drive bird-mediated ecosystem service supply, suggesting a link between habitat variables and ecosystem services. To explicitly examine the links between effect traits, habitat, and bird-mediated ecosystem service supply at the community scale, we assessed how the summed effect traits in bird communities varied with habitat variables. Then we assessed how ecosystem services calculated from community-scale effect trait totals were influenced with habitat variables. All analyses were conducted in R (R version 4.0.0; R Core Team, 2015); code and data to replicate our procedures are provided at https://doi.org/10.6084/m9.figshare.19251758.

2.7. Identifying key response traits and habitat variables

We identified the key response traits driving bird species' responses to habitat variables using the "traitglm" function in the R package *mvabund* (Wang et al., 2012). This approach models the abundance of species across multiple sites as a function of the species' traits, environmental habitat variables, and the interaction between traits and habitat (Brown et al., 2014; Warton et al., 2015). The relative magnitude of the coefficients of the trait-habitat interactions are an indicator of their importance in determining abundance bird species at sites (Bartomeus et al., 2018) and are a way to identify the key response traits with respect to habitat variables. Three matrices were used as inputs for this 'fourth-corner model' (see Legendre et al., 1997): 1) a site-by-species abundance matrix of average species counts at each of the 60 sites, 2) a species-by-trait matrix consisting of the trait values for each species, and 3) a site-by-habitat matrix for measurements of local- and landscape-scale variables. The abundance matrix consisted of the number of individuals of each species averaged across the sampling events at each site, rounded up to the nearest integer. The landscape-scale variables were percent cover of impervious surface and tree cover within 500 m of our study sites. Local-scale variables were the first two axes derived from a principal components analysis (PCA) performed using the "rda" function from the *vegan* package in R (Oksanen et al. 2019) on our full set of local habitat variables (see Table 1) to reduce the dimensionality of the data. These two axes captured 52.02 % of the variation in our local-scale variables and represent gradients of vegetation density. Specifically, the first axis (PC1 – 34.82 % of variation) represents a gradient in woody vegetation density from open lawn sites to natural, complex forest vegetation with high shrub and large tree density. The second axis (PC2 – 17.2 %) represents a gradient of herbaceous vegetation density, from those with extensive bare ground to sites with unmown, overgrown herbaceous vegetation (Figs. S4 & S5).

We used the default negative binomial family and specified the "glm1path" method to employ a LASSO penalty to perform model selection and avoid overfitting by reducing to zero the coefficients of trait-habitat interactions that do not improve model fit (Warton et al., 2015). This procedure resulted in the identification of all trait-environment relationships with statistical support, however, some of these relationships were rather weak, suggesting the response traits are not very important for explaining bird responses to the environment. As a result, we selected the most important response traits for our subsequent analyses by ranking the traits by their standardized interaction coefficients and then carrying forward those traits found in the 90th percentile for absolute effect size ($\geq |0.075|$).

2.8. Correlations between response and effect traits

Effect traits have no presumed relationship with habitat conditions (Suding et al., 2008). Rather, habitat conditions impact ecosystem services via correlations between species' response and effect traits. We investigated these relationships by testing for correlations between the important response traits we identified and our 14 effect traits across all species observed in this study using an abundance-weighted linear Pearson correlation (after Pakeman, 2011). The mean abundance of each species across all study sites was used for weighting. This allowed us to account for the contribution of each species to the analysis in proportion to their abundance across the whole data set. This procedure was performed with the "weightedCorr" function from the *wCorr* package (Emad & Bailey, 2017). To test for significance, we used a Bonferroni-corrected alpha value (alpha = 0.0007) to generate a critical t value (3.394) which we compared to the absolute value of each correlation's t value (after Pakeman, 2011).

2.9. Community-scale effect trait-habitat associations

The ecosystem services produced in a site depend on the entire community of service providers (Suding et al., 2008). Accordingly, we used a redundancy analysis (RDA) to identify associations between habitat variables and community-summed effect traits to determine how effect traits vary across the urban landscape. RDA is a constrained ordination method that explains variation in community data using habitat variables (Borcard et al., 2018; Ter Braak, 1986). Here, our community data consisted of a community-summed effect trait matrix where effect trait values were multiplied by each species' site-level mean abundance then summed for all species (see Table 2 for traits). These community-summed effect traits represent the total amount of effect trait produced by the bird community at each site. The habitat data were a matrix of the two local habitat PC axes (see *Identifying key response traits and habitat variables* above) and the two landscape context variables (Table 1). Community-summed effect trait and habitat variables were mean-centered and scaled by the standard deviation. The RDA was performed using the "rda" function in *vegan* (Oksanen et al., 2019). We used the "anova.cca" function, also in *vegan*, to perform permutation tests of the significance of the overall ordination and the significance of each RDA axis and environmental variable. An adjusted R-squared value was generated with the "RsquareAdj" function as a measure of goodness of fit for the overall ordination solution.

2.10. Estimating bird-mediated ecosystem service supply

To quantify how the habitat-effect trait associations scale to affect ecosystem services, we used hypothesized trait-ecosystem service relationships to calculate seven ecosystem service scores from the community-summed effect traits (after Tran et al., 2020; Table S4). In short, we calculated simple additive measures for each effect trait family (visual, acoustic, and diet) by summing the scaled values for each effect trait at each site, with each trait either contributing positively or negatively to a service, based on the literature (Table S4). We used linear models to assess the relationship between the supply of each ecosystem service quantified from the model and all significant environmental variables from the RDA. We adjusted our alpha level to account for multiple tests (N = 7) using a Bonferroni correction (alpha = 0.007).

3. Results

Across our 60 sites, 3,604 individuals from 44 bird species (Table S5) were observed in our sampling. Mean site-level species richness was 8 (SD = 3.5, range = 2–21). The three most common species, which comprised 66.7 % of all individuals observed, were House Sparrow (*Passer domesticus*; 38.5 %), European Starling (*Sturnus vulgaris*; 17.2 %), and American Robin (*Turdus migratorius*; 11.0 %). The average site-level abundance of individuals per visit was 8.6 (SD = 5.4, range = 1–52).

3.1. Identifying key response traits and habitat variables

Across all trait-habitat interactions, there were six response traits and three habitat variables with strong interaction coefficients (magnitude in the 90th percentile; Fig. 1). Species that nest in human-built structures, species with greater relative wing length, and species with a higher proportion of seeds in their diets were more abundant in sites with higher landscape-scale impervious surface cover. Species with larger clutch sizes were less abundant in high impervious surface sites, but more abundant in sites with higher landscape-scale tree cover. Canopy-foraging species and species with a higher proportion of invertebrates in their diets were more abundant in sites with more woody vegetation at the local scale. Overall, interactions between response traits and habitat variables were stronger for landscape than for local habitat variables. The average magnitude of interaction coefficients for landscape variables was 0.078 (range −0.150–0.180), which was twice that of the interaction coefficients for local scale variables (0.034, range −0.048–0.101; Fig. 1).

3.2. Correlations between response and effect traits

The abundance-weighted Pearson correlation showed that five of the six important response traits we identified were significantly correlated to effect traits related to regulating and cultural ecosystem services (clutch size, invertebrate diet, seed diet, nesting in built structures, and wing length; Fig. 2). The sixth response trait, canopy foraging, was not correlated with any regulating or cultural effect trait. For response traits related to regulating effect traits, nesting in structures, invertebrate diet, and seed diet correlated with each of the diet effect traits, except diet evenness. Structure nesters were more likely to consume seeds and less likely to consume invertebrates or fruits. Invertebrate consumers tended to also be fruit eaters and not seed eaters while seed consumers tended to eat fewer invertebrates and fruits. For response traits related to cultural effect traits, species with larger clutches tended to be those with smaller

body size and longer bills. Those that nest in structures and those with longer wings tended to have shorter tails. Those with longer wings also tended to be those with high diet evenness and were more likely to have black plumage.

3.3. Community-scale effect trait-habitat associations

Our ordination of site-level community-summed effect trait values revealed several links between effect traits and impervious surface cover, but not the other habitat variables (Fig. 3). Overall, the explanatory local and landscape habitat variables significantly captured variation in the effect traits ($F_{4,55}$ = 5.43, p < 0.001; adjR^2 = 0.23) and multicollinearity among explanatory habitat variables was low (VIF < 5 for all). Together, the habitat variables explained 28.29 % of the total variance in community-summed effect traits in our redundancy analysis (RDA). Permutation tests indicated that only the first RDA axis explained a significant amount of variation in community-summed trait values (RDA1: $F_{1,55}$ = 18.07, p < 0.001; 24.70 % of total variance explained) and the only explanatory variable that had a significant relationship with RDA1 was impervious surface (i.e., Impervious surf; RDA1: $F_{1,55}$ = 18.02, p < 0.001), which had a negative relationship with RDA1. RDA2 explained substantially less variation in summed trait values and was not statistically significant ($F_{1,55}$ = 1.29, p = 0.76; 1.68 %).

For the most part, effect traits that contribute positively to the supply of plumage- and shape-related aesthetic cultural services (filled red and blue symbols in Fig. 3) were more prevalent at sites with lower impervious surface cover (positive relationship with RDA1) (Fig. 3). In contrast, traits that supply acoustic cultural services (filled yellow symbols) were more prevalent at sites with high impervious surface cover (negative relationship with RDA1). For regulating services, relationships between community-summed effect traits and RDA1 varied by service, with a negative relationship with RDA1 for granivory and diet evenness and a positive one for invertivory.

3.4. Estimating predicted ecosystem service supply

To understand how bird-mediated ecosystem service supply is predicted to vary with environmental variables, we related ecosystem service scores to impervious surface, the only significant environmental variable from our RDA (Fig. 4). Services associated with diet evenness, granivory, and acoustic aesthetics are predicted to increase with impervious surface cover, whereas services related to invertivory, plumage, and shape aesthetics are expected to decrease. Frugivory services did not strongly correspond to impervious surface levels.

4. Discussion

In this study, we applied a functional trait approach to understand how the response of bird species to local and landscape habitat characteristics shape the community-scale supply of ecosystem services provided in urban green spaces. Most urban animals and their associated services cannot easily be managed through direct introductions of species into green spaces. Functional trait approaches can help inform the management of green spaces for ecosystem services provided by animals, yet have rarely been applied in this context (de Bello et al., 2010). Here we show how response and effect functional traits can be used to identify habitat characteristics important for supporting urban bird communities that provide ecosystem services that may be important for human well-being. Although all of our sites are located within the boundary of Philadelphia's city limits and can be considered 'urban', bird species still responded strongly to the habitat gradient generated by land use intensification. In our study, landscape-scale impervious surface cover was associated with significant variation in effect traits and thus indicates significant variation in regulating and cultural ecosystem services provided by bird communities across the urban landscape. In light of the ongoing expansion and intensification of urban land cover
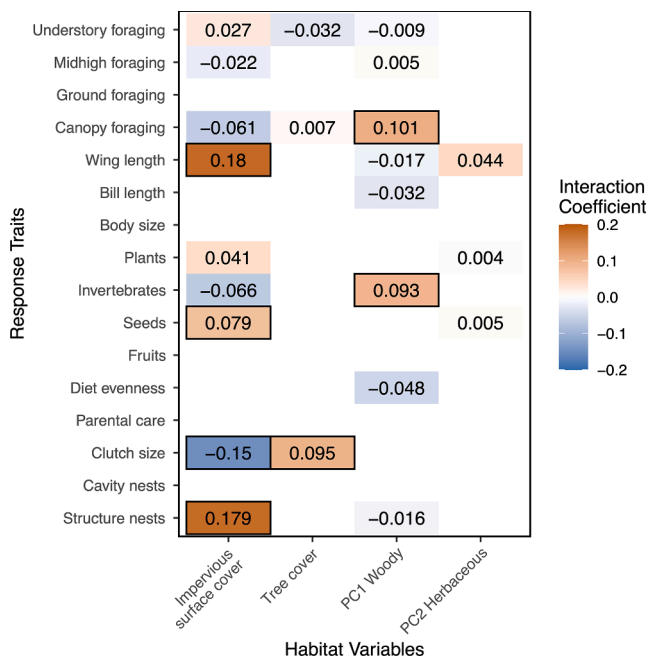

Fig. 1. Tile plot indicating the direction and strength of interaction coefficients between avian response traits and landscape context (Impervious surface and Tree cover) and local habitat (PC1.Woody and PC2.Herbaceous) variables from multiple linear regression modeling. Interactions are blank if they had insufficient statistical support. Black-outlined boxes highlight the strongest response trait-environmental variable interactions (magnitude of coefficients in the 90th percentile across all interactions; ≥ |0.075|).
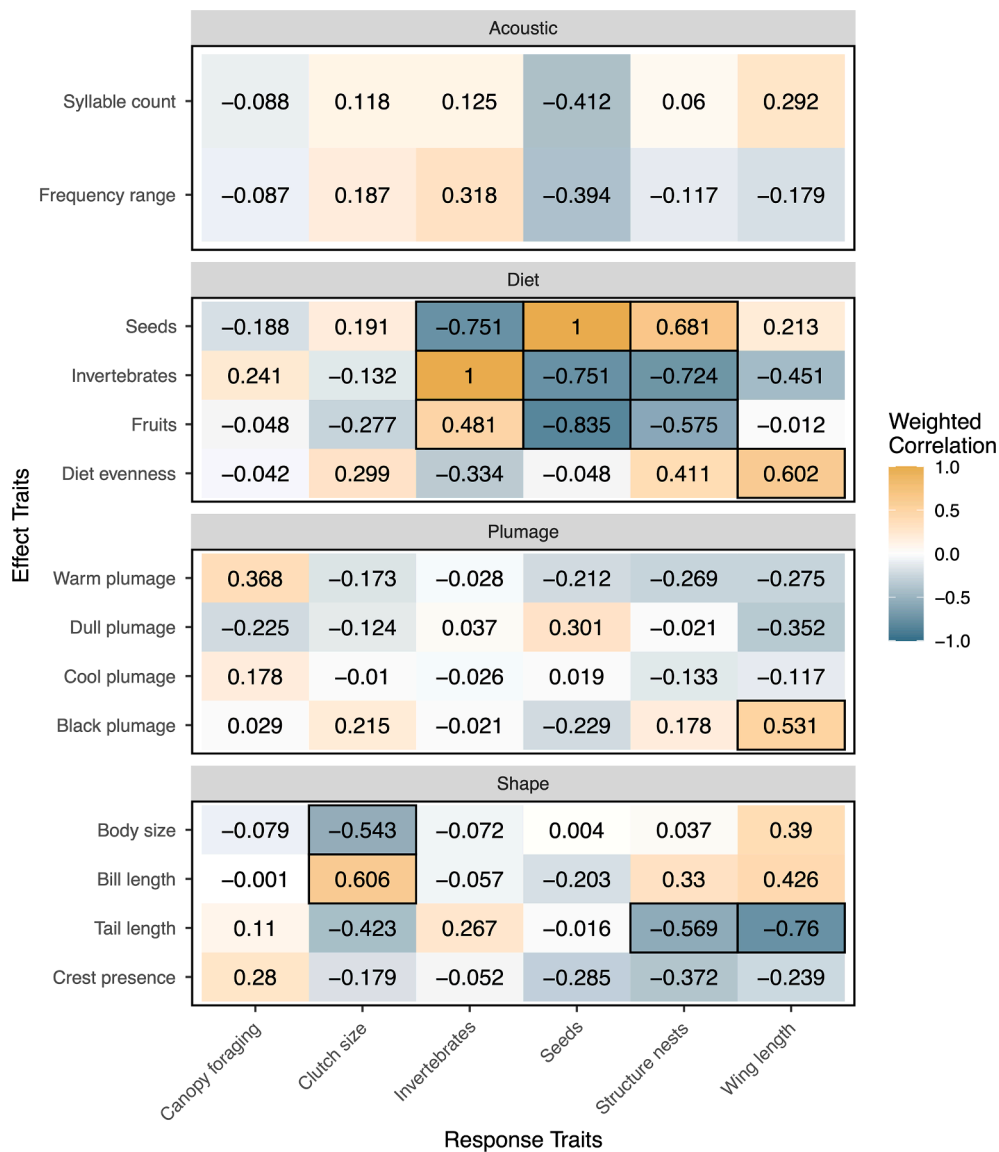
Fig. 2. Tile plots of pairwise abundance-weighted Pearson correlations between avian response and effect traits, grouped by effect trait family. Acoustic, plumage, and shape families contribute to cultural ecosystem services whereas diet traits contribute to regulating services. Significant correlations, based on comparison to a critical t value that represents an α = 0.0007, are outlined with a black border.

(Seto et al., 2011; Seto et al., 2012), these findings are relevant to urban ecosystem service management.

A major component of managing urban green spaces for ecosystem services entails identifying interactions between habitat and species' response traits, since these interactions affect the presence and abundance of potential service-providing species. The urban green spaces we studied varied considerably in their local-scale habitat structure and composition, but the strongest relationships were found between response traits and landscape-scale variables. This suggests that the scale at which green spaces are managed (local) may not match the scale at which bird communities respond to habitat (landscape). The influence of landscape-context on urban bird diversity has been clear for some time (Donnelly & Marzluff, 2004; Luther et al., 2008) and a recent multi-city analysis has underscored the role of impervious surface cover in shaping urban bird communities (Lerman et al., 2021). At the same time, local-scale habitat interventions remain a major component of green space management efforts (Aronson et al., 2017; Strohbach et al., 2013) and can be crucial to conserving local urban bird biodiversity (e.g., Lerman et al., 2021; Narango et al., 2017; Reynolds et al., 2019; Threlfall et al., 2017), especially rare species, which are the focus of

many conservation efforts (Cadotte & Davies, 2010). These local efforts should be coupled with landscape-scale planning (Jokimäki et al., 2018; Liordos et al., 2021) to conserve both species of conservation concern and the communities that provide ecosystem services.

Correlations between response and effect traits are key to the effective management of habitats for the ecosystem services provided by biological communities. Lack of such correlations simultaneously increases the resilience of ecosystem services, as they are less likely to be affected by environmental change (Stachewicz et al., 2021; Suding et al., 2008), while also reducing the possibility that their supply can be increased through habitat management. Our abundance weighted response-effect trait correlation analysis revealed connections between response traits and some, but not all, effect traits. For example, structure-nesting correlated with diet effect traits, suggesting that the proliferation of anthropogenic nest sites in areas with high impervious surface cover could affect the supply of diet-based regulating services. This response-effect trait correlation helps explain the trends noted in our redundancy analysis as well as our models of predicted ecosystem services – diet-related traits and services are strongly associated with impervious surface cover in both positive (granivory, evenness) and
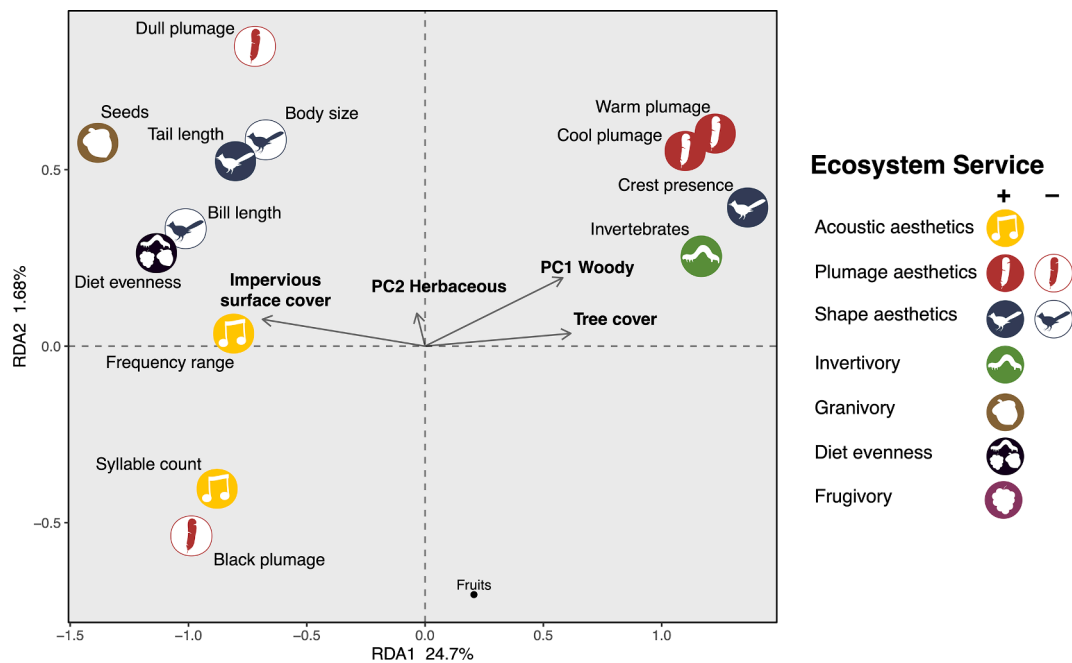
Fig. 3. Redundancy analysis (RDA) biplot showing the centroids of avian effect traits as explained by environmental variables (vector arrows, bold text). Effect traits are grouped by the ecosystem service to which they contribute (symbol and color) as well as the direction of their contribution to the service (positive or negative, see Table S3). Note, RDA axes displayed on different scales.
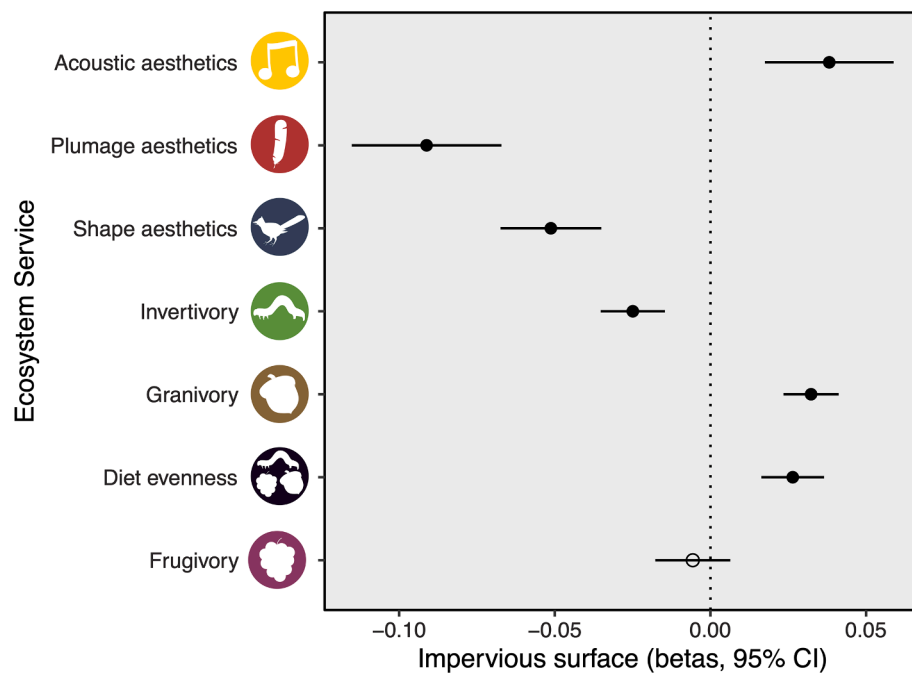

Fig. 4. Plot depicting the effect of impervious surface on 7 ecosystem service scores. Standardized model coefficients and 95 % confidence intervals from linear regression models are displayed, filled circles denote statistically significant coefficient (alpha = 0.007).

negative (frugivory, intertivory) directions.

In contrast, the mechanisms that link habitat, response traits, and effect traits related to cultural ecosystem services are less clear. Except for the relationship between wing length and black plumage coloration, correlations between response traits and plumage and acoustic effect traits were particularly weak. Yet, our redundancy analysis showed a clear association between landscape cover of impervious surface and community-summed effect trait values for both plumage and acoustic traits. Given this, there likely are response traits that correlate with

plumage and acoustic aesthetic traits that were not considered in our correlation analysis because they were not identified as important in the response trait-environment analysis or simply because we did not measure them. For example, the acoustic effect traits we used (syllable count and frequency range) could be correlated with unmeasured acoustic response traits that shape how species are affected by urbanization. Indeed, noise pollution in urban areas can affect community composition by filtering out species that produce low frequency vocalizations (Francis et al., 2011) and favoring those with high frequency

vocalizations (Hu & Cardoso, 2009). Future efforts to identify response traits related to plumage and acoustic effect traits could help pave the way to managing bird-mediated cultural services in urban areas.

Our redundancy analysis and models of bird-mediated ecosystem service supply showed how trait-habitat associations scale up to influence ecosystem services at the community scale. Notably, we found that the services that granivores could provide, like the consumption of carbohydrate-rich littered food waste (Youngsteadt et al., 2015), may be relatively high in sites with high landscape impervious surface cover. In contrast, invertebrate pest control is likely low. In some respects, this pattern may match demand for such services, with a higher need for litter removal in population-dense areas. However, invertebrate pest outbreaks often occur in urban areas and isolated green spaces within a high impervious surface context may be more vulnerable to such outbreaks (Long & Frank, 2020). Furthermore, despite particularly high demand for cultural ecosystem services in areas with more impervious surface cover (Goodness et al., 2016; Valente-Neto et al., 2021), they are likely most scarce there due to the absence of colorful species. By increasing natural cover in the landscape context surrounding urban parks, managers may be able to attract more presumably visually appealing species and improve cultural service supply.

Our functional trait approach revealed that acoustic aesthetics may be a cultural ecosystem service that is generally higher in green spaces surrounded by high impervious surface land cover. While some abundant urban birds (including House Sparrow [*Passer domesticus*]) possess vocalizations consisting of simple, repeating syllables, European Starling (*Sturnus vulgaris*), another abundant species, has an extensive song repertoire, counterbalancing the simple House Sparrow song in our community-scale analyses. Other research approaches have shown contrasting results. In one of the few studies to explore the influence of House Sparrow songs on human perception of the urban soundscape, not only were their vocalizations found to be the least appealing but they reduced overall soundscape appeal when their songs were added to a multi-species chorus (Hedblom et al., 2014). Given the current paucity of research on the relationship between bird song and ecosystem services (Goodness et al., 2016), this is an area where future study of the links between traits and human perception in real-world contexts is warranted.

The need to understand how animal traits generate ecosystem services at a community-scale applies to aesthetic traits and to cultural services more broadly. The links we have made between visual and acoustic traits and the cultural services supplied by green space bird communities are reasonable given present evidence (Goodness et al., 2016), but some are untested. We represented these relationships with unweighted additive measures since existing research has focused on directionality of trait contributions to aesthetic appeal and on rankings of appeal across species (Echeverri et al., 2019b; Lišková & Frynta, 2013; Lišková et al., 2015). Describing the relative importance of and interactions between different traits is needed to develop more refined estimates. Such measures must also account for the scale at which humans experience birds (see Cox et al., 2017). A species' rarity and the difficulty of observing it may contribute to a positive response (Zoeller et al., 2020), but this likely varies depending on the human observers involved (e.g., birdwatchers vs non-birdwatchers; Echeverri et al., 2019a). If a visually appealing species is too rare for most people to observe it, then it may make a lower contribution to real-world ecosystem service supply than an abundant, gregarious species that is more readily observed by the average green space visitor. Furthermore, the characteristics of the landscape in which birds are observed also impacts their perceived appeal (Zoeller et al., 2022). There is also growing evidence that demographic characteristics, like wealth, age, and education shape the value people ascribe to bird-mediated ecosystem services (Belaire et al., 2015). Future research should build on species-level studies of aesthetics to link bird communities to cultural service supply (Cumming & Maciejewski, 2017; Hedblom et al., 2014) while taking a place-based approach that centers the values and attributes of local human communities (Jones et al., 2020; Potschin & Haines-Young, 2013).

In providing a step toward functional trait approaches to managing urban green spaces, our study highlights several future avenues for investigation. First, we expect services to shift with the temporal dynamics of bird communities (e.g., Leveau, 2022) including the loss of migratory breeding species in winter and the influx of transitory non-breeding migrants in spring and fall (Graves et al., 2019). While breeding bird communities provide a constant supply of cultural services to summer-time park visitors, non-breeding migrants may provide a strong pulse of services over a short period. Additionally, birds are just one of many urban animal taxa which provide ecosystem services. Other services and their associated communities, like biological control by predatory arthropods (Burkman & Gardiner, 2014; Gardiner et al., 2014) or cultural benefits provided by charismatic butterflies (López-Hoffman et al., 2010), may be a more easily be managed through local-scale actions (i.e., mowing, tree planting, seeding native plants). These opportunities should be investigated within a functional trait framework. Applying a trait-based approach to other taxa and seasons would undoubtedly provide further insight into the feasibility of managing local green space habitats for ecosystem services.

Finally, it is also important to note that urban ecosystems are social-ecological systems where ecosystem services are co-produced through complex interactions between people and nature (Palomo et al., 2016; Raymond et al., 2018). As such, the relative value of a particular ecosystem service may differ from place to place and person to person (e. g., Echeverri et al., 2019b; Lamarque et al., 2011). In this study, we have focused on applying our functional trait approach to urban ecosystem services that are broadly defined and generally considered to be valued across studies conducted in a range of contexts. However, given that ecosystem services can be assigned context-specific definitions and value, we strongly encourage those responsible for assessing and managing ecosystem services within urban environments to consider their particular city and collection of green spaces when defining the parameters of their assessment and monitoring (Heckert & Rosan, 2016).

5. Conclusion

Urban green spaces are a centerpiece in cities' efforts to create thriving urban landscapes. In this endeavor, cities face a difficult task of balancing the demands placed on urban green spaces to provide ecosystem services including carbon storage, urban heat mitigation, recreation, psychological benefits, wildlife habitat, as well as space for cultural enrichment and social interaction (Aronson et al., 2017; Madureira & Andresen, 2014; Tran et al., 2020). Our goal here has been to implement an approach using functional traits to quantify the relationships between habitat and the service-providing organisms it supports. We suggest that if managers are equipped with knowledge about community-scale functional responses to management actions, they could pursue targeted interventions to augment desirable services. In this process, tradeoffs among ecosystem services are likely (Dennis & James, 2017; Haase et al., 2014) and the decision-making process needs to account for the relative value of the various services in question (Manning et al., 2018). Our approach offers a transparent way to address this challenge by making relationships between habitat, functional traits, and services explicit. Careful, community-engaged management is needed to ensure that green spaces and their biodiversity continue to provide healthy, livable conditions for the world's growing population of urban residents.

CRediT authorship contribution statement

Timothy M. Swartz: Conceptualization, Formal analysis, Methodology, Investigation, Writing – original draft. **Jason M. Gleditsch:** Methodology, Writing – review & editing. **Jocelyn E. Behm:** Conceptualization, Resources, Funding acquisition, Writing – review & editing.

Declaration of Competing Interest

Data availability

The R code and data used for the analyses described in this manuscript are available at https://doi.org/10.6084/m9.figshare.19251758.

Acknowledgements

Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.landurbplan.2023.104724.

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