

1 **Urban greenspace drivers of bird species richness differ between migratory and resident**
2 **species across the full-annual cycle**

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Urban greenspace drivers of bird species richness differ between migratory and resident species across the full-annual cycle

ABSTRACT

Urban greenspaces are increasingly under pressure from urbanization. Greenspaces provide some of the last remaining resources for biodiversity in cities, but their ecological value varies substantially among sites. Despite their importance, we still lack a comprehensive understanding of which urban greenspaces species use across the full-annual cycle and among migratory groupings. To investigate this, we assessed the impact of area, isolation, and urbanization intensity on occupancy by migratory and resident bird species in urban greenspaces across their full-annual cycle. We aggregated community science data from eBird for 66 urban greenspaces across Broward, Miami-Dade, and Palm Beach Counties in South Florida, USA. Data were selected via spatial filtering and the integration of eBird checklists from 2010 to 2024. Our analyses included 366 bird species, classified as migratory or resident. To assess the influence of the 3 greenspace attributes on avian species richness, we fit generalized linear mixed models. We found that migratory and resident species richness were differentially impacted throughout the full-annual cycle by greenspace attributes. Resident species were more likely to be found in more urbanized regions, whereas migratory species were more likely to avoid these areas. However, both groups declined in richness the more isolated a greenspace was, and this effect was more pronounced for residents. Species richness across all species increased with area. We showed that area, isolation, and level of urbanization impacted overall species richness but were moderated by seasons and migratory status. Understanding these fundamental differences is

increasingly important for managers of greenspaces to curate areas that benefit avian species with different life-history traits throughout the year.

Keywords: *birds; citizen science; eBird; migratory; resident; species-area relationship; urban greenspace*

Lay Summary

- Urbanization is rapidly transforming landscapes, making urban greenspaces increasingly important for conserving biodiversity.
- We used eBird checklists across South Florida to assess the impact of area, isolation, and level of urbanization of urban greenspaces on bird species richness.
- Migratory and resident bird species were documented in different urban greenspaces across their full-annual cycles.
- In contrast to migratory species, resident species were more frequently found in greenspaces with higher levels of urbanization.
- Our findings highlight that migratory and resident species have distinct ecological needs across their full-annual cycles and demonstrate how different urban greenspace attributes shape bird diversity in cities.

INTRODUCTION

Over half of the world's human population lives in cities, and that number is expected to grow to 70% by 2050 (United Nations 2018). This rapid rate of urbanization makes it a leading driver of global biodiversity loss (Czech et al. 2000, Parnell et al. 2013). Increasing urbanization transforms landscapes through fragmentation and resource restriction for many species (Kondratyeva et al. 2020, Li et al. 2022, Urban et al. 2024). Despite the negative consequences of cities on biodiversity, they also serve as important areas for some species including, threatened taxa (Ives et al. 2015). To understand how and why urban areas impact biodiversity differentially, it is necessary to identify the mechanisms that allow some species to persist in cities and to recognize that these effects are not static but can vary across seasons and stages of the full-annual cycle.

Within cities, urban greenspaces (i.e., parks and reserves) are key locations where biodiversity persists by maintaining ecological functions (Rakhshandehroo et al. 2017, Gizachew 2021). Larger greenspaces typically harbor higher species richness due to higher environmental heterogeneity, and reduced edge effects (Batáry and Báldi 2004, La Sorte et al. 2020, Moreno-Arias et al. 2020). These patterns tend to conform with the general pattern of the classic species-area relationship (Lack 1983, Lomolino 2001) and the theory of island biogeography (MacArthur and Wilson 2001). However, there is some evidence that larger greenspaces do not always equate to higher biodiversity (Oddi et al. 2025), and some work has shown that small greenspaces can be proportionately very important (Carbó-Ramírez and Zuria 2011). Urban greenspaces range from heavily anthropogenically modified to somewhat natural reserves of remnant habitats (Miguez et al. 2024), leading to differential impacts on biodiversity. Their value for biodiversity

also varies widely depending on area, connectivity, and environmental complexity (Taylor and Hochuli 2017, Zhao et al. 2022, Egerer et al. 2024, Itescu and Jeschke 2024). Urban greenspaces also differ in the degree of surrounding urbanization (for example, the extent of built-up landcover, such as buildings, concrete walkways, lights, or any other human modification) and their spatial isolation within the urban matrix (Zabihi et al. 2025). Greenspaces embedded in highly urbanized landscapes may experience increased anthropogenic disturbance, altered resource availability, and greater exposure to edge effects, compared with greenspaces in periurban areas (Li et al. 2024, Oropeza-Sánchez et al. 2025). Similarly, isolated greenspaces (i.e., further distance from other greenspaces) may be less accessible to mobile species, particularly during energetically demanding periods such as migration (Liu et al. 2025, Oropeza-Sánchez et al. 2025). Yet more isolated greenspaces could represent proportionately more important ‘islands’ within the urban matrix, providing resources in an otherwise resource-sparse environment (Leveau et al. 2024). Together, variation in greenspace area, isolation, and urbanization intensity help explain how urban greenspaces support biodiversity differentially.

The role of urban greenspaces for biodiversity within cities is particularly pronounced for species that rely on different resources and habitat types throughout their full-annual cycle. Birds provide an ideal study system for examining these dynamics because they are highly mobile, occupy a wide range of ecological niches, and occupy urban areas to varying degrees across the full-annual cycle (Callaghan et al. 2021, Alba et al. 2025). Despite the importance of full-annual cycle research, much of the existing research of urban birds has instead focused on the breeding season (Báldi 2007, Whittaker and Marzluff 2009, La Sorte et al. 2017, De Groot et al. 2021, Song et al. 2025). Similarly, the foundations of species-area relationship research have been built

largely on breeding season dynamics (Rafe et al. 1985, Craig 2008, Di Petro et al. 2021). This approach obscures how the strength and ecological interpretation of species-area relationships may shift across seasons and between resident and migratory species (i.e., species that have regular, seasonal movements between separate breeding and non-breeding localities) in urban greenspaces. Addressing this limitation requires explicitly examining how bird species occupy urban greenspaces across the full-annual cycle, allowing for comparisons with the breeding season, noting that resource demands differ across the full-annual cycle.

Migratory and resident bird species inherently differ in their movement strategies, seasonal resource requirements, and occupancy of urban systems; thus, understanding how migratory and resident species differentially occupy urban greenspaces across the full-annual cycle is necessary. Seasonal patterns of resource availability and predation risk shape the use of urban greenspaces by birds (Callaghan et al. 2021). Much previous research has focused on dynamics during the breeding season, but such emphasis provides only a partial view of ecological dynamics, leaving seasonal patterns outside of the reproductive period largely understudied. During the spring and fall migration, migratory birds exhibit stopover events (i.e., when migratory birds stop to rest, recover, or refuel), and during these stages, the environment can differ drastically between localities, and often stopover events pass through cities (Feng et al. 2025). During migration, many species rely on urban greenspaces as temporary stopover refuges (Thorup et al. 2006, Somveille et al. 2013, Lepczyk et al. 2023). Thus, identifying when and how these regions are most valuable can integrate ecological insights with strategies to maintain urban biodiversity throughout the entire year, and can help construct future greenspaces with these practices at the forefront.

Here, we examine how bird species richness (i.e., the number of species present) varies among urban greenspaces across the full-annual cycle and how these patterns differ between migratory and resident species. We evaluate how 3 urban greenspace attributes influence patterns of species richness: (1) patch area; (2) the isolation of the urban greenspace from other greenspace within the urban system; and (3) the level of urbanization within each urban greenspace. To do this, we have two specific objectives: 1) to quantify the relative importance of greenspace area, isolation, and urbanization in explaining bird species richness and assess whether the strength of these relationships differ between migratory and resident species and 2) to determine if the effects of individual attributes vary across seasons and migratory groups to determine whether these relationships are consistent throughout the full annual cycle (Supplementary Material Figure S1). Our objectives were accomplished using 15-years of citizen science data derived from eBird (Sullivan et al. 2009).

METHODS

Study Area

Our study examines urban greenspaces in Broward, Miami-Dade, and Palm Beach Counties in Florida, USA; hereafter, South Florida (Figure 1). Respectively, these areas represent the second, first, and fourth largest counties in Florida by population size ([Census Bureau Tables](#) 2025). This region is experiencing rapid urbanization, with a combined population size of 6.14 million people ([Data USA](#) 2025) and is a global hotspot for avian biodiversity (Merker and Chandler 2020). South Florida has a subtropical climate with wet (May-October) and dry (November-April) seasons. Seasonal temperature variations are not pronounced. This area has an extensive

greenspace network built within the city matrix. Due to its subtropical climate and extensive greenspace network, South Florida can sustain year-round bird populations. Thus, this area serves as an excellent case study for understanding how birds occupy urban greenspaces throughout their full-annual cycle (Merker and Chandler 2020).

eBird Citizen Science Data

We used complete bird observation checklist data, defined as those where a single checklist included every bird detected during sampling, submitted through eBird, where observers record all the bird species they see or hear at a specific location, during a self-chosen time, and within a defined area (Wood et al. 2011, Sullivan et al. 2014, 2017, Johnston et al. 2021). Complete checklists allow researchers to infer the presence and absence of species, which is necessary for estimating species richness (Johnston et al. 2021). Each checklist is automatically checked against filters set by regional volunteers (Gilfedder et al. 2019) tailored to the time and place of the observation to flag anything unusual. When there are uncertainties, regional experts review the data and reach out to confirm observations. We downloaded eBird data from January 1, 2010, to December 31, 2024, for each county (version ebd_rel-Jan2025). Furthermore, we removed any checklists with species records that denoted the number of individuals as X, as this reflects species presence without an associated count (Kinnunen et al. 2024, Barratt Heitmann et al. 2025, Callaghan et al. 2025). Additionally, observers may use this code for a variety of reasons, potentially introducing additional uncertainty into count-based analyses. To assess the decision to exclude checklists with species records recorded as X in our results, we ran a sensitivity analysis and found nearly identical results (Supplementary Material Figure S2). We further removed any checklist with survey duration of < 5 minutes and >240 minutes, and those of >5

km length, following prior protocols of using eBird data (Kinnunen et al. 2024, Barratt Heitmann et al. 2025, Callaghan et al. 2025).

Each species was subsequently categorized as migratory or resident using the lifestyle groupings from AVONET (Tobias et al. 2022), where species scored 2 (partial migrants: species that have migratory, as well as resident populations) or 3 (full migrants) were classified as migratory, and species scored 1 were classified as residents. For species not included in the AVONET data (N = 21; Supplementary Material Table S1), we sourced information from All About Birds data maps, which shows if a species occupies South Florida year-round or seasonally (All About Birds 2025). Non-native species were considered resident for South Florida, as there are year-round populations for all species included in the analyses (e.g., *Myiopsitta monachus* [Monk Parakeet], *Acridotheres tristis* [Common Myna]).

To examine patterns across the full-annual cycle, we grouped observations into 4 biologically meaningful categories based on presence during the non-breeding season (December – February), spring migration (March – May), breeding season (June – August), and fall migration (September – November). These groupings align with the timing of key annual cycle in the Northern Hemisphere and are used in full-annual cycle research (Culp et al. 2017).

Defining Urban Greenspaces

Urban greenspaces were obtained from the ParkServe dataset ([The ParkServe® database - Trust for Public Land \(tpl.org\)](#)), which provides polygons of greenspaces across the United States as of

2024 in a shapefile format. We filtered these polygons to South Florida and identified 4,318 greenspaces. To focus on urban greenspaces, we filtered out extremely small parcels and very large natural areas (e.g., the Everglades), only retaining greenspaces between 0.0005 ha and 150 ha (i.e., $5 \text{ m}^2 \leq \text{area} \leq 1,500,000 \text{ m}^2$). We filtered extremely small and very large parcels because they did not meet the functionality criteria defined by Callaghan et al. (2020)—urban spaces that are managed and designated as parks or recreational spaces, which are capable of being utilized by the surrounding community and are adjacent to built-up landcover. This definition, along with Taylor and Hochuli’s (2017) definition that urban greenspaces must be predominantly surrounded by urban development and generally accessible to the public, eliminates tree patches that run down highways and small parcels that are not accessible to the public. Next, we overlaid the shapefiles with the locations of eBird checklists, retaining greenspaces ($n = 76$) with at least 10 complete checklists per season of the full-annual cycle for the entirety of the study. To ensure these greenspaces met all criteria and our definition for inclusion in downstream analyses, we manually inspected the resulting 76 greenspaces and removed the 7 localities that did not meet the functionality criteria (Juno Beach Ocean Park, Boynton Beach Oceanfront Park, Fort Lauderdale Beach Park to Oakland, Hillsboro Blvd, 400 N State Road A1A, SW 360th Street / SW 192nd Avenue, and Pahokee State Park), and 3 localities, for which we could not calculate all necessary data (i.e., Global Human Modification Index—GHMI) for modeling (Arch Creek Park, Jupiter Inlet Outstanding Natural Area, and Seacrest Scrub Preserve). Thus, 66 greenspaces were used in our analysis.

Urban Greenspace Attributes

For each step, we used R version 4.4.1 (R Core Team 2025), specifically the *tidyverse* package (Wickham et al. 2019) to clean and organize, *ggplot2* (Wickham 2011) to plot, and *gt* (Sjoberg et al. 2021) to create tables. For each urban greenspace delineated and included above, we calculated the following 3 urban greenspace attributes: (1) area; (2) isolation; and (3) GHMI (hereafter, level of urbanization). Greenspace area was calculated directly from the ParkServe polygons in m² using the *sf* R package (Pebesma 2018). Greenspace isolation was calculated as the distance from the nearest greenspace edge to any greenspace in the original dataset, which included all 4,318 greenspaces. Without including all greenspaces, we would have misinterpreted the results, and greenspaces that are surrounded by more green patches would have been misconstrued as isolated when they have either large patches of green or small parcels neighboring them (*sensu* La Sorte et al. 2020). We subsequently categorized each greenspace by the level of urbanization. We quantified the level of urbanization from within the greenspaces on a continuous scale from 0 (least urbanized) to 1 (most urbanized) relative to a global baseline using the Global Human Modification Index that categorizes data based on a 1,000-m resolution (Kennedy et al. 2019), obtained from the Google Earth Engine CSP gHM dataset (developers.google.com/earth-engine/datasets/catalog/CSP_HM_GlobalHumanModification).

Statistical Analysis

To assess our first objective, the relative influence of greenspace attributes on predicting species richness, we fit two separate models for migratory and resident species. These models were intended to compare the relative strength of the 3 greenspace attributes. For each model, the response variable was species richness of the respective group, and the predictor variables were the greenspace attributes (i.e., area, isolation, or level of urbanization), season, and their

interactions (attribute $\times$ season). This framework allowed us to test whether the importance of each attribute on species richness varied between groups, and whether importance changed between seasons for each group. In addition to these predictor variables of interest, we included sampling effort as a predictor variable, calculated as the total number of checklists submitted per greenspace. Sampling effort was included as a stand-alone fixed effect to account for variation in observer effort. The distribution of the number of checklists was highly right-skewed, with a small number of urban greenspaces receiving many checklist submissions while most received relatively few; thus, we log-transformed this variable before statistical analyses to improve model fit. Additionally, we fit a random effect for greenspace to account for the non-independent measures of species richness from each greenspace. Both models were fit as generalized linear mixed models (GLMMs; Supplementary Material Figure S1) using the *glmmTMB* package (Brooks et al. 2017). Because species richness is count data, we initially explored model diagnostics using both a Poisson distribution and a negative binomial distribution for fitting. The Poisson model was not over-dispersed and model comparison using Akaike Information Criterion (AIC) and residual diagnostics indicated that the Poisson distribution provided the best-fit model; therefore, we fit our models with a Poisson distribution. To assess model fit, we used the *DHARMa* package (Hartig and Hartig 2017) to run simulated-based residual diagnostics to assess residual patterns. We also created a correlation plot to show how each attribute was correlated to one another (Supplementary Material Figure S3). No pairwise correlations exceeded 0.3, indicating that multicollinearity was not a concern.

Because objective 1 focused on relative importance among predictors, we then fit attribute-specific models to evaluate how the effect of each attribute varied across seasons and migratory

groups. Fitting attribute-specific models allowed us to test interactions between each attribute, season, and migratory group explicitly without confounding effects among associated landscape variables. For each model, the response variable was species richness and the predictor variables were the respective greenspace attribute (i.e., area, isolation, or level of urbanization), season, migratory group, and their interactions, including two-way and three-way interaction terms (attribute $\times$ season; attribute $\times$ migratory status; and attribute $\times$ season $\times$ migratory status). As each attribute was a different measurement unit and scale, we z-transformed them for adequate comparisons across the 3 attributes (Bartlett 1993). This framework allowed us to test whether the effect of each greenspace attribute varied across seasons, differed between migratory and resident species, and whether seasonal patterns in attribute effects differed between migratory groups (see Supplementary Material Figure S1). For objective 2, we fit separate models for each greenspace attribute because this provided a more parsimonious and interpretable framework for evaluating interactions with season and migratory group while avoiding confounding effects among predictors. As with the models for objective 1, we included sampling effort as a predictor variable and a random effect for greenspace. Full model specifications, including fixed and random effects structures, are provided in Supplementary Material Figure S1. For both models, we fit separate models without the number of checklists included to test the marginal R^2 value with and without sampling effort (*sensu* Lilkendey et al. 2025).

We extracted and interpreted model outputs for the two objectives using the *broom.mixed* (Bolker et al. 2019) and *marginalEffects* (Makowski et al. 2025) R packages. These packages allowed for the visualization of partial dependence plots showing predicted species richness based on greenspace area, isolation, and level of urbanization, while holding other variables

constant. For both models, we ran a type III Anova using the *car* package (Fox and Weisberg 2018) to test each hypothesis. This approach properly accounts for interaction variables by individually testing each predictor for explanatory power (for similar methods see Hoiss et al. 2012). Statistical significance was assessed using a priori $\alpha = 0.05$. Parameter estimates were considered statistically significant when $p < 0.05$ or, equivalently, when 95% confidence intervals did not overlap zero.

RESULTS

We analyzed 66 urban greenspaces across South Florida, with an average area of 39.9 ha (range: 2.3 – 147.5 ha). Across all greenspaces, we compiled 366 bird species (Supplementary Material Table S1) by integrating 1,618 eBird checklists and 9,581,045 bird observations, comprising 263 migratory and 103 resident species. Species richness varied widely among greenspaces (Supplementary Material Figure S4). The mean species richness per greenspace was 112.0 ± 40.8 SD, with the highest and lowest richness recorded at Green Cay Wetlands and Nature Center (N = 232 species) and at Camp Redlands (N = 18 species), respectively.

Objective 1 – Relative Influence of Greenspace Attributes

We assessed all 3 variables in 2 models: one for resident species (Table S2.A) and one for migratory species (Supplementary Material Table S2.B). These models showed that resident and migratory species responded differently to greenspace attributes, as area significantly affected migratory species richness ($\log_{10}(\text{area})$: $z = 3.21$, $P = 0.001$; level of urbanization: $z = 0.13$, $P = 0.894$; isolation: $z = -0.35$, $P = 0.724$), while the level of urbanization and area significantly affected resident species richness ($\log_{10}(\text{area})$: $z = 3.78$, $P < 0.001$; level of urbanization: $z =$

3.78, $P < 0.001$; isolation: $z = -1.53$, $P = 0.127$; Figure 2). Overall, migratory richness was more strongly tied to greenspace area, while resident richness appeared more responsive to level of urbanization. Both models explained a substantial proportion of variation in richness (resident, marginal $R^2 = 0.671$; migratory, marginal $R^2 = 0.876$). However, much of this variance was due to sampling effort (i.e., the number of checklists), and when sampling effort was removed, the marginal R^2 values were lower (resident, marginal $R^2 = 0.213$; migratory, marginal $R^2 = 0.380$). The greenspace attributes and sampling effort correlated weakly ($r \leq 0.24$; Supplementary Material Figure S3), which indicated that more heavily surveyed greenspaces were not strongly associated with larger area ($r = 0.17$), greater isolation ($r = 0.24$), or higher levels of urbanization ($r = -0.03$).

Objective 2 – Individual Greenspace Attributes

We found that all 3 attributes affected species richness differently across migratory groups and between each season of the full-annual cycle. We tested the three-way and two-way interactions between each variable with season and migratory status in separate models.

Area model. Species richness significantly increased with the area of greenspaces for both migratory and resident species ($\log_{10}(\text{area})$, $z = 2.31$, $P = 0.021$; Figure 3; Supplementary Material Table S2.C). The strength of this relationship differed between migratory groups ($\chi^2 = 4.66$, $P = 0.031$; Figure 3), with estimated marginal trends showing a stronger positive response for migratory species (slope = 0.158, SE = 0.039, $z = 4.08$, $P < 0.001$) than for resident species (slope = 0.101, SE = 0.044, $z = 2.31$, $P = 0.021$). In contrast, there was no significant interaction between greenspace area, season, and migratory group ($\chi^2 = 1.02$, $P = 0.797$), which indicated

that the positive relationship of area on richness was consistent across seasons for both migratory groups. The model explained a large proportion of variance in species richness with (marginal $R^2 = 0.882$), and without (marginal $R^2 = 0.516$) the number of checklists (i.e., sampling effort) in the model.

Isolation model. Species richness significantly decreased as greenspace isolation increased ($\log_{10}(\text{isolation})$, $z = -2.31$, $P = 0.021$; Figure 4; Supplementary Material Table S2.D). Estimated marginal trends showed that resident species richness declined significantly with increasing isolation (slope = -0.046 , SE = 0.020 , $z = -2.31$, $P = 0.021$), whereas migratory species richness was not significantly related to isolation (slope = -0.003 , SE = 0.018 , $z = -0.15$, $P = 0.881$). There was no significant three-way interaction among isolation, season, and migratory group ($\chi^2 = 0.14$, $P = 0.986$), which indicated consistent isolation effects across seasons of the full-annual cycle for both groups. The model accounted for a substantial proportion of variation in species richness with (marginal $R^2 = 0.870$), and without (marginal $R^2 = 0.468$) the inclusion of sampling effort.

Urbanization intensity model. We found that migratory and resident species richness responded differently to level of urbanization (Figure 5; Supplementary Material Table S2.E). The level of urbanization had a significant overall effect on species richness ($\chi^2 = 6.49$, $P = 0.011$), and this effect differed between migratory groups ($\chi^2 = 19.99$, $P < 0.001$). Estimated marginal trends indicated that resident species richness increased significantly with a higher level of urbanization (slope = 0.469 , SE = 0.184 , $z = 2.55$, $P = 0.011$). The three-way interaction between level of urbanization, season, and migratory group was not significant (total, $\chi^2 = 1.92$,

$P = 0.589$). The model accounted for a substantial proportion of the variation in species richness both when excluding (marginal $R^2 = 0.870$) and including (marginal $R^2 = 0.460$) sampling effort.

DISCUSSION

By analyzing a large citizen science dataset, we found that species richness in urban greenspaces was structured by area, isolation, and the level of urbanization, but that the relative importance of these attributes differed between migratory and resident species. For migratory species, richness was driven by area alone. For resident species, richness was influenced by urbanization and greenspace area, but not by greenspace isolation. The significance and effect size of each greenspace attribute varied throughout the full-annual cycle and between migratory and resident species. Specifically, migratory species exhibited a non-significant relationship with greenspace area in the spring, but a significant relationship during the other seasons. Our results illustrate the importance of full-annual cycle research (Marra et al. 2015) when it comes to understanding how bird species respond to increasing urbanization and greenspace modification (Apfelbeck et al. 2025). Taken together, this suggests that local environmental conditions significantly influence species richness (Bhakti et al. 2025), with the ecological community behaving dynamically between each greenspace, across time, and among migratory and resident species.

Species Richness Patterns

Migratory species disproportionately depended on larger greenspaces during most of the annual cycle. Area was the only significant predictor of migratory species richness, supporting previous findings that park size is the primary driver of avian richness in urban greenspaces (La Sorte et al. 2020). During migration, many species—particularly Neotropical migrants—face high

energetic demands and strict time constraints, making access to high-quality and predictable foraging resources critical (McWilliams et al. 2004, La Sorte et al. 2018). Larger greenspaces may better meet these needs by providing greater environmental heterogeneity, reduced edge effects, and higher prey availability than smaller, more fragmented patches embedded within urban landscapes (Evans et al. 2009, Callaghan et al. 2021). However, this dependence was not uniform across seasons. During spring migration, migratory species richness was not significantly predicted by area. This likely reflects the faster pace of spring migration compared to fall migration (Alerstam et al. 2011, Schmaljohann et al. 2012, Nilsson et al. 2013), which may reduce selectivity of urban greenspaces during stopover events. Stopover events require different resources depending on the function of each stopover event (Schmaljohann et al. 2022), which in turn, might lead to lowered habitat preferences and a heightened preference to individual resources instead (Matthews and Rodewald 2010). Although our findings differ somewhat from those of La Sorte et al. (2020), who found that area explained avian species richness patterns across seasons and throughout the year without distinguishing migratory status, our results suggest that area remains the dominant driver for migratory species when life-history groups are considered separately.

Resident species richness was driven by both the area of the greenspace and the level of urbanization. With both attributes, resident species richness increased, likely indicating that resident species in South Florida may be well adapted to the urban environment. The positive relationship with urbanization may indicate that many resident species are well adapted to modified environments, potentially reflecting greater behavioral flexibility and urban tolerance (Morelli et al. 2022, Liu et al. 2025). Urban-adapted residents may exploit anthropogenic food

resources, novel nesting substrates, and fragmented greenspaces throughout the year (Aronson et al. 2016, La Sorte et al. 2018). Resident species also exhibited relatively moderate and stable responses to the area of the greenspace throughout the annual cycle compared with migratory species, further suggesting that residents may be less dependent on large greenspaces. However, higher richness in more urbanized greenspaces does not necessarily indicate higher habitat quality, as urban-tolerant species may benefit from anthropogenic resources, while other species are excluded. Thus, species richness alone cannot distinguish between urban adaptation and potential ecological traps.

Isolation was not a significant predictor of migratory richness and was the weakest predictor of resident richness. This may reflect the highly urbanized landscape of South Florida and the ability of individual birds to move through or use the urban matrix. Birds may also be less affected by patch isolation than less mobile taxa (Neuschulz et al. 2013, Hiron et al. 2015, Kale et al. 2018, Korányi et al. 2021, Callaghan et al. 2024). However, our measure of isolation was based on nearest-neighbor distance, which may not fully capture functional connectivity or the quality of the surrounding landscape. Future studies could therefore evaluate alternative measures, such as the proportion of natural area surrounding each greenspace (Callaghan et al. 2018, Arévalo et al. 2022).

Sampling effort explained substantial variation in observed species richness and was therefore retained as a covariate to account for differences in detection and observer coverage among greenspaces. Greater sampling effort increases the probability of detecting species and consequently influences observed richness (Azovsky 2011). Sampling effort may also be

associated with greenspace characteristics; for example, larger greenspaces may attract more observers due to greater recreational opportunities, while highly urbanized locations may receive greater visitation because of their accessibility and proximity to human populations. Although checklist effort was accounted for in our analyses, future studies should explicitly evaluate relationships between sampling effort and greenspace characteristics to better identify potential sources of bias in citizen science datasets.

An additional limitation is that abundance may respond differently to urbanization than species richness (Carbó-Ramírez and Zuria 2011, Thompson et al. 2022). Because eBird checklists do not provide standardized counts of individuals across sites and observers, our analyses were limited to species richness. Designed surveys, such as point counts or mist-netting, could provide standardized abundance estimates and help determine whether changes in abundance contribute to the richness patterns observed across seasons and spatial scales (Dunn and Ralph 2004).

Management Implications and Future Directions

Our results show that the ecological value of urban greenspaces varies across seasons and between migratory groups, indicating that a single management approach is unlikely to maximize benefits for all bird communities. Consequently, effective management must incorporate temporal planning—ensuring that resources, microhabitats, and disturbance regimes align with periods of peak migratory occupancy, requirements during the non-breeding season, and resident breeding cycles. For migratory species, maintaining and protecting larger greenspaces should be a priority because area was consistently associated with greater richness during most of the annual cycle. Larger greenspaces may provide greater structural complexity

and the resources necessary during stopover and the non-breeding season (Buler et al. 2007, Chiron et al. 2024). Additionally, migratory species richness was predicted to decrease with increasing urbanization levels, except during spring migration and during breeding (which had a positive prediction). This suggests that migratory species are sensitive to environmental modification and may require greenspaces with greater structural complexity and natural resource availability (Machar et al. 2022, Egerer et al. 2024). Management should therefore prioritize diverse native vegetation and natural water features that provide food, shelter, and breeding resources throughout the year (Wang et al. 2023).

Tailoring management to seasonal ecological demands not only improves environmental suitability but may also reduce maintenance costs by concentrating effort and resources when and where they are most effective, rather than applying uniform management throughout the year. For example, delaying mowing in early spring can boost insect prey availability for both migratory and resident species (Leung et al. 2022, de Araújo et al. 2025), while planting late-season fruiting plant species can support fall migratory species without year-round maintenance (Smallwood et al. 2023). Yet, our results suggest that management should focus on reducing the level of urbanization and increasing the area of urban greenspaces. During spring and fall migration, birds are heavily impacted by urbanization. One way to decrease this anthropogenic disturbance is to reduce the amount of artificial light at night exposure in the urban greenspace during these periods (this is a measure involved in calculating the level of urbanization: GHMI). Light pollution can disrupt migration and can cause birds to become confused or disoriented (La Sorte et al. 2022, Burt et al. 2023). Another way to reduce the level of urbanization is to increase woody plant cover (Von Thaden et al. 2025), so planting a mix of native trees, shrubs, and palms

can benefit ecological integrity and help bird populations persist. This is particularly important for non-breeding and breeding populations that rely on a constant supply of resources in urban greenspaces (Aida et al. 2016, Smallwood & Wood 2023).

Future research should explicitly evaluate how management interventions, restoration strategies, and more specific greenspace attributes (e.g., quantity of native and non-native plants or percent roadways/bike paths) influence the year-round ecological function of urban greenspaces.

Additional work should combine fine-scale movement data with detailed structural environmental metrics to analyze how birds occupy urban localities across seasons (Byer et al. 2025, Guo et al. 2025). Future studies could integrate urban greenspace analyses with building-collision datasets generated through lights-out programs to clarify how urban infrastructure influences bird movements and mortality across cities (Nemes et al. 2023). Incorporating fine-scale data, including lights-out building strike data, can help inform scientists on where birds are moving and if they are using or avoiding urban greenspaces near taller building structures. This could help improve management design to curate urban greenspaces that better mitigate urbanization. Because our analyses focus on species richness rather than direct measures of environmental use, future studies integrating occupancy models, movement data, or individual-level tracking could help determine the behavioral mechanisms underlying these observed richness patterns. In this study, we intentionally used broad classifications of species as either residents or migratory because the non-breeding season of many species in South Florida is rapidly changing (Al Rifat and Liu 2022). However, future studies could investigate whether responses to urbanization differ between partial and full migratory species. Understanding these interactions will allow managers to design and curate greenspaces that support both migratory

512 and resident species under increasing pressures from urbanization throughout their full-annual
513 cycles.

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Ethics statement

Data collection was entirely through open-source data, no ethics guidelines were applicable.

Conflict of interest statement

The authors declare no conflict of interest.

Author contributions

Conceived the idea: LPH and CTC; Conducted the analyses: LPH and BMM; Developed models: LPH, CTC, BB; Wrote or substantially edited the paper: LPH, BMM, BB, CTC; Secured funding: CTC.

Data availability

Analyses reported in this article can be reproduced using the data provided by [Hoskins \(2026\)](#).

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818 **Data Accessibility Statement:** Reproducible code and datasets are archived on Zenodo
819 ([https://github.com/Global-Ecology-Research-Group/Levi_et_al-2026-Ornithological-](https://github.com/Global-Ecology-Research-Group/Levi_et_al-2026-Ornithological-Applications)
820 [Applications](https://github.com/Global-Ecology-Research-Group/Levi_et_al-2026-Ornithological-Applications)).

Figures

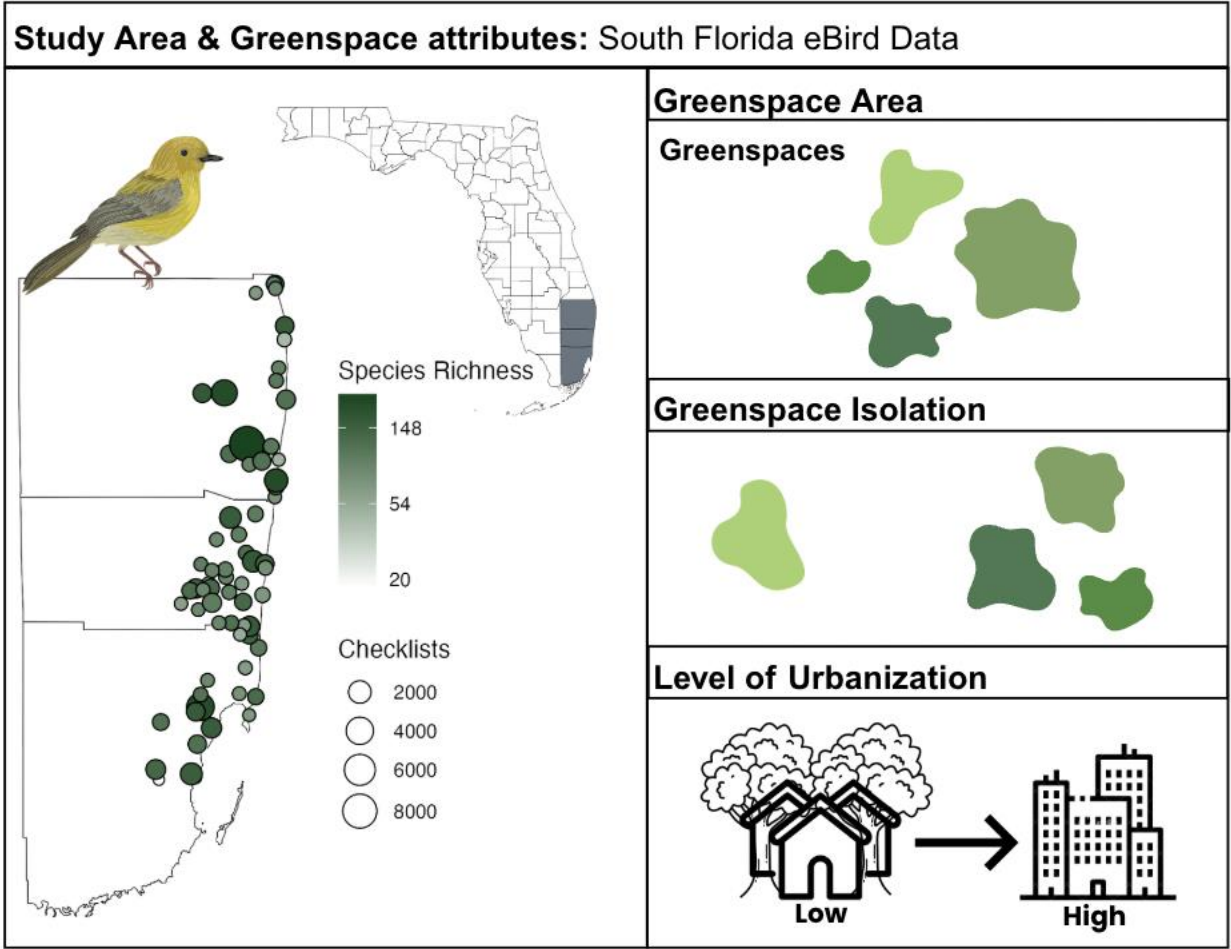


Figure 1. Sampled greenspaces of Broward, Miami-Dade, and Palm Beach counties, Florida, USA, and associated greenspaces attributes. The circle radius represents the total number of checklists, and the color-scale represents the number of species found in each greenspace. The study area is on the left and the greenspace attributes are on the right.

ALT TEXT: Graphical abstract showing study area in South Florida and urban greenspaces attributes assessed, along with species richness and checklist count for each urban greenspace.

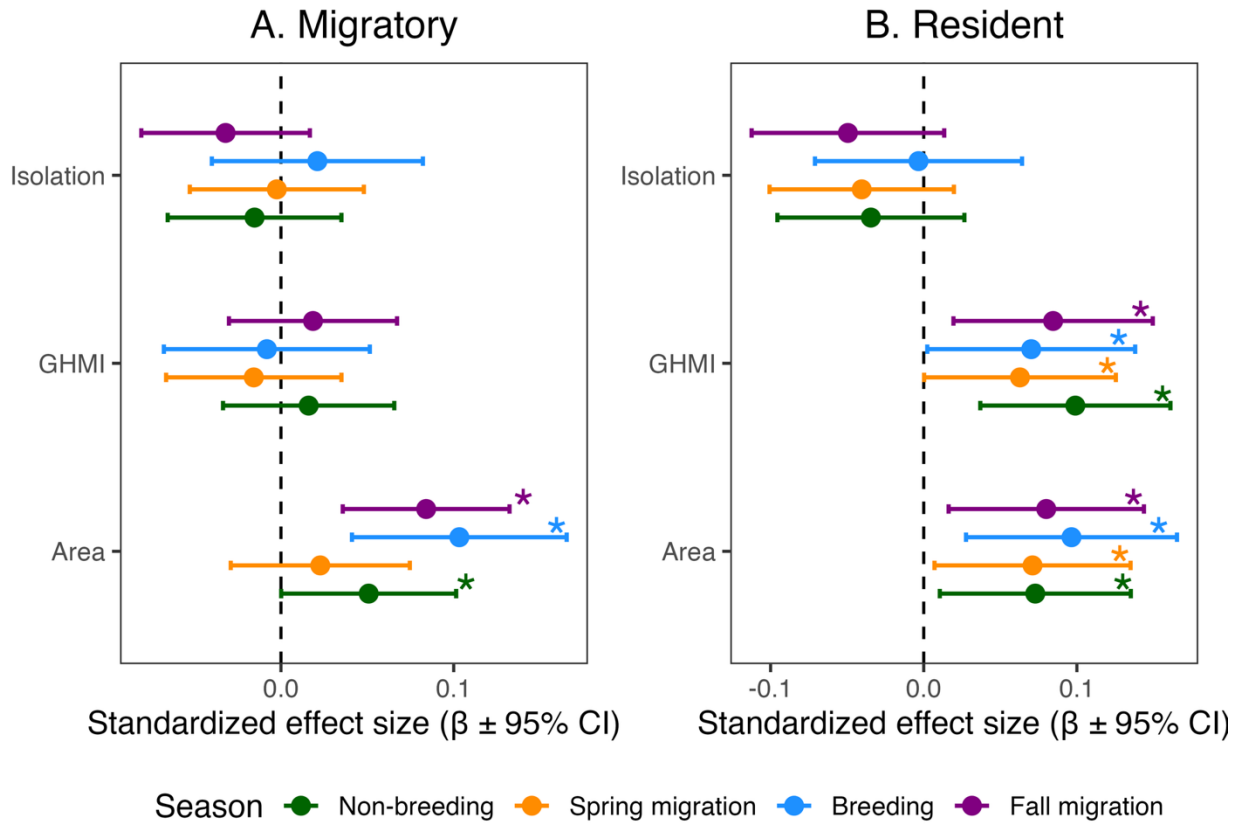


Figure 2. Effect size of each greenspace attribute (area, isolation, Global Human Modification Index [GMHI]), on species richness for migratory group and between seasons of the full-annual cycle. Whiskers represent the 95% confidence intervals. Each predictor variable was z-transformed to address the varying units of measurement. Asterisks denote significant trends ($p < 0.05$).

ALT TEXT: Graphs showing the effect size of each greenspace attribute for migratory and resident species richness during each season of the full-annual cycle.

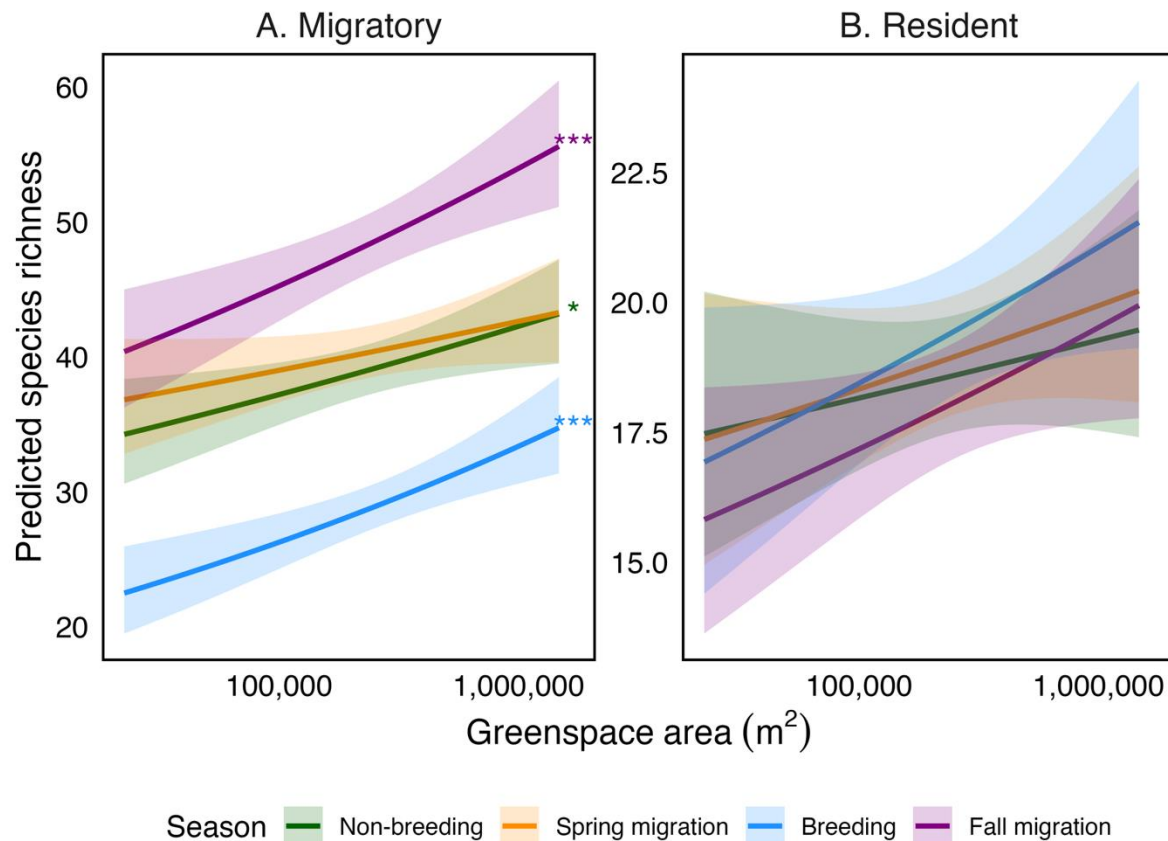


Figure 3. Predicted species richness for each season of the full-annual cycle based on greenspace area for each greenspace, plotted on the log-scale. Ribbons represent the 95% confidence intervals. Asterisks denote significant trends ($P < 0.001 = \text{"***"}\text{"}$, $p < 0.01 = \text{"**"}\text{"}$, $P < 0.05 = \text{"*"}\text{"}$).

ALT TEXT: Line graphs showing the predicted species richness for each season of the full-annual cycle, split between migratory and resident species, based on greenspace area (m²).

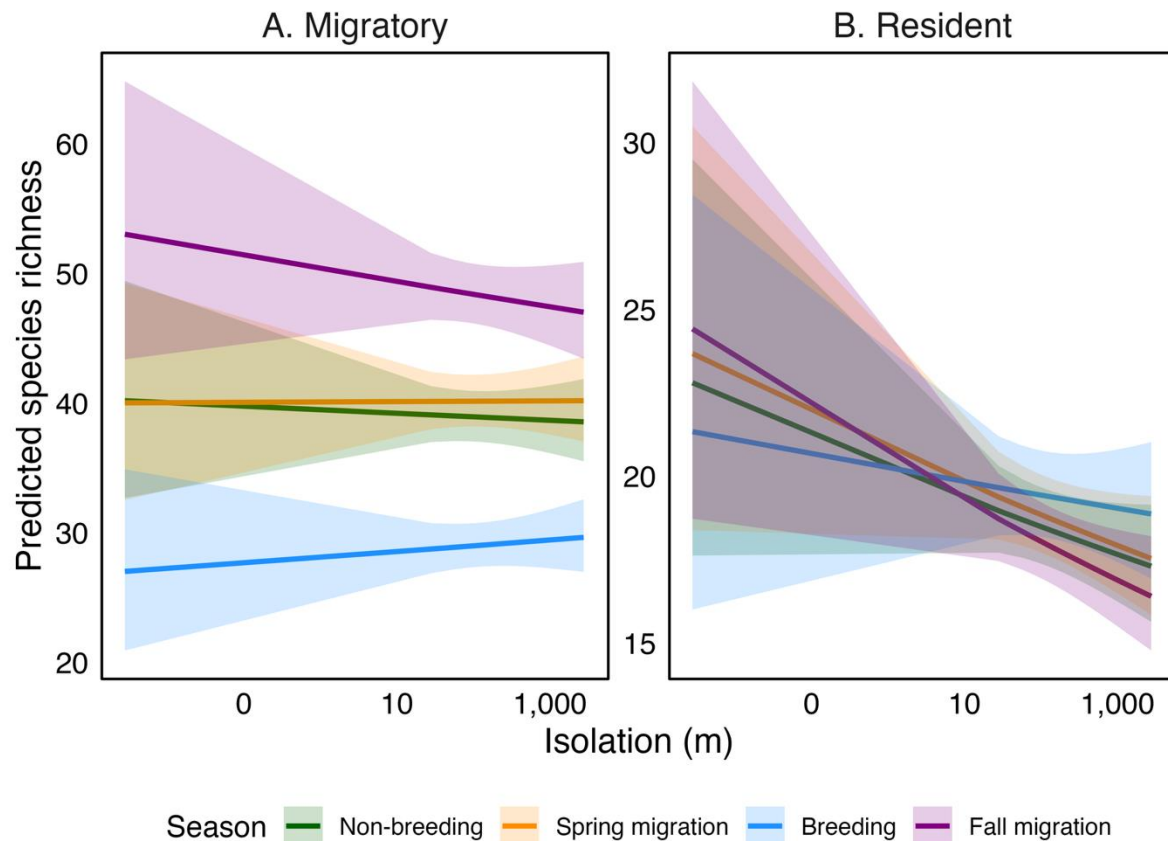


Figure 4. Predicted species richness for each season of the full-annual cycle based on nearest neighbor distance (in meters) for each greenspace, plotted on the log-scale. Ribbons represent the 95% confidence intervals. Fall migration for residents is significant ($P < 0.05$).

ALT TEXT: Line graphs showing the predicted species richness for each season of the full-annual cycle, split between migratory and resident species, based on isolation of each urban greenspace (m).

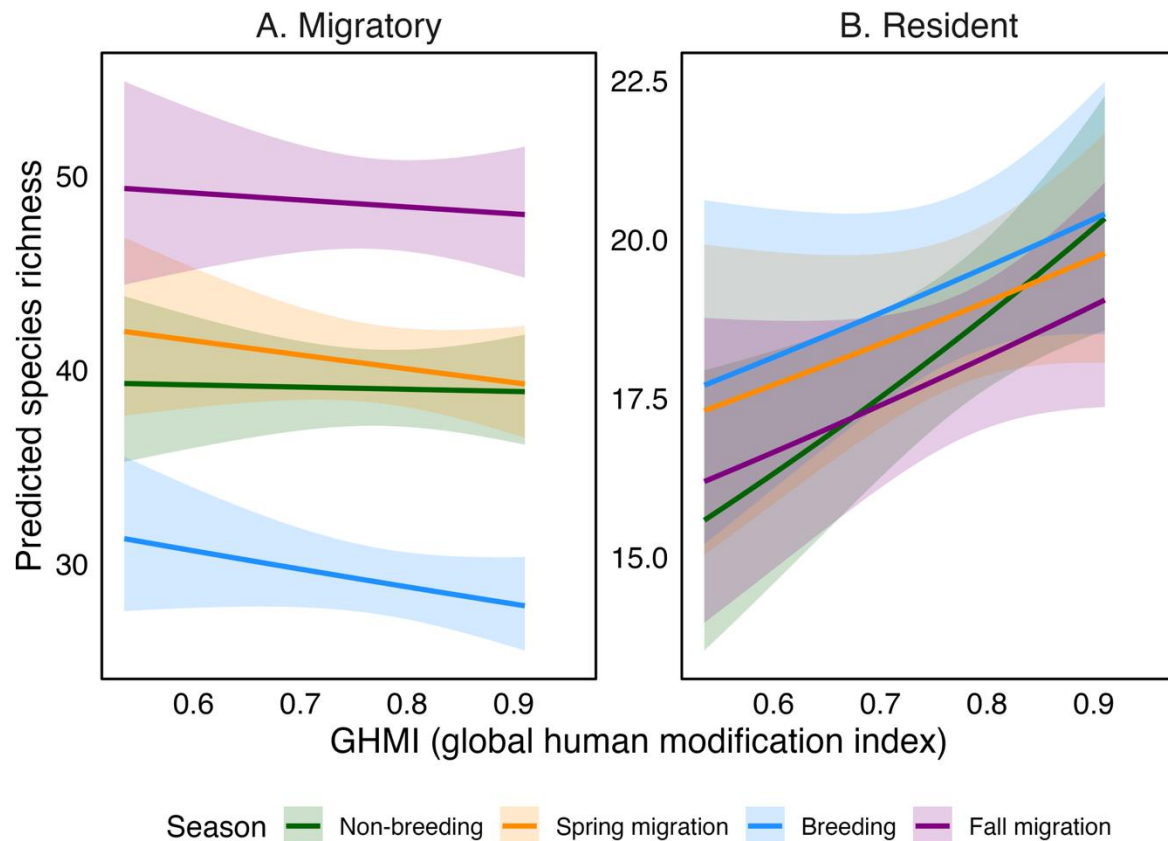


Figure 5. Predicted species richness for each season of the full-annual cycle based on Global Human Modification Index for each greenspace. Ribbons represent the 95% confidence intervals. Non-breeding for residents is significant ($P < 0.01$).

ALT TEXT: Line graphs showing the predicted species richness for each season of the full-annual cycle, split between migratory and resident species, based on GHMI for each urban greenspace (m²).