

RESEARCH ARTICLE OPEN ACCESS

Land Cover and Area Influence Bird Biodiversity in Geographically Isolated Wetlands

Jackson Barratt Heitmann 💿 | Brittany M. Mason | Corey T. Callaghan

Department of Wildlife Ecology and Conservation, Fort Lauderdale Research and Education Center, University of Florida, Gainesville, Florida, USA

Correspondence: Jackson Barratt Heitmann (j.barrattheitman@ufl.edu) | Corey T. Callaghan (c.callaghan@ufl.edu)

Received: 16 July 2024 | Revised: 21 February 2025 | Accepted: 26 February 2025

Editor: Christine Howard

Funding: This work was supported by College of Liberal Arts and Sciences, University of Florida.

Keywords: biodiversity | eBird | geographically isolated wetlands | species richness | species-area relationship | temporary wetlands

ABSTRACT

Aim: Geographically isolated wetlands, wetlands surrounded by upland habitat, harbour high amounts of bird biodiversity but are rapidly being lost across the United States. Yet, we do not know which characteristics, such as wetland area or land cover, influence the level of bird biodiversity supported. We assessed the influence of wetland area and local (size of the wetland, 0.001–4.20 km²) and landscape (25 km) land cover on bird biodiversity in geographically isolated wetlands.

Location: Conterminous United States.

Methods: We quantified the impacts of the wetland area and different land cover on overall bird species richness and richness estimates within five functional groups. We integrated 207 geographically isolated wetlands, selected based on eBird sampling locations with over 100 total checklists. We computed land cover metrics within wetland sites and landscape buffers (25km) around each site. Using a generalised linear modelling approach, we examined how species richness was impacted by area and six remotely sensed land cover variables.

Results: Species richness increased with area for all species and functional groups of birds, but aquatic (e.g., ducks) and terrestrial (e.g., wading birds) functional groups had the steepest species–area slopes. Constructed wetlands exhibited a steeper species–area relationship slope compared to natural wetlands. Species richness was negatively correlated with built land cover at the local and landscape scales and was positively associated with flooded vegetation at the local scale and grass cover at the local and landscape scales. All functional group richness estimates responded negatively to build land cover but showed unique responses in their associations with other land cover variables.

Main Conclusions: Anthropogenic disturbance at the local and landscape scales significantly reduces species richness. Land managers looking to create or restore wetlands, which have steeper species–area curves, should consider local-scale management changes in flooded vegetation or grass cover to improve habitat for birds.

1 | Introduction

Geographically isolated wetlands (GIWs)—wetlands which are surrounded by upland habitat—provide an assortment of ecosystem services including biochemical processing, flood protection and habitat for flora and fauna (Cohen et al. 2016; Cowardin 1979; Kirkman et al. 1999; Leibowitz 2003; Tiner 2003). GIWs represent an estimated 29% of all wetland types in the United States and may represent up to 16% of total wetland area in the United States (Fluet-Chouinard et al. 2023; Lane et al. 2023; Lane and D'Amico 2016; Leibowitz and Nadeau 2003). These wetlands come in a variety of shapes and sizes, depending on

This is an open access article under the terms of the Creative Commons Attribution License, which permits use, distribution and reproduction in any medium, provided the original work is properly cited.

 ${\small ©}$ 2025 The Author(s). Diversity and Distributions published by John Wiley & Sons Ltd. their geographic position, whether they are naturally occurring or were constructed, and the degree to which they have been impacted by human activities at local and landscape scales (McKinney et al. 2011; McKinney and Charpentier 2009). The variability in GIWs, including area (Snodgrass et al. 2000) and vegetation (Aronson and Galatowitsch 2008; Zamora-Marín et al. 2021), influences the amount of biodiversity held in these systems (Comer et al. 2005), but how these characteristics influence bird biodiversity amongst different wetland types across large spatial scales is not well documented.

GIWs may act as isolated or fragmented 'island habitats', which are part of a much larger habitat mosaic (Golden et al. 2017). The paucity of information regarding bird biodiversity in these systems embedded within larger habitat mosaics highlights the need to explore the species-area relationship. The species-area relationship (SAR) is a key concept from Island Biogeography Theory stipulating that larger areas will support more species (Macarthur and Wilson 1967). GIW conditions and characteristics across the entire spatial extent of the United States can vary quite dramatically in area, depending on hydrology, soil conditions, climate or precipitation (Cowardin 1979; Tiner 2003). Managers or engineers constructing wetlands (Almeida et al. 2020; Rajpar et al. 2022) may take these conditions into account when evaluating the biodiversity value of GIWs (Golden et al. 2017). Due to greater availability of microhabitats for foraging, nesting and cover from predators, bird species richness generally increases with area (Guadagnin et al. 2009, 2005). This has been documented in prairie potholes (a type of GIW) of the Midwestern US, where waterbird richness was positively associated with increases in wetland area (Fairbairn and Dinsmore 2001; Naugle et al. 2001). Additionally, reptile distribution and dragonfly species richness and diversity have been documented to be positively associated with wetland size (Pryke et al. 2015; Attum et al. 2008). However, this contrasts with other studies that found no correlation between wetland area and species richness in vernal pools or depression wetlands (other types of GIWs) in both birds and amphibians (McKinney and Paton 2009; Oertli et al. 2002; Riffell et al. 2006). This makes a large-scale macroecological study of GIWs necessary to discern if the SAR is consistent amongst wetland types (Carolina bays, vernal pools, prairie potholes, excavated ponds, etc.).

In addition to area, the diversity of land cover types within and surrounding GIWs likely plays a role in promoting biodiversity (Martínez-Ruiz and Renton 2018; Luther et al. 2008). The influence of land cover on biodiversity can vary amongst different spatial scales, influencing the local patterns of biodiversity (Callaghan et al. 2018; Chase et al. 2018; Newbold et al. 2015). For example, higher landscape wetland cover estimates have been positively associated with higher bird biodiversity at the local scale (Dertien et al. 2020; Elliott et al. 2020). Furthermore, amphibian richness and abundance in wetlands are positively correlated with adjacent forest cover (Houlahn and Findlay 2003), and dragonfly richness and diversity in ponds are positively associated with higher habitat heterogeneity (Pryke et al. 2015). However, adjacent habitat type has variable influence on reptile species; common species are not impacted by impervious land cover, but rare species are negatively impacted by impervious land cover (Attum et al. 2008). Conversely, urbanisation and intense land use for agriculture have been associated with an overall decrease in amphibian diversity in GIWs (Surdick 2005). A dual-scale perspective, which considers how land cover at the local and landscape scales influences biodiversity, is crucial for understanding how biodiversity persists in GIWs and for identifying effective conservation strategies and management actions.

The biodiversity of GIWs has predominantly been studied across relatively small spatial scales, restricted to single wetland types in distinct ecosystems (Barratt Heitmann et al. 2025; Herteux et al. 2020). This limitation is partly due to the logistical and financial challenges of conducting fieldwork over broad geographic regions. However, GIWs have a continental distribution. Ecoregions support different regional species pools that currently lack crucial generalizable biodiversity patterns for GIWs (Spake et al. 2022). Advances in research tools from participatory and community science efforts like eBird (Sullivan et al. 2009; Wood et al. 2011) offer opportunities to overcome logistical constraints to expand the scope of GIW biodiversity studies. eBird has over 1 billion bird observations and provides broad spatiotemporal coverage, making it a powerful tool for investigating local and broad-scale ecological processes (Callaghan and Gawlik 2015; Fink et al. 2021; Wood et al. 2011). As a semi-structured platform, eBird data requires careful filtering and sorting to address biases in checklist submissions and spatial biases related to observer effort (Grade et al. 2022). Additionally, challenges such as observer variability, uneven taxonomic expertise and validation of rare or unusual records highlight the need for careful use of such data. Despite these limitations, the scale and breadth of eBird make it an invaluable resource for advancing macroecological studies, including those focused on GIWs.

Birds are excellent study organisms for exploring how wetland biodiversity is influenced by habitat area and land cover, due to their diverse ecological roles and adaptations across lifestyles (e.g., aquatic, aerial, terrestrial), trophic levels (e.g., herbivores, omnivores, carnivores) and niches (e.g., open water, dense vegetation, grasslands). However, studies often focus on taxonomic diversity, such as species richness, to assess biodiversity changes, which can overlook important functional and ecological differences amongst bird groups. For instance, functional diversity, which captures the variety of ecological roles species play, may not always align with taxonomic or phylogenetic diversity (Almeida et al. 2020; Devictor et al. 2010). In some cases, restored and constructed wetlands can even enhance functional diversity compared to natural wetlands, though this outcome varies depending on the ecological context (Almeida et al. 2020).

Our overall objective was to assess the ecological dynamics of bird biodiversity amongst GIWs (Figure 1). We tested support for the species–area relationship amongst GIWs across the conterminous United States. We hypothesized that bird species richness in GIWs would conform to the species–area relationship, with larger wetlands having higher species richness due to increased availability of habitat resources and microhabitats. We then quantified how land cover variables (i.e., vegetation cover, water cover and built cover) within local and landscape contexts impact bird species richness amongst GIWs across the United States. We hypothesised that local vegetation and water cover would be positively associated with species richness, and built cover would be negatively associated with species richness. Lastly, we tested if these hypothesised relationships remain the



FIGURE 1 | Graphical outline of research objectives: (A) species–area relationship (SAR) for bird biodiversity in geographically isolated wetlands, (B) impact of local and landscape characteristics on bird biodiversity, and (C) contribution of different functional group diversity (primary lifestyle) to the SAR and impacts from local and landscape land cover.

same when species richness is broken down into functional groups (i.e., primary lifestyle; Tobias et al. 2022). This analysis advances our understanding of how spatial and ecological factors interact at multiple scales, providing insights for managing GIWs.

2 | Methods

2.1 | Sampling Design

Our goal was to identify GIWs throughout the conterminous United States that had sufficient sampling to estimate bird biodiversity. We selected potential wetland sites using eBird by filtering all site names (i.e., Hotspots in eBird nomenclature) that contained the word "wetland" or "Wetland" (eBird basic dataset: ebird_vrs_April2022). We recognise that naming conventions for GIWs, also called ponds, potholes, vernal pools and others, likely reduced and/or altered the available list of eBird hotspots. We did not spatially select wetlands based on correspondence with the National Wetlands Inventory because of its failure to accurately map many GIWs (Tiner et al. 2002). Therefore, we felt that the most generic term, "wetland" was helpful in selecting the greatest number of potential sampling locations. We only included eBird registered sites (i.e., Hotspots) to acquire sampling locations at publicly accessible birding locations. Because our goal was to minimise the amount of manual work of looking at each wetland balanced with selecting sites that would have a reasonable amount of eBird data, we only

considered sites that had ≥ 100 submitted checklists (Callaghan et al. 2022; Freckleton 2002). We were conservative in our site selection, requiring ≥ 100 submitted checklists; however, we wanted to ensure we had adequate sampling coverage for our sites and minimised the likelihood of missing rare or cryptic species. Hereafter, eBird sites are denoted as site or site location.

We visually assessed each potential site (eBird hotspots with ≥ 100 submitted checklists, n = 534) by overlaying the site with National Agriculture Imagery Program (NAIP) imagery from 2010 to 2022 (Earth Resources Observation And Science [EROS] Center 2017), the most recent National Wetlands Inventory (NWI) shapefile (US Fish and Wildlife Service 2022), Google Dynamic World dataset 2018 (Brown et al. 2022), and Google Earth Imagery from 1985 to 2022 (Google Earth 1985-2022) to identify standing water and relative surface level hydrological connectivity. While GIWs are known to have below-ground hydrologic connectivity with other wetlands and waterways, we defined GIWs as wetlands surrounded by upland habitat (Cohen et al. 2016; Mushet et al. 2015) based on delineation using the NWI shapefiles (US Fish and Wildlife Service 2022), land categorisation from Google Dynamic World (Brown et al. 2022) and aerial NAIP (EROS Center 2017) and Google Earth Imagery (Google Earth 1985-2022) for at least part of the year to be considered a GIW. GIWs encompass a suite of heterogeneous habitat types in the conterminous United States, and delineating them can often be difficult given that some of these wetland types dry up seasonally, can be connected to other water bodies for short periods of the year, and may be forested, making it difficult to identify the wetland boundaries. We dealt



FIGURE 2 | Number of mapped wetlands by state, with image inlays from three different ecoregions.

with these various issues by only selecting wetlands where water was visible on aerial imagery, the NWI or hydrology maps at any point during the year (even if they were only inundated for a short period of time). We then delineated n = 207 sites (i.e., manually drew a polygon) based on the coverage of the entire eBird site; i.e., we did not map only the wetlands, but rather the entire eBird site area (Figure S1). All mapped sites' main feature(s) were GIW(s) (Figure S1, Figure 2).

When delineating GIWs, we categorised them as either constructed, natural or unknown. To categorise wetlands, we used a combination of web searching the eBird hotspot name in Google and inspecting historical aerial imagery in Google Earth. GIWs were denoted as 'constructed' if they were created as part of a restoration project, a water management tool or a water feature in a park (Table S1). GIWs were denoted as 'natural' if they had uneven perimeters, long aerial imagery histories, no indication of construction from a web search and other features mentioned in (Tiner 2003). If we could not decide, we simply denoted them as 'unknown'. Out of our 207 wetlands, 66 were classified as natural, 101 were classified as constructed and 40 were classified as unknown.

2.2 | Calculating Land Cover and Area

We calculated environmental variables at both the local scale (the mapped site location: 0.001–4.20 km², also see Table S1),

and at the landscape scale (site location +25 km buffer). Buffers were calculated relative to wetland size; we applied a proportional buffer for the landscape scale, where the buffer area was scaled relative to the size of the wetland. This ensured that smaller wetlands were analysed with buffers that adequately captured their broader landscape context, while larger wetlands had buffers that reflected their inherently larger local footprint. This approach ensured that the distinction between local and landscape effects was meaningful across wetlands of varying sizes. We used Google Earth Engine to obtain six land cover variables from the Google Dynamic World data set, including: built (anthropogenic), flooded vegetation, grass, shrub and scrub, trees and water (Brown et al. 2022). We calculated annual mean values of the daily total pixel percentage (%) representing each land cover type from daily satellite imagery taken from 1/1/2019-12/31/2019, using the ee.Mean.Reducer function. We calculated the wetland area using the area function in the sf package in R (Pebesma et al. 2024). To measure the level of heterogeneity in land cover at the local and landscape scale, we calculated Shannon's diversity index of the six land cover types for each local wetland site and the landscape 25 km buffer using the diversity function in the package vegan in R (Oksanen et al. 2022). Finally, we identified the EPA Level I Ecoregion (US EPA, ORD 2015) for each wetland by finding the intersection of each wetland polygon centroid with the EPA Ecoregion shapefile using the sf package in R.

For measurements of richness for functional groups, we appended primary lifestyle groupings to each bird species as derived from AVONET (Tobias et al. 2022). Primary lifestyle is a combination of trophic level and trophic niche, which largely reflects a species primary method for foraging (aerial, aquatic, generalist, terrestrial and insessorial) (Tobias et al. 2022). We used primary lifestyle as our functional grouping variable and calculated richness for each group in GIWs as it combines morphological bird traits, as well as ecological congruence between species that are similar functionally, which reveal primarily how birds use habitats to meet their life history needs (Madrigal-Roca 2024).

2.3 | eBird Data

For each of our delineated sites (n = 207) we downloaded all eBird data from within that site from 01/01/2010-04/30/2022. To clean the eBird data, we only included complete checklists (i.e., where birding was the primary objective of the observer, and they identified all species they saw/heard) with a duration $\geq 5 \text{ min}$. From the complete checklists, we included species and species identifiable to subspecies (code in eBird: issf). We collated abundances of species and subspecies (code in eBird: issf) on individual checklists if they were of the same higher order species (e.g., Yellow-rumped Warbler (species) and Yellow-rumped Warbler (Myrtle's) (a subspecies)). We excluded entire checklists from potential analysis if any species on the checklist had an 'X' recorded instead of an abundance count, as this indicates that the observer may not have been systematically reporting all species present. We also excluded any observations that were not made to the species level. We excluded all domestic species except Muscovy Duck and Rock Pigeon because they are now considered naturalised in many portions of the United States and do contribute meaningfully to urban biodiversity and ecosystem functioning (Schlaepfer 2018). If checklists were submitted as part of a group of 2 or more observers, we randomly selected 1 checklist to avoid pseudo-replication of the exact same checklist by multiple observers.

We calculated local-scale diversity at each site location as total species richness from all submitted checklists for overall species richness and separately stratified by the five functional groups at each wetland site (n=207). Due to unequal sampling amongst all GIWs in our dataset, we also used a bootstrapping approach to calculate richness at equal sampling effort across all sites. To do this, we randomly selected 50 checklists from each site and calculated species richness using those 50 checklists. We repeated this process 100 times per site and calculated the mean of all 100 iterations. Total richness and mean resampled richness had a correlation coefficient of 0.87, suggesting that total richness appropriately samples the 'amongst-GIW' diversity differences. Therefore, we chose to use total richness as our response variable in our main analysis but accounted for differences in sampling effort (see Statistical analysis section). To check the robustness of our results, we confirmed that our models and figures of total richness and mean resampled richness estimates revealed similar patterns, and we report figures for resampled richness in the supplement (Figures S3 and S4).

2.4 | Statistical Analysis

For our analyses, we employed generalised linear models (GLM) and generalised linear mixed models (GLMM) to investigate bird species richness in GIWs. This statistical approach was chosen to appropriately model count data (species richness), which typically follows a Poisson distribution, and to account for potential non-independence amongst wetlands within the same ecoregion for mixed-effects models. GLMMs were specifically used for the land cover questions to account for variation in land cover composition across the United States, incorporating EPA Level I ecoregion as a random effect to control for unobserved heterogeneity amongst ecoregions, which was not of interest to our study questions per se. We assessed model assumptions (e.g., residuals, collinearity, homogeneity of variance) using the 'performance' package in R (Lüdecke et al. 2021) and standardised all predictor variables to improve the interpretability of model coefficients (Gelman 2009). An overview of the models, the questions they pertain to, and the specification in R is provided in Table S2.

For our first objective, to assess the species-area relationship (SAR) in GIWs for species richness, we used a GLM. We fitted the model with two predictor variables: number of submitted checklists to control for variation in sampling effort (Freckleton 2002) between wetland sites and area, our primary variable of interest. We log transformed area and the number of checklists to meet assumptions of normality and homogeneity of variance.

For our second objective, to assess the impacts of local versus landscape land cover on species richness, we used a GLMM approach for all our models. We log transformed area and the land cover variables to meet assumptions of normality. We fit a GLMM model with 15 predictor variables: number of submitted checklists, six land cover metrics at the local and landscape scale, as well as a heterogeneity variable (Shannon's diversity index of the six land cover variables at the local and landscape scale). We fit our GLMM models with ecoregion (EPA Level I) as a random effect. Ecoregion was used to control for unobserved heterogeneity in overall ecoregion type and spatial autocorrelation with wetlands within the same ecoregion context. In all models, we standardised predictor variables using the 'rescale' function in the scales package in R (Wickham et al. 2023). We standardised our predictor variables to make coefficient outputs in the model comparable in marginal effect plots (Gelman 2009). We constructed land cover models that also included area as a predictor variable and found that area was indeed the strongest predictor of total richness, with similar results amongst the importance of land cover variables (Figure S4). However, our focus for this second analysis was on the land cover variables within a wetland and in the surrounding landscape; therefore, we focused on reporting models that do not include area in the main text.

For our third objective, we modelled species richness of each primary lifestyle individually: aquatic, aerial, generalist, insessorial and terrestrial. To assess how the SAR impacts functional group richness, we utilised the same model structure as species richness mentioned above, fit with a Poisson family distribution GLM model. To assess the impacts of local and landscape land cover on each functional group, we employed the same model structure as we did for species richness mentioned above, using a GLMM model fit with 15 predictor variables: number of submitted checklists, six land cover variables at the local and landscape scale, and two land cover heterogeneity variables, one each at the local and landscape scale, with ecoregion as a random effect.

2.5 | Sensitivity Analysis of Land Cover Predictors at Multiple Buffers

We analysed the effect sizes of local and landscape land cover models at three different landscape buffer sizes (5 km, 10 km and 25 km). Our models performed similarly across all three landscape buffers (Figures S6 and S7) for both total richness and across all five functional groups of birds. We report on minor differences in the discussion. We report results on the 25 km landscape buffer below for two reasons. (1) Previous studies have also shown that larger scale buffers can account for available habitat at the metacommunity level (i.e., overlapping ranges for multiple communities with variable dispersal and home range sizes), as opposed to the home range sizes of a single species (Callaghan et al. 2018; Radford et al. 2005), and (2) landscape level predictors for wetlands may be relative to the range size of the focal species, but we evaluated community level biodiversity and 25 km represents a more holistic matrix of available habitats for selection and habitat use by all possible species (Fairbairn and Dinsmore 2001; McKinney and Charpentier 2009).

3 | Results

Overall, we sampled 207 wetlands with a median area of $0.16 \,\mathrm{km^2}$ (range: $0.001-4.20 \,\mathrm{km^2}$, standard deviation: $0.75 \,\mathrm{km^2}$, Figure S2). Across all sampled wetlands, we had 2,885,558 species observations, representing 590 bird species. There were 48 species in the aquatic functional group, 58 in aerial, 84 in generalist, 185 in terrestrial and 216 in insessorial. For examples of species within each functional group, see Table S3. The range of complete checklists submitted at each site was between 87 and 16,118. These were collected by 131,056 unique observers, averaging 633 observers per wetland site. The average species richness per wetland site was 150 ± 42 . Sweetwater Wetlands, Arizona (eBird ID: L208918) had the highest total with 288 species, and Five Mile and Victory Wetland, Idaho (eBird ID: L3962950) had the lowest total with 55 species.

3.1 | Species-Area Relationship for Species Richness and Functional Group Richness

We found that total species richness significantly increased with area (log(area), z = 17.33, p < 0.001) and total number of submitted checklists (log(checklists), z = 31.66, p < 0.001) (Figure 3). We found that total species richness for all primary lifestyles significantly increased with area (log transformed) and total number of submitted checklists (log transformed) (Figure 3). Increasing area was the strongest predictor for aquatic (parameter estimate = 1.08) and terrestrial (parameter estimate = 0.98) primary

6 of 13

lifestyles and the weakest predictor for insessorial primary lifestyle (parameter estimate = 0.13).

3.2 | Important Land Cover Predictors of Species Richness

After accounting for the total number of checklists, we found the strongest negative predictors were trees at the landscape scale (parameter estimate = -0.15) and built area at the local (parameter estimate = -0.11) and landscape scale (parameter estimate = -0.11) (Figure 4). We found that land cover heterogeneity at the landscape scale (parameter estimate = -0.05) had a significantly negative impact on total richness. However, the strongest positive predictor variables were grass cover at the local (parameter estimate = 0.05) and landscape scale (parameter estimate = 0.05) and landscape scale (parameter estimate = 0.05) and flooded vegetation cover at the local scale (parameter estimate = 0.05) (Figure 4).

3.3 | Important Land Cover Predictors of Functional Group Richness

We found that all functional group species richness estimates decreased with built land cover at the landscape scale, indicating all functional groups were negatively impacted by urbanisation (Figure 5A-E). Aerial species richness also decreased with higher tree cover at the landscape scale (parameter estimate = -0.18) and was not positively associated with any land cover variables at the local or landscape level (Figure 5A). The only other negative predictors we identified occurred with aquatic and terrestrial functional group richness estimates. Aquatic species richness was negatively correlated with flooded vegetation (parameter estimate = -0.14), grass (parameter estimate = -0.19) and tree cover (parameter estimate = -0.27) at the landscape scale (Figure 5B). Terrestrial species richness was also negatively associated with tree cover (parameter estimate = -0.15, -0.23) at both the local and landscape scales, as well as built cover locally and land cover heterogeneity at the landscape scale (parameter estimate = -0.25, -0.12, Figure 5E). Higher tree cover at the landscape scale reduced functional group species richness estimates for three different functional groups (i.e., aerial, aquatic and terrestrial), while built land cover at the landscape scale reduced richness estimates across all functional groups but was particularly strong for aquatic and terrestrial functional group richness (Figure 5A-E).

Generally, across all functional group richness estimates, we found that positive predictors were unique depending on the functional group and largely occurred only at the local scale. Aquatic species richness was the only functional group to have positive predictors at multiple scales, being positively associated with water (parameter estimate = 0.12) and grass (parameter estimate = 0.15) cover at the local scale, as well as land cover heterogeneity at the landscape scale (parameter estimate = 0.14) (Figure 5B). Insessorial species richness was positively associated with tree (parameter estimate = 0.20) and scrub land cover (parameter estimate = 0.06) at the local scale (Figure 5D). Terrestrial species were positively associated with increases in flooded vegetation cover (parameter estimate = 0.06) at the local



FIGURE 3 | Species-area relationship for all species and for five different functional groups (from AVONET) with slopes (aquatic (m = 1.08), terrestrial (m = 0.98), generalist (m = 0.46), aerial (m = 0.41), all species (m = 0.17), and insessorial (m = 0.13)) and 95% confidence intervals.

scale and grass (parameter estimate = 0.13) cover at the land-scape scale (Figure 5E).

4 | Discussion

Our study of over 200 GIWs across the United States reveals that species richness estimates are mediated by area and land cover across multiple spatial scales. Area was the most significant predictor, suggesting that larger wetlands are more important for contributing to higher bird biodiversity in GIW systems. This result follows the typical SAR for both species richness and species richness of all functional groups. Additionally, aquatic and terrestrial functional group richness had the steepest slopes, suggesting that these species are more influential on the overall species–area relationship within GIWs. Land cover impacts on bird biodiversity are driven by changes at both the local and landscape scales. Both overall species richness and each functional group's richness are negatively impacted by built land cover at the landscape scale. However, positive predictors of diversity were different amongst functional groups at both spatial scales, likely due to species sorting driven by foraging preferences amongst different land covers, which vary amongst functional groups of birds at multiple spatial scales (Özkan et al. 2013). Importantly, our results suggest that land management professionals and conservation practitioners looking to construct GIWs or improve and/or restore natural ones can make alterations to wetlands that can have a positive impact on bird biodiversity. Such alterations could include planting native emergent wetland vegetation (flooded vegetation land cover) around wetland buffers or incorporating grass cover to enhance habitat heterogeneity and foraging opportunities for multiple bird functional groups (Cannon et al. 2024).

Our finding that species richness increased as wetland area increased contrasted with some previous results in GIW systems (McKinney and Paton 2009; Riffell et al. 2006). This could be



FIGURE 4 | Effect sizes for generalised linear mixed model outputs of total richness explained by seven land cover metrics at the local and landscape scale. Dots represent means and error bars represent 95% confidence intervals. Effect sizes not overlapping 0 are statistically significant. Variables highlighted in red are significantly negative, blue are significantly positive, and black are not significant. The number of checklists was also included in the model as a predictor variable but is not shown here as this was not a variable of interest.

because previous studies contained a smaller number of wetlands (<30) of a single type that did not vary enough in their respective areas to find a significant SAR (Barratt Heitmann et al. 2025; Czapka and Kilgo 2011). Additionally, smaller patches are not frequented by larger-bodied birds, which make up several species in the aquatic and terrestrial functional groups, potentially creating an environmental filter that reduces the number of birds that could use smaller GIWs (Winter et al. 2006). We extended previous work by assessing the SAR amongst functional groups and found that all functional groups increased significantly with respective increases in wetland area, but that aquatic and terrestrial birds had the steepest slopes (Figure 3). Aquatic birds included ducks (Mallard, Blue-winged Teal) and water-dependent species like Anhinga, Double-crested Cormorant and American Coot, while terrestrial species in our study included many wading birds (Great Blue Heron, Little Blue Heron), shorebirds (Greater Yellowlegs, Short-billed Dowitcher) and corvids (Blue Jay, American Crow). Based on results of overall species richness and individual functional group responses, terrestrial and aquatic species richness are driving the SAR in GIWs, likely due to larger wetlands being visited by a greater number of larger-bodied species in the terrestrial and aquatic functional groups, compared to those relatively smaller insessorial and aerial species with relatively smaller species–area slopes. However, smaller-bodied species may also be less likely to be detected by eBird users, potentially influencing the observed patterns. We recommend a direct study of bird body size in wetlands as a future study that could help to determine how body size influences habitat use, detection probabilities and species–area relationships in geographically isolated wetlands (Winter et al. 2006).

Overall species richness and functional group estimates responded to land cover differently at both the local and landscape scales. Built land cover was the strongest predictor across all land cover variables, with a consistently negative impact on overall species richness and all functional group species richness estimates.



FIGURE 5 | Effect sizes of functional groups species richness (A) Aerial, (B) Aquatic, (C) Generalist, (D) Insessorial, (E) Terrestrial explained by land cover predictors at the local and landscape level. Dots represent means and error bars represent 95% confidence intervals. Effect sizes not overlapping 0 are statistically significant. Variables highlighted in red are significantly negative, blue are significantly positive, and black are not significant. The number of checklists was also included in the model as a predictor variable but is not shown here as this was not a variable of interest.

This was true at both the local and landscape scales. This finding supports previous work on urbanisation's impact on biodiversity (Di Pietro et al. 2021; Mao et al. 2019) confirming a general pattern of the negative influences of urbanisation on bird diversity (Callaghan et al. 2024), likely a result of the lack of connectivity, habitat availability through fragmentation and the overall presence of humans (Xu et al. 2018). Our findings contrast with previously published work documenting higher richness in urban GIWs compared to rural ones (McKinney et al. 2011; Rahlin et al. 2022). This is likely a product of sampling scale in previous studies,

whose wetlands were confined to smaller spatial scales than our study (i.e., all within the same county or state). Land cover data came from relatively small buffers around wetlands (1km buffers around GIWs) that did not consider larger landscape contexts (25km buffers around GIWs), which better capture the amount of available habitats for high dispersal organisms like birds (Martin et al. 2021). We also found that habitat heterogeneity was not an important predictor at either the local or landscape scale for overall species richness. This suggests that a greater variety of habitat patches does not improve richness estimates for bird species in GIW systems, as previously documented in many other studies of birds (Meynard et al. 2011). Tree cover at the landscape scale was a negative predictor of overall species richness, likely a result of regional species pool filtering in the Northeastern Temperate Forests ecoregion. GIWs surrounded by forest may be less likely to be visited by wetland-obligate species that require large open habitats for adequate habitat selection, like GIWs in the Midwest that are hotspots for many wetland-obligate species (Paracuellos 2006; Lorenzón et al. 2019). It is also possible that the composition of the avian community shifts in forested landscapes, with fewer wetland-dependent species and more generalist or forest-adapted species dominating, which could reduce overall richness when focused on the birds within a GIW. We found generally that overall species richness was reduced by landscape predictors (built and tree cover), likely due to environmental filtering of the regional species pool, but that urbanisation played an outsized role in reducing diversity ubiquitously across overall species diversity, as well as the five different functional groups.

Overall results from the 5, 10 and 25 km landscape buffers were quite similar for overall richness and across functional group richness (Figures S6-S12). This likely means that GIWs are part of larger landscape mosaics that filter the metacommunity at a fairly coarse grain. However, results for functional group richness did have some variation based on the landscape buffer chosen (5, 10, 25km) (Figures S8-S12). Insessorial species responded negatively to build land cover only at the 25 km buffer size, meaning that environmental filtering of the metacommunity for these species likely occurs at a larger spatial scale. Urban intolerance in this functional group occurs at a coarse spatial grain. Aerial functional group richness responded negatively to tree cover at 10 and 25km buffers, but not at 5km. This may be due to this functional group having a relatively small number of species with relatively large home ranges that may be impacted at a larger spatial scale more strongly.

Restoration and conservation of GIWs are essential for maintaining bird biodiversity, particularly in landscapes where built land cover reduces species richness (Callaghan et al. 2021). Enhancing wetlands at the local scale by increasing flooded vegetation and grass cover can help improve bird diversity. We advocate for restoring vegetation surrounding well-manicured and mowed stormwater ponds across the United States (Adams et al. 1985; Cannon et al. 2024; Hassall and Anderson 2015). We found that constructed GIWs had a steeper SAR slope than natural ones, meaning that these systems *can* be managed and manipulated to provide higher biodiversity than naturally occurring GIWs (Figure S5). Managers looking to conserve GIW systems should identify their priority functional bird groups and key ecosystem functions when undertaking management. For example, conserving and/or improving wetlands for aquatic and terrestrial target species, such as ducks, should prioritise larger wetlands with open water for foraging and sparse tree cover (Ma et al. 2010). These novel ecosystems can support high amounts of biodiversity, but engineers and restoration ecologists should consider the ecosystem context, priority ecosystem functions and species of interest during construction or restoration (Hassall and Anderson 2015; Oertli and Parris 2019).

We leveraged broad-scale citizen science data to assess fundamental questions about wetland macroecology. However, we acknowledge that there are some limitations to using these data. We had an unbalanced study design with an unequal number of samples across ecoregions, and we did not account for different detection probabilities across the different ecoregions. Future work should test whether these SAR and land cover patterns are generalisable across different ecoregions, which could aid in conservation planning for especially biodiverse regions that would complement well-documented rates of rare and threatened plant and herpetofauna in GIWs more generally (Dertien et al. 2020). Our investigation of overall species richness and richness of five functional groups of birds identifies important components of richness, like wetland area and land cover. However, we suggest that future work also analyse the abundance and evenness of birds in these systems. Abundance and evenness provide additional information about biodiversity value, such as dominance by common versus rare species that are not captured solely by species richness (Elliott et al. 2020; McGlinn et al. 2019). For example, investigating beta diversity can be helpful to identify especially unique communities or ecoregions where GIWs may require special conservation attention.

Geographically isolated wetlands across the United States conform to the typical SAR, increasing in all functional groups with relative increases in area. The SAR is driven primarily by an increase in the number of aquatic and terrestrial functional groups that specialise in these habitats for foraging and other life history needs. Built land cover at both the local and landscape scale negatively impacts species richness in wetland habitats. However, increasing emergent wetland vegetation (flooded vegetation cover) and grass cover can increase terrestrial functional group species, such as wading birds and shorebirds. Landscapes with high amounts of both flooded vegetation and grass cover promote species richness of aquatic and terrestrial species and may be important conservation priority areas for conserving GIWs.

Author Contributions

J.B.H. and C.T.C. conceived the study. J.B.H. and B.M.M. collected the data. J.B.H. and C.T.C. analysed the data. J.B.H wrote the manuscript. All authors edited and reviewed the manuscript.

Acknowledgements

This work was funded in part through the CALS Dean Fellowship and Jennings Scholarship in the Department of Wildlife Ecology and Conservation at the University of Florida. C.T.C acknowledges that this research was supported in part by the intramural research program of the US Department of Agriculture, Hatch, FLA-FTL-006297.

Conflicts of Interest

The authors declare no conflicts of interest.

Data Availability Statement

Code and data is freely available on Anonymous GitHub at https://anonymous.4open.science/r/iso_wetlands_ebird-3DC5/README.md. and Zenodo at DOI: 10.5281/zenodo.14967758.

Peer Review

The peer review history for this article is available at https://www.webof science.com/api/gateway/wos/peer-review/10.1111/ddi.70012.

References

Adams, L. W., L. E. Dove, and T. M. Franklin. 1985. "Use of Urban Stormwater Control Impoundments by Wetland Birds." *Wilson Bulletin* 97, no. 1: 120–122.

Almeida, B. A., E. Sebastián-González, L. dos Anjos, and A. J. Green. 2020. "Comparing the Diversity and Composition of Waterbird Functional Traits Between Natural, Restored, and Artificial Wetlands." *Freshwater Biology* 65, no. 12: 2196–2210. https://doi.org/10.1111/fwb. 13618.

Aronson, M. F. J., and S. Galatowitsch. 2008. "Long-Term Vegetation Development of Restored Prairie Pothole Wetlands." *Wetlands* 28, no. 4: 883–895. https://doi.org/10.1672/08-142.1.

Attum, O., Y. M. Lee, J. H. Roe, and B. A. Kinsbury. 2008. "Wetland Complexes and Upland-Wetland Linkages: Landscape Effects on the Distribution of Rare and Common Wetland Reptiles." *Journal of Zoology* 275, no. 3: 245–251. https://doi.org/10.1111/j.1469-7998.2008.00435.x.

Barratt Heitmann, J., T. H. Folk, L. J. Lord, and D. J. McGlinn. 2025. "Geographically Isolated Wetlands Have Higher Alpha Diversity Than Surrounding Uplands in Pine Savanna Ecosystems." *Wetlands Ecology and Management* 33, no. 1: 18. https://doi.org/10.1007/s11273-025-10035-6.

Brown, C. F., S. P. Brumby, B. Guzder-Williams, et al. 2022. "Dynamic World, Near Real-Time Global 10 m Land Use Land Cover Mapping." *Scientific Data* 9, no. 1: 251. https://doi.org/10.1038/s41597-022-01307-4.

Callaghan, C. T., and D. E. Gawlik. 2015. "Efficacy of eBird Data as an Aid in Conservation Planning and Monitoring." *Journal of Field Ornithology* 86, no. 4: 298–304. https://doi.org/10.1111/jofo.12121.

Callaghan, C. T., D. E. Bowler, S. A. Blowes, J. M. Chase, M. B. Lyons, and H. M. Pereira. 2022. "Quantifying Effort Needed to Estimate Species Diversity From Citizen Science Data." *Ecosphere* 13, no. 4: e3966. https://doi.org/10.1002/ecs2.3966.

Callaghan, C. T., J. M. Chase, and D. J. McGlinn. 2024. "Anthropogenic Habitat Modification Causes Nonlinear Multiscale Bird Diversity Declines." *Ecography* 2024, no. 1: e06759. https://doi.org/10.1111/ecog. 06759.

Callaghan, C. T., R. E. Major, M. B. Lyons, J. M. Martin, and R. T. Kingsford. 2018. "The Effects of Local and Landscape Habitat Attributes on Bird Diversity in Urban Greenspaces." *Ecosphere* 9, no. 7: e02347. https://doi.org/10.1002/ecs2.2347.

Callaghan, C. T., A. G. B. Poore, R. E. Major, W. K. Cornwell, J. H. Wilshire, and M. B. Lyons. 2021. "How to Build a Biodiverse City: Environmental Determinants of Bird Diversity Within and Among 1581 Cities." *Biodiversity and Conservation* 30, no. 1: 217–234. https://doi.org/10.1007/s10531-020-02088-1.

Cannon, S., A. Prochaska, K. Stewart, T. Callahan, and M. Nowlin. 2024. "Identifying Barriers Preventing Stormwater Pond Buffer Implementation in Coastal South Carolina." *Journal of South Carolina Water Resources* 9, no. 2: 7.

Chase, J. M., B. J. McGill, D. J. McGlinn, et al. 2018. "Embracing Scale-Dependence to Achieve a Deeper Understanding of Biodiversity and Its Change Across Communities." *Ecology Letters* 21, no. 11: 1737–1751. https://doi.org/10.1111/ele.13151.

Cohen, M. J., I. F. Creed, L. Alexander, et al. 2016. "Do Geographically Isolated Wetlands Influence Landscape Functions?" *Proceedings of the National Academy of Sciences* 113, no. 8: 1978–1986. https://doi.org/10. 1073/pnas.1512650113.

Comer, P., K. Goodin, A. Tomaino, et al. 2005. *Biodiversity Values of Geographically Isolated Wetlands in the United States*. NatureServe.

Cowardin, L. M. 1979. *Classification of Wetlands and Deepwater Habitats of the United States*. Fish and Wildlife Service, U.S. Department of the Interior.

Czapka, S. J., and J. C. Kilgo. 2011. "Importance of Carolina Bays to the Avifauna of Pinelands in the Southeastern United States." *Southeastern Naturalist* 10, no. 2: 321–332.

Dertien, J. S., S. Self, B. E. Ross, K. Barrett, and R. F. Baldwin. 2020. "The Relationship Between Biodiversity and Wetland Cover Varies Across Regions of the Conterminous United States." *PLoS One* 15, no. 5: e0232052. https://doi.org/10.1371/journal.pone.0232052.

Devictor, V., D. Mouillot, C. Meynard, F. Jiguet, W. Thuiller, and N. Mouquet. 2010. "Spatial Mismatch and Congruence between Taxonomic, Phylogenetic and Functional Diversity: The Need for Integrative Conservation Strategies in a Changing World." *Ecology Letters* 13, no. 8: 1030–1040. https://doi.org/10.1111/j.1461-0248.2010. 01493.x.

Di Pietro, S., C. Mantoni, and S. Fattorini. 2021. "Influence of Urbanization on the Avian Species-Area Relationship: Insights From the Breeding Birds of Rome." *Urban Ecosystems* 24, no. 4: 779–788. https://doi.org/10.1007/s11252-020-01081-4.

Earth Resources Observation And Science (EROS) Center. 2017. *National Agriculture Imagery Program (NAIP)*. Tiff. U.S. Geological Survey. https://doi.org/10.5066/F7QN651G.

Elliott, L. H., L. D. Igl, and D. H. Johnson. 2020. "The Relative Importance of Wetland Area Versus Habitat Heterogeneity for Promoting Species Richness and Abundance of Wetland Birds in the Prairie Pothole Region, USA." *Condor* 122, no. 1: duz060. https://doi.org/10.1093/condor/duz060.

Fairbairn, S. E., and J. J. Dinsmore. 2001. "Local and Landscape-Level Influences on Wetland Bird Communities of the Prairie Pothole Region of Iowa, USA." *Wetlands* 21, no. 1: 41–47. https://doi.org/10.1672/0277-5212(2001)021[0041:LALLIO]2.0.CO;2.

Fink, D., T. Auer, A. Johnston, et al. 2021. *eBird Status and Trends*. Cornell Lab of Ornithology. https://doi.org/10.2173/ebirdst.2021.

Fluet-Chouinard, E., B. D. Stocker, Z. Zhang, et al. 2023. "Extensive Global Wetland Loss Over the Past Three Centuries." *Nature* 614, no. 7947: 281–286. https://doi.org/10.1038/s41586-022-05572-6.

Freckleton, R. P. 2002. "On the Misuse of Residuals in Ecology: Regression of Residuals vs. Multiple Regression." *Journal of Animal Ecology* 71, no. 3: 542–545. https://doi.org/10.1046/j.1365-2656.2002. 00618.x.

Gelman, A. 2009. "When to Standardize Regression Inputs and When to Leave Them Alone | Statistical Modeling, Causal Inference, and Social Science." https://statmodeling.stat.columbia.edu/2009/07/11/when_to_standar/.

Golden, H. E., I. F. Creed, G. Ali, et al. 2017. "Integrating Geographically Isolated Wetlands Into Land Management Decisions." *Frontiers in Ecology and the Environment* 15, no. 6: 319–327. https://doi.org/10.1002/fee.1504.

Google Earth. 1985–2022. "Imagery From Landsat/Copernicus." Google Earth Pro v.7.7.3.6.9796.

Grade, A. M., N. W. Chan, P. Gajbhiye, D. J. Perkins, and P. S. Warren. 2022. "Evaluating the Use of Semi-Structured Crowdsourced Data to Quantify Inequitable Access to Urban Biodiversity: A Case Study with eBird." *PLoS One* 17, no. 11: e0277223. https://doi.org/10.1371/journal. pone.0277223.

Guadagnin, D. L., L. Maltchik, and C. R. Fonseca. 2009. "Species-Area Relationship of Neotropical Waterbird Assemblages in Remnant Wetlands: Looking at the Mechanisms." *Diversity and Distributions* 15, no. 2: 319–327. https://doi.org/10.1111/j.1472-4642.2008.00533.x.

Guadagnin, D. L., Â. S. Peter, L. F. C. Perello, and L. Maltchik. 2005. "Spatial and Temporal Patterns of Waterbird Assemblages in Fragmented Wetlands of Southern Brazil." *Waterbirds* 28, no. 3: 261–272. https://doi. org/10.1675/1524-4695(2005)028[0261:SATPOW]2.0.CO;2. Hassall, C., and S. Anderson. 2015. "Stormwater Ponds Can Contain Comparable Biodiversity to Unmanaged Wetlands in Urban Areas." *Hydrobiologia* 745, no. 1: 137–149. https://doi.org/10.1007/s1075 0-014-2100-5.

Herteux, C. E., D. E. Gawlik, and L. L. Smith. 2020. "Habitat Characteristics Affecting Wading Bird Use of Geographically Isolated Wetlands in the U.S. Southeastern Coastal Plain." *Wetlands* 40, no. 5: 1149–1159. https://doi.org/10.1007/s13157-019-01250-y.

Houlahn, J. E., and C. S. Findlay. 2003. "The Effects of Adjacent Land Use on Wetland Amphibian Species Richness and Community Composition." *Canadian Journal of Fisheries and Aquatic Sciences* 60, no. 9: 1078–1094. https://doi.org/10.1139/f03-095.

Kirkman, L. K., S. W. Golladay, L. Laclaire, and R. Sutter. 1999. "Biodiversity in Southeastern, Seasonally Ponded, Isolated Wetlands: Management and Policy Perspectives for Research and Conservation." *Journal of the North American Benthological Society* 18, no. 4: 553–562. https://doi.org/10.2307/1468387.

Lane, C. R., and E. D'Amico. 2016. "Identification of Putative Geographically Isolated Wetlands of the Conterminous United States." *JAWRA Journal of the American Water Resources Association* 52, no. 3: 705–722. https://doi.org/10.1111/1752-1688.12421.

Lane, C. R., E. D'Amico, J. R. Christensen, H. E. Golden, W. Qiusheng, and A. Rajib. 2023. "Mapping Global Non-Floodplain Wetlands." *Earth System Science Data* 15, no. 7: 2927–2955. https://doi.org/10.5194/essd-15-2927-2023.

Leibowitz, S. G. 2003. "Isolated Wetlands and Their Functions: An Ecological Perspective." *Wetlands* 23, no. 3: 517–531. https://doi.org/10. 1672/0277-5212(2003)023[0517:IWATFA]2.0.CO;2.

Leibowitz, S. G., and T.-L. Nadeau. 2003. "Isolated Wetlands: State-Of-The-Science and Future Directions." *Wetlands* 23, no. 3: 663–684. https://doi.org/10.1672/0277-5212(2003)023[0663:IWSAFD]2.0.CO;2.

Lüdecke, D., M. S. Ben-Shachar, I. Patil, P. Waggoner, and D. Makowski. 2021. "Performance: An R Package for Assessment, Comparison and Testing of Statistical Models." *Journal of Open Source Software* 6, no. 60: e03139. https://doi.org/10.21105/joss.03139.

Lorenzón, R. E., A. H. Beltzer, P. F. Olguin, et al. 2019. "Temporal Variation of Bird Assemblages in Dynamic Fluvial Wetlands: Seasonality and Influence of Water Level and Habitat Availability." *Revista de Biología Tropical* 67, no. 6: 1131–1145. https://doi.org/10. 15517/rbt.v67i6.36734.

Luther, D., J. Hilty, J. Weiss, C. Cornwall, M. Wipf, and G. Ballard. 2008. "Assessing the Impact of Local Habitat Variables and Landscape Context on Riparian Birds in Agricultural, Urbanized, and Native Landscapes." *Biodiversity and Conservation* 17, no. 8: 1923–1935. https://doi.org/10. 1007/s10531-008-9332-5.

Ma, Z., Y. Cai, B. Li, and J. Chen. 2010. "Managing Wetland Habitats for Waterbirds: An International Perspective." *Wetlands* 30, no. 1: 15–27. https://doi.org/10.1007/s13157-009-0001-6.

Macarthur, R. H., and E. O. Wilson. 1967. *The Theory of Island Biogeography*. Princeton University Press.

Madrigal-Roca, L. J. 2024. "Assessing the Predictive Value of Morphological Traits on Primary Lifestyle of Birds Through the Extreme Gradient Boosting Algorithm." *PLoS One* 19, no. 1: e0295182. https://doi.org/10.1371/journal.pone.0295182.

Mao, Q., C. Liao, Z. Wu, et al. 2019. "Effects of Land Cover Pattern Along Urban-Rural Gradient on Bird Diversity in Wetlands." *Diversity* 11, no. 6: 86. https://doi.org/10.3390/d11060086.

Martin, C. A., R. Proulx, M. Vellend, and L. Fahrig. 2021. "How the Relationship Between Vegetation Cover and Land-Cover Variance Constrains Biodiversity in a Human Dominated World." *Landscape Ecology* 36, no. 11: 3097–3104. https://doi.org/10.1007/s10980-021-01312-9.

Martínez-Ruiz, M., and K. Renton. 2018. "Habitat Heterogeneity Facilitates Resilience of Diurnal Raptor Communities to Hurricane Disturbance." *Forest Ecology and Management* 426: 134–144. https://doi.org/10.1016/j.foreco.2017.08.004.

McGlinn, D. J., X. Xiao, F. May, et al. 2019. "Measurement of Biodiversity (MoB): A Method to Separate the Scale-Dependent Effects of Species Abundance Distribution, Density, and Aggregation on Diversity Change." *Methods in Ecology and Evolution* 10, no. 2: 258–269. https://doi.org/10.1111/2041-210X.13102.

McKinney, R. A., and M. A. Charpentier. 2009. "Extent, Properties, and Landscape Setting of Geographically Isolated Wetlands in Urban Southern New England Watersheds." *Wetlands Ecology and Management* 17, no. 4: 331–344. https://doi.org/10.1007/s11273-008-9110-x.

McKinney, R. A., and P. W. C. Paton. 2009. "Breeding Birds Associated With Seasonal Pools in the Northeastern United States." *Journal of Field Ornithology* 80, no. 4: 380–386. https://doi.org/10.1111/j.1557-9263. 2009.00244.x.

McKinney, R. A., K. B. Raposa, and R. M. Cournoyer. 2011. "Wetlands as Habitat in Urbanizing Landscapes: Patterns of Bird Abundance and Occupancy." *Landscape and Urban Planning* 100, no. 1: 144–152. https://doi.org/10.1016/j.landurbplan.2010.11.015.

Meynard, C. N., V. Devictor, D. Mouillot, W. Thuiller, F. Jiguet, and N. Mouquet. 2011. "Beyond Taxonomic Diversity Patterns: How Do α , β and γ Components of Bird Functional and Phylogenetic Diversity Respond to Environmental Gradients Across France?" *Global Ecology and Biogeography* 20, no. 6: 893–903. https://doi.org/10.1111/j.1466-8238.2010.00647.x.

Mushet, D. M., A. J. K. Calhoun, L. C. Alexander, et al. 2015. "Geographically Isolated Wetlands: Rethinking a Misnomer." *Wetlands* 35, no. 3: 423–431. https://doi.org/10.1007/s13157-015-0631-9.

Naugle, D. E., R. R. Johnson, M. E. Estey, and K. F. Higgins. 2001. "A Landscape Approach to Conserving Wetland Bird Habitat in the Prairie Pothole Region of Eastern South Dakota." *Wetlands* 21, no. 1: 1–17. https://doi.org/10.1672/0277-5212(2001)021[0001:ALATCW]2.0.CO;2.

Newbold, T., L. N. Hudson, S. L. L. Hill, et al. 2015. "Global Effects of Land Use on Local Terrestrial Biodiversity." *Nature* 520, no. 7545: 45–50. https://doi.org/10.1038/nature14324.

Oertli, B., D. Auderset Joye, E. Castella, R. Juge, D. Cambin, and J.-B. Lachavanne. 2002. "Does Size Matter? The Relationship Between Pond Area and Biodiversity." *Biological Conservation* 104, no. 1: 59–70. https://doi.org/10.1016/S0006-3207(01)00154-9.

Oertli, B., and K. M. Parris. 2019. "Review: Toward Management of Urban Ponds for Freshwater Biodiversity." *Ecosphere* 10, no. 7: e02810. https://doi.org/10.1002/ecs2.2810.

Oksanen, J., G. L. Simpson, F. G. Blanchet, et al. 2022. "Vegan: Community Ecology Package." https://cran.r-project.org/web/packa ges/vegan/index.html.

Özkan, K., J.-C. Svenning, and E. Jeppesen. 2013. "Environmental Species Sorting Dominates Forest-Bird Community Assembly Across Scales." *Journal of Animal Ecology* 82, no. 1: 266–274. https://doi.org/10. 1111/j.1365-2656.2012.02019.x.

Paracuellos, M. 2006. "How Can Habitat Selection Affect the Use of a Wetland Complex by Waterbirds?" *Biodiversity and Conservation* 15, no. 14: 4569–4582. https://doi.org/10.1007/s10531-005-5820-z.

Pebesma, E., R. Bivand, E. Racine, et al. 2024. "Sf: Simple Features for R." https://cran.r-project.org/web/packages/sf/index.html.

Pryke, J. S., M. J. Samways, and K. De Saedeleer. 2015. "An Ecological Network Is as Good as a Major Protected Area for Conserving Dragonflies." *Biological Conservation* 191: 537–545. https://doi.org/10. 1016/j.biocon.2015.07.036.

Radford, J. Q., A. F. Bennett, and G. J. Cheers. 2005. "Landscape-Level Thresholds of Habitat Cover for Woodland-Dependent Birds." *Biological Conservation* 124, no. 3: 317–337. https://doi.org/10.1016/j. biocon.2005.01.039.

Rahlin, A. A., S. P. Saunders, and S. Beilke. 2022. "Spatial Drivers of Wetland Bird Occupancy Within an Urbanized Matrix in the Upper Midwestern United States." *Ecosphere* 13, no. 9: e4232. https://doi.org/10.1002/ecs2.4232.

Rajpar, M. N., S. Ahmad, M. Zakaria, et al. 2022. "Artificial Wetlands as Alternative Habitat for a Wide Range of Waterbird Species." *Ecological Indicators* 138: e108855. https://doi.org/10.1016/j.ecolind.2022.108855.

Riffell, S., T. Burton, and M. Murphy. 2006. "Birds in Depressional Forested Wetlands: Area and Habitat Requirements and Model Uncertainty." *Wetlands* 26, no. 1: 107–118. https://doi.org/10.1672/0277-5212(2006)26[107:BIDFWA]2.0.CO;2.

Schlaepfer, M. A. 2018. "Do Non-Native Species Contribute to Biodiversity?" *PLoS Biology* 16, no. 4: e2005568. https://doi.org/10.1371/journal.pbio.2005568.

Snodgrass, J. W., M. J. Komoroski, A. L. Bryan JR., and J. Burger. 2000. "Relationships Among Isolated Wetland Size, Hydroperiod, and Amphibian Species Richness: Implications for Wetland Regulations." *Conservation Biology* 14, no. 2: 414–419. https://doi.org/10.1046/j.1523-1739.2000.99161.x.

Spake, R., R. E. O'Dea, C. Shinichi Nakagawa, et al. 2022. "Improving Quantitative Synthesis to Achieve Generality in Ecology." *Nature Ecology & Evolution* 6, no. 12: 1818–1828. https://doi.org/10.1038/s4155 9-022-01891-z.

Sullivan, B. L., C. L. Wood, M. J. Iliff, R. E. Bonney, D. Fink, and S. Kelling. 2009. "eBird: A Citizen-Based Bird Observation Network in the Biological Sciences." *Biological Conservation* 142, no. 10: 2282–2292. https://doi.org/10.1016/j.biocon.2009.05.006.

Surdick, J. A. 2005. Amphibian and Avian Species Composition of Forested Depressional Wetlands and Circumjacent Habitat the Influence of Land Use Type and Intensity. University of Florida.

Tiner, R. W., H. C. Bergquist, G. P. DeAlessio, and M. J. Starr. 2002. "Geographically Isolated Wetlands a Preliminary Assessment of Their Characteristics and Status in Selected Areas of the United States." Hadley, MA: US Department of the Interior, Fish and Wildlife Service. https://digitalmedia.fws.gov/digital/collection/document/id/1334/.

Tiner, R. W. 2003. "Geographically Isolated Wetlands of the United States." *Wetlands* 23, no. 3: 494–516. https://doi.org/10.1672/0277-5212(2003)023[0494:GIWOTU]2.0.CO;2.

Tobias, J. A., C. Sheard, A. L. Pigot, et al. 2022. "AVONET: Morphological, Ecological and Geographical Data for all Birds." *Ecology Letters* 25, no. 3: 581–597. https://doi.org/10.1111/ele.13898.

US EPA, ORD. 2015. "Ecoregions of North America." Data and Tools. Accessed November 25, 2015. https://www.epa.gov/eco-research/ecore gions-north-america.

US Fish and Wildlife Service. 2022. "National Wetland Inventory Wetlands Mapper."

Wickham, H., T. L. Pedersen, D. Seidel, and Posit and PBC. 2023. "Scales: Scale Functions for Visualization." https://cran.r-project.org/ web/packages/scales/index.html.

Winter, M., D. H. Johnson, and J. A. Shaffer. 2006. "Does Body Size Affect a Bird's Sensitivity to Patch Size and Landscape Structure?" *Condor* 108, no. 4: 808–816. https://doi.org/10.1093/condor/108.4.808.

Wood, C., B. Sullivan, M. Iliff, D. Fink, and S. Kelling. 2011. "eBird: Engaging Birders in Science and Conservation." *PLoS Biology* 9, no. 12: e1001220. https://doi.org/10.1371/journal.pbio.1001220.

Xu, X., Y. Xie, K. Qi, Z. Luo, and X. Wang. 2018. "Detecting the Response of Bird Communities and Biodiversity to Habitat Loss and Fragmentation due to Urbanization." *Science of the Total Environment* 624: 1561–1576. https://doi.org/10.1016/j.scitotenv.2017.12.143.

Zamora-Marín, J. M., A. Zamora-López, M. V. Jiménez-Franco, J. F. Calvo, and F. J. Oliva-Paterna. 2021. "Small Ponds Support High Terrestrial Bird Species Richness in a Mediterranean Semiarid Region." *Hydrobiologia* 848, no. 7: 1623–1638. https://doi.org/10.1007/s10750-021-04552-7.

Supporting Information

Additional supporting information can be found online in the Supporting Information section.