Biological Conservation 249 (2020) 108708

Contents lists available at ScienceDirect

Biological Conservation

journal homepage: www.elsevier.com/locate/biocon

Prioritizing coastal wetlands for marsh bird conservation in the U.S. Great Lakes

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ARTICLE INFO

Keywords:
Abundance
Boosted regression trees
Marsh birds
Occurrence
Wetland-dependent
Zonation

ABSTRACT

Human activity surrounding the Laurentian Great Lakes basin has significantly degraded coastal wetland habitats, resulting in severe marsh bird population declines and reduced coastal resilience to changing environmental conditions. Given the need to conserve remaining coastal wetlands for wildlife and people, we developed a spatial prioritization to identify the most important U.S. Great Lakes coastal wetlands for 14 marsh bird species. We modeled occurrence and relative abundance of each species using boosted regression trees, a machine learning algorithm, to relate standardized monitoring data to ten remotely-sensed environmental covariates. We then used Zonation conservation planning software to rank every wetland cell based on its importance for the suite of marsh bird species. Evaluation of the drivers of marsh bird occurrence and abundance revealed that open water, herbaceous wetland, latitude, longitude, and impervious surface were the most important predictors across focal species. The high-priority wetlands for marsh birds (defined as grid cells ranked in the top 20%) occurred along the shores of eastern Lake Ontario, western Lake Erie/St. Clair, Saginaw Bay, Green Bay, northern lakes Michigan and Huron, and western Lake Superior. Overall, less than half (42%) of high-priority coastal wetlands across the Great Lakes basin are currently under some level of protection, with Lake Ontario priority wetlands being the least protected (25%). Our findings represent an opportunity to improve coastal wetland conservation in a region where wetland loss and degradation continue to threaten marsh bird populations and the integrity of one of the world's largest freshwater ecosystems.

1. Introduction

Coastal wetlands (i.e., wetlands adjacent to freshwater or marine waterbodies) provide critical habitat for birds, fish, amphibians, and other taxa, while also supporting terrestrial biodiversity within the surrounding landscape. Additionally, these ecosystems contribute up to 40% of global annual renewable ecosystem services (in U.S. dollars/year), including carbon sequestration, pollutant filtration, and protection against storm surges (Gedan et al., 2009; Meli et al., 2014). Despite their significance, coastal wetlands worldwide have declined by > 60% during the twentieth century (primarily due to land conversion; Wolter et al., 2006), and their biota are now considered among the most endangered in the world (Jenkins, 2003; Nel et al., 2009). Thus, there is a need to identify freshwater coastal wetlands that optimize biodiversity, which can be mutually beneficial to both wetland-reliant wildlife and human well-being (Finlayson et al., 2005; Howe et al., 2007; Niemi et al., 2007), as well as help direct future protection and restoration efforts where they may have the greatest impact.

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https://doi.org/10.1016/j.biocon.2020.108708
Received 7 February 2020; Received in revised form 8 July 2020; Accepted 11 July 2020

Spatial prioritization is an important tool for conservation planning because it balances multiple factors (e.g., ecological processes, species rarity) that may be indicative of the importance of an area for biodiversity within a spatially efficient configuration (Kujala et al., 2018Sinclair et al., 2018). The use of multi-species prioritizations to identify key areas has increased recently (Carvalho et al., 2017; Kujala et al., 2018), but considerable research is still required to improve both the implementation of resulting conservation plans and their scientific rigor, especially in the context of coastal wetland systems. For example, broad-scale datasets such as the North American Breeding Bird Survey do not adequately sample emergent wetlands (Conway, 2011). Consequently, relatively few freshwater protected areas have been created compared to terrestrial or marine reserves, likely because distribution data are limited for many wetland-dependent species (Moilanen et al., 2008).

Marsh birds are an ideal indicator guild to advance freshwater conservation because they are reliant on a variety of wetland vegetation characteristics (e.g., emergent vegetation interspersed with open water; DeLuca et al., 2004, Howe et al., 2007), and many are sensitive to anthropogenic disturbances within and around wetlands (Tozer et al., 2010; Glisson et al., 2017; Saunders et al., 2019). In the Laurentian Great Lakes region, several marsh bird populations are in steep decline, with some long-term declines exceeding 60% since the 1990s (Wires et al., 2010; Tozer, 2016; Soulliere et al., 2018). Today, < 50% of historical Great Lakes coastal wetlands remain (Krieger, 1992), and remnant wetlands are located in highly modified landscapes (Anteau and Afton, 2008), where they are subject to stressors from neighboring land uses and other factors related to human activities (e.g., sedimentation, nutrient loading, invasive species) that impact wetland quality and aquatic vegetation. Thus, protection and restoration of coastal wetlands across the Great Lakes are required, both to prevent further decline of marsh birds and to sustain the valuable ecosystem services that their wetland habitats confer.

To provide decision support for basin-wide conservation planning in U.S. Great Lakes coastal wetlands, we developed a spatial conservation prioritization to identify the most important wetlands for a suite of marsh bird species by (1) synthesizing seven years (2011–2017) of Great Lakes Coastal Wetland Monitoring Program survey data for 14 marsh bird species; (2) using a machine learning approach to model species occurrence and relative abundance as a function of remotely-sensed habitat variables; and (3) employing Zonation systematic conservation planning software (Moilanen et al., 2014) to rank each wetland cell based on its importance for our suite of marsh bird species. The purpose of this study was two-fold: to advance our understanding of marsh bird-habitat associations, and to harness the power of a robust dataset coupled with a rigorous, multi-step modeling approach to provide decision support for both marsh bird and wetland conservation planning at the landscape scale.

2. Methods

2.1. Study area

Our study area encompasses the U.S. Great Lakes coastal wetland system, which we defined as wetlands within 30 km of the shoreline (Fig. 1A) to include all wetlands of interest to both non-profit and U.S. government stakeholders. We excluded Canada because the results were intended to inform conservation efforts within the U.S. portion of the Great Lakes basin. To create a comprehensive map of all current and potential U.S. Great Lakes coastal wetlands, we combined data from three sources: (1) the Great Lakes Coastal Wetland Monitoring Program (CWMP) survey wetlands, which include all coastal wetlands within the Great Lakes basin > 4 ha in area with a surface water connection to a Great Lake and herbaceous vegetation (in addition to a small number of reference sites not meeting these criteria; see Uzarski et al., 2017a for details on CWMP sampling design); (2) the U.S. Environmental Protection Agency (EPA) potential wetland occurrence and important adjacent habitat dataset that considered elevation, coastal vegetation, and water level fluctuations, and resulted in a 356% increase in coastal wetland area over previous mapping efforts (U.S. EPA, 2017); and (3) the emergent wetland class from the National Wetlands Inventory (NWI; U.S. Fish and Wildlife Service, 2020), clipped to 30 km of the shoreline. Thus, all coastal wetlands were included in our analysis, regardless of size or connection to a Great Lake.

2.2. Focal species

We selected a suite of marsh bird species as the conservation features on which to base our prioritization. The focal species breed in the Great Lakes region and exemplify the variety of wetland vegetation associations that occur across the basin (Tozer, 2016; Panci et al., 2017). Several studies have demonstrated correlations between wetland quality/availability and reproductive success and abundance of our focal species (Lor and Malecki, 2006; Hanowski et al., 2007; Rehm and Baldassarre, 2007; Saunders et al., 2019). A total of 14 species were included in the analyses: American Bittern (*Botaurus lentiginosus*), Black-crowned Night Heron (*Nycticorax nycticorax*), Black Tern (*Chlidonias niger*), Blue-winged Teal (*Anas discors*), Common Gallinule (*Gallinula galeata*), Least Bittern (*Ixobrychus exilis*), Marsh Wren (*Cistothorus palustris*), Osprey (*Pandion haliaetus*), Pied-billed Grebe (*Podilymbus podiceps*), Sandhill Crane (*Grus canadensis*), Sedge Wren (*Cistothorus platensis*), Sora (*Porzana carolina*), Swamp Sparrow (*Melospiza georgiana*), and Virginia Rail (*Rallus limicola*). These species are considered either marsh-obligate or marsh-facultative, depending on whether the species preferentially uses specific habitat features associated with wetlands. Marsh-obligate species select for water level, interspersion, and vegetation type, while marsh-facultative species have more general habitat requirements and may also breed or forage in non-wetland areas. We assume that areas predicted by our models to have high occurrence or relative abundance will support the focal species only if the unmeasured, local-scale features (e.g., interspersion of open water and herbaceous vegetation) are present or restored.

2.3. Analytical workflow

We followed a five-step approach for prioritizing coastal wetlands for marsh bird conservation in the U.S. Great Lakes region (Fig. 1B). First, we collected marsh bird count data at an average of three points per sampled wetland. Second, we accounted for observational factors impacting detectability of species by estimating detection offsets to ‘correct’ CWMP counts prior to building the species-habitat models. Third, we assembled pertinent environmental covariates based on relevant literature and expert opinion. Fourth, we modeled species-specific occurrence and abundance as a function of the aforementioned covariates, and predicted the probability of occurrence or relative abundance (depending on species; see Section 2.7) for each of the 14 focal species across our study area. In the final step, we used the results of our species-habitat models as inputs to an optimization algorithm to produce a multi-species prioritization map for all U.S. Great Lakes coastal wetlands.

2.4. Step 1: marsh bird survey data collection

The CWMP was initiated in 2011 to assess biotic conditions in all major coastal wetlands in the Great Lakes (approx. 1000 wetlands; Uzarski et al., 2017a). Data were collected on birds, anurans, fish, macroinvertebrates, and macrophytes; our analysis focused on marsh birds and hence only includes the bird monitoring data from the CWMP. Wetland sites were selected using a stratified random sample, based on wetland type (lacustrine, riverine, and barrier) and region (Uzarski et al., 2017a). Selected sites were surveyed every five years, and rotating subsets of those sites were randomly selected to be surveyed two

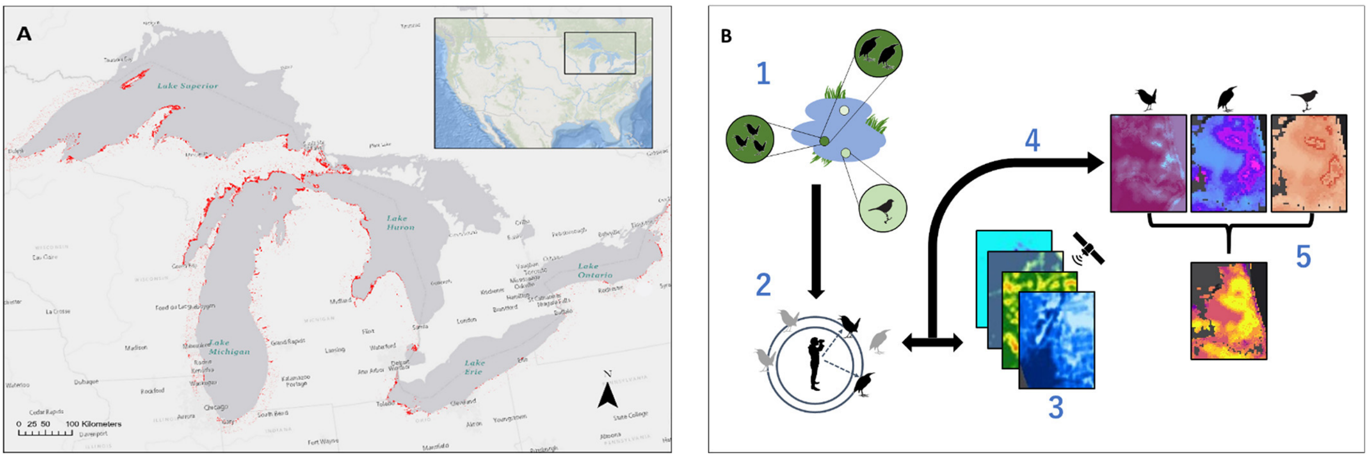

Fig. 1. (A) Coastal wetlands of the U.S. Great Lakes that were included in our spatial prioritization (shown in red; the analysis excluded coastal wetlands in Canada). (B) Flowchart visualizing the five-step analytical workflow for prioritizing U.S. Great Lakes coastal wetlands for marsh bird conservation: (1) Birds were counted at an average of three points within a wetland as part of the Great Lakes Coastal Wetland Monitoring Program; (2) counts were corrected for imperfect detection; (3) environmental covariates were assembled from remotely-sensed data; (4) species-habitat models were built by relating corrected counts to environmental covariates, and used to predict occurrence/abundance for 14 focal species across the study area (shown: focal images of Marsh Wren, American Bittern, and Swamp Sparrow prediction layers); and (5) predicted occurrences/abundances for all focal species were used as inputs to an optimization algorithm to create a multi-species prioritization map for U.S. Great Lakes coastal wetlands (shown: focal image of rank raster with colors representing the scale from zero to one). (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

years in a row as a temporal control. The number of points sampled in a given wetland depended on total wetland area, shape, accessibility, and wetland vegetation heterogeneity (Uzarski et al., 2017a); an average of three points, a minimum of 250 m apart, were sampled per wetland site during 2011–2017 (see Coastal Wetland Monitoring Program sampling design details in Appendix A).

The basic sampling unit for breeding marsh bird surveys was a point count. Observers sampled each survey point twice during each breeding season; once in the morning (0.5 h before to 4 h after sunrise) and once in the evening (4 h before to 0.5 h after sunset) between 20 May and 10 July. The duration of each point count was 15 min, which consisted of 5 min passive listening, 5 min of call-broadcasts, and 5 min of passive listening. During point counts, observers recorded all birds detected aurally or visually in any direction (full circle) at an unlimited distance. Data recorded at each survey point include GPS coordinates, the distance of each bird detection from the observation point (< 50 m, 50–100 m, or > 100 m), the type of detection (e.g., observed, calling, singing, flyover), and the minute interval (e.g., 0 for minute 0–1) when the species was first detected (Uzarski et al. 2017b).

2.5. Step 2: detection offset estimation

We used CWMP bird survey data collected during 2011–2017, including observations at Canadian Great Lakes coastal wetlands, to maximize species-specific sample sizes for estimating the potential factors influencing detection of marsh birds across the Great Lakes basin (n = 9057 bird observations at 1501 unique survey points). Our dataset included both time of first detection and distance of birds from the observer, so we used a formulation of time removal and distance sampling models developed by Sólymos et al. (2013) and implemented in the R package *detect* (Sólymos et al., 2018) to estimate detection correction factors (or 'offsets'). Although two surveys were conducted at a given point during each breeding season, we retained only the survey with the most detections per species within each point-year combination for use in estimating offsets because our analytical approach could not accommodate temporal replication in addition to time removal and distance sampling (Sólymos et al., 2013).

We estimated point-level, species-specific offsets that correct for two components of detection probability (availability and perceptibility) using conditional multinomial maximum likelihood estimation. Availability, which is the probability that a bird provided a visual or auditory cue during sampling and was thus available to be detected, was estimated as the 'singing rate' using the first minute of detection. Each individual was counted only once (i.e., individuals were 'removed' once detected). Perceptibility, which is the conditional probability that birds available for detection were actually detected, was estimated using the effective detection radius as a function of distance from observer (Sólymos et al., 2013).

To account for non-detection, we created zero observation records for all surveys at which each species was not observed. We grouped observations into 15 one-minute time intervals (0–1 min, 1–2 min, … 14–15 min) and three distance bins: 0–50 m, 51–100 m, and > 100 m. Singing rate was collapsed across distance bins and modeled as a log-linear function. We controlled for temporal and environmental variables affecting singing rate by including linear terms for year, weather (ordinal; 1 = dry, 2 = damp, 3 = drizzle, 4 = rain), noise (ordinal; 0 = no effect to 4 = profoundly affecting sampling), and wind (ordinal; 0 = calm to 5 = large branches and small trees sway), as well as both linear and quadratic terms for day of year and time since local sunrise, in addition to the intercept. We controlled for environmental variables affecting perceptibility by including linear terms for year, weather, noise, and wind, in addition to the intercept. Null models (i.e., no covariates) and models including all combinations of covariates were built; model selection was conducted using AIC (Burnham and Anderson, 2003). Singing rate and effective area sampled (in ha), defined as the area within the effective detection radius buffer, were calculated at the point level and then used to estimate a correction factor for each species during each survey to account for imperfect detection (see Methodological details on detection offset estimation in Appendix A for more details). Correction factors were entered as offsets in species-habitat models (see Section 2.7).

2.6. Step 3: environmental covariate data collection

We used the Focal Statistics tool in ArcGIS Pro version 2.4 (Environmental Systems Research Institute ESRI, 2019) to conduct a moving window analysis with a 400 m circular neighborhood (50.3 ha area) to derive all land cover covariates at a 100 m resolution, and sampled the resulting rasters at each survey point. We selected a resolution of 100 m as it represented the approximate radius of detection of most calling marsh birds (Allen et al., 2004; Johnson et al., 2009). Although response to spatial scale is species-dependent (Wiens, 1989), we selected a scale of 400 m because (1) recent work has suggested that land cover characteristics measured at this scale have greater explanatory power for avian species richness, occupancy, and abundance than those measured at larger spatial scales (e.g., 5 km; Cunningham and Johnson, 2006, Chocron et al., 2015, Saunders et al., 2019, Elliott et al., 2020); and (2) we assessed the correlations of covariates measured at the 400 and 800 m scales and all covariates were highly correlated ($r > 0.8$). Therefore, we opted to retain the scale with the most support in the literature.

Our suite of environmental variables was selected based on previously identified relationships with the distribution and abundance of wetland-dependent birds (Lor and Malecki, 2006; Harms and Dinsmore, 2013; Glisson et al., 2017; Gnass Giese et al., 2018; Saunders et al., 2019; Wiest et al., 2019). We incorporated ten covariates in our species-habitat models: proportions of open water, herbaceous wetland, woody wetland, agriculture (pooled cereals, oil seeds, legumes, wildflowers, herbs, and pasture; Saunders et al., 2019), and *Phragmites australis* (common reed) stands > 0.2 ha; mean impervious surface, annual lake levels, year, latitude, and longitude. All land cover variables were derived from remotely-sensed data. Although remotely-sensed measures of landscape characteristics have known limitations (e.g., land classified as open water may actually be emergent marsh), they nevertheless provide valuable information for landscape-scale conservation planning.

We estimated proportions of open water, herbaceous wetland, and woody wetland from the National Oceanic and Atmospheric Administration (NOAA) Coastal Change Analysis Program (C-CAP) 2010 Regional Land Cover Data (Office for Coastal Management, 2020). C-CAP 2010 was the most recent version of the dataset available at the time of analysis, and it represented landscape characteristics at the beginning of our time series. To control for changes in the extent of open water over the 7-year period in response to fluctuating water levels, we included an annual lake level covariate that accounted for potential variation in habitat characteristics within wetlands hydrologically connected to a Great Lake. Annual (2011–2017) average Great Lakes water levels were derived from monthly mean lake-wide average water level data (May–July) collected by the U.S. Army Corp of Engineers (2019). We obtained *Phragmites* distribution data from the U.S. Geological Survey *Phragmites* Decision Support Tool (v2.0.0; Bourgeau-Chavez et al., 2013; see Appendix A for more details on inclusion of *Phragmites*), and we used the 2016 National Land Cover Database Imperviousness (Multi-Resolution Land Characteristics Consortium, 2016) to calculate mean impervious surface (a continuous measure ranging from 0 to 1). To calculate the proportion of pooled agricultural classes, we used the 2016 Cropland Data Layer (National Agricultural Statistics Service, 2016). We lumped agricultural classes to limit the number of covariates included in model fitting and because a previous study conducted in southern Ontario demonstrated no differences in marsh bird response to cropland alone compared to cropland combined with pasture (Tozer et al., 2020). Although agricultural land within 400 m of our sampling points was generally scarce, our inclusion of *Phragmites* as a covariate may capture the bird response to eutrophication due to agriculture at larger landscape scales. Inclusion of latitude and longitude partially controlled for known spatial variation in both wetland availability and wetland use by some focal species (Brazner and Trebitz, 2016). Finally, we included year in our models to account for additional temporal fluctuations in wetland water levels not captured by our other variables (Elith et al., 2008; Timmermans et al., 2008; Hohman, 2019). We specified 2017 (the most recent survey year) as the year for all predictions of species occurrence and relative abundance.

2.7. Step 4: species-habitat modeling

We developed species-habitat models to both quantify the relationships with the aforementioned environmental covariates and predict focal species occurrence and abundance (depending on model fit; see below) across U.S. Great Lakes coastal wetlands ($n = 1111$ unique survey points at 376 unique wetlands). Because many marsh birds have low detection rates, species-specific abundance distributions were highly skewed with large numbers of zero counts (i.e., absences), prohibiting the use of traditional parametric modeling methods (Martin et al., 2005). Instead, we implemented a hierarchical hurdle model approach, in which we separately fit a presence-absence model that estimated the probability of focal species occurrence, and an abundance model that estimated relative abundance only where the species was predicted to occur (Wenger and Freeman, 2008; Oppel et al., 2012; Wilsey et al., 2019b).

We built species occurrence and abundance models using boosted regression trees (BRTs), a machine learning approach that is ideal for modeling complex curvilinear relationships with multiple, and often highly correlated (collinear and multicollinear), environmental variables (Elith et al., 2008). For the first model of each species, we iteratively tuned the following BRT parameters to optimize model fit while ensuring a minimum of 1000 trees using default parameter ranges recommended by Elith et al. (2008): learning rate 0.0001–0.1, bag fraction 0.55–0.75, and tree complexity 1–3. At each step, we used 10-fold cross-validated area under the curve (AUC) and residual deviance to select the optimal parameter value. This process resulted in models with the following parameters: occurrence models had a learning rate of 0.005, a bag fraction of 0.55 and a tree complexity of 1, and abundance models had a learning rate of 0.0005, a bag fraction of 0.55 and a tree complexity of 1 (see Methodological details on boosted regression trees in Appendix A for more details).

The response variables were presence for the occurrence model, and count for the abundance model. The detection offset correction factors described above were added to the BRTs as offsets to account for imperfect detection (Sólymos et al., 2013). Count data were modeled using a Poisson distribution where possible; if Poisson models failed to converge, we used a Gaussian distribution on log-transformed count data (to meet the normality assumption). All ten environmental covariates were included in each species-specific model, with the exception of latitude and longitude for species with fewer than 200 detections, as the models failed to converge with those two variables included (see Appendix A for more details). Models were fit using packages *dismo* (Hijmans et al., 2017) and *gbm* (Ridgeway, 2019) in R version 3.5.1 (R Core Team, 2018). We evaluated model performance using AUC for occurrence models, and cross-validated deviance explained for relative abundance models, and assessed the influence of each predictor by calculating the relative variable importance, as well as the mean relative importance (with associated 95% confidence intervals) averaged across all species. Relative importance represents the proportion of the total model deviance explained by each predictor, as measured by its contribution to tree splits and model improvement (Elith et al., 2008).

We identified a minimum threshold for probability of occurrence below which grid cells were classified as unoccupied for each focal species (Wilsey et al., 2019b). Thresholds were identified with the R package *SDMTools* using the maximum sensitivity + specificity criterion (VanDerWal et al., 2014). Predicted relative abundance estimates were generated only for grid cells that exceeded this probability of occurrence threshold. For each species, we considered the performance of the relative abundance model adequate for inclusion in the prioritization when the residual cross-validated deviance explained was less than the null cross-validated deviance explained. When this criterion was not met, we used the occurrence model to represent the species in the prioritization (see Section 3.1). Thus, all 14 species were represented in the prioritization via either occurrence or abundance model estimates.

Species-habitat models such as these are susceptible to spatial autocorrelation, which can result in biased species-environment relationships. To assess spatial autocorrelation in models, we used spatially stratified cross-validation by dividing the datasets into 5 bins by longitude and 3 bins by latitude, while withholding one longitudinal/latitudinal bin for testing at each fold (Roberts et al., 2017). We tested for residual spatial autocorrelation in the final models using Moran's I, calculated with the R package *ape* (Paradis et al., 2004).

2.8. Step 5: coastal wetland prioritization

We used Zonation conservation planning software (version 4.0; Moilanen et al., 2014) to rank every 100-m coastal wetland cell in the landscape based on probability of occurrence or relative abundance of all focal species (depending on model fit for a given species; see Section 3.1). Zonation is a decision-support tool that identifies balanced reserve networks that represent all species in an efficient configuration. It applies a complementarity-based algorithm to distribution data to produce a priority ranking based on the importance of each cell to the suite of target species. The algorithm starts with the full landscape and incrementally removes the grid cell that leads to the smallest aggregate loss of conservation value, resulting in a hierarchy or ranking of cell importance for biodiversity ranging from 0 to 1. We used the Core Area Zonation (CAZ) cell-removal algorithm, which calculates the marginal value of each cell based on the species with the highest weighted proportion of its distribution remaining in each cell at each iteration of the ranking process. Thus, it has the benefit of identifying biodiversity-poor cells that are important for a single rare or highly weighted feature (for more details see: Moilanen et al., 2014).

We ran the prioritization analysis using a coastal wetland mask to exclude all other land cover types from the ranking. The coastal wetland mask was comprised of the three aforementioned datasets: CWMP wetlands (Uzarski et al. 2017b), EPA potential wetlands (U.S. Environmental Protection Agency, 2017), and NWI emergent wetlands (U.S. Fish and Wildlife Service, 2020). We used a warp factor of 1 (a single cell was removed at each iteration) and no edge removal (preferential removal of edge cells to force aggregation of high-ranked cells), as computation time was not a limiting factor and we wanted to identify all high value cells for marsh birds, irrespective of location within the wetland.

We assigned weights to each of the 14 species based on a combination of the North American Bird Conservation Initiative Conservation Concern Score (*NABCI score*; NABCI, 2016), Audubon Climate Status (*ACS*; where climate vulnerable = 2, not climate vulnerable = 1; Wilsey et al., 2019a), and Species of Greatest Conservation Need list status in Great Lakes states (*SGCN*; U.S. Geological Survey, 2017) using the following formulae:

$$\textit{Regional score} = ACS + (SGCN.\ states_{end}\cdot 3) + (SGCN.\ states_{thr}\cdot 2) + (SGCN.\ states_{con})$$

$$\textit{Species weight} = \frac{(\textit{Regional score} + \textit{NABCI score})}{2}$$

where $SGCN.states_{end}$ refers to the number of states for which the species is listed as endangered on the Species of Greatest Conservation Need list; $SGCN.states_{thr}$ is the number of states for which the species is listed as threatened; $SGCN.states_{con}$ is the number of states for which the species is listed as of concern. Therefore, the *Regional score* for a given species is higher if the species is listed in multiple states and/or if the species is of greater conservation need (i.e., endangered vs. threatened). We also included the *ACS* to account for potentially severe range losses predicted for focal species under climate change (vulnerable status = higher conservation priority). Climate-vulnerable was defined as projected loss of > 50% of a species' current range by 2080 (with no net gain from potential range expansion). The calculated *Regional score* was then averaged with the *NABCI score*, which employs biological criteria to evaluate vulnerability, including population size, distribution, threats, and population trend (see Panjabi et al., 2012 for more details).

We defined high-priority wetlands as the top 20% of the prioritization ranks (i.e., ≥0.8). For each Great Lake, we calculated median wetland rank, proportion of high-priority wetlands, and proportion of high-priority wetlands under some form of protection, which we defined as located within areas designated as GAP status 1–4 in the Protected Areas Database of the U.S. (U.S. Geological Survey (USGS) Gap Analysis Project (GAP), 2018). GAP status designations range from permanent protection combined with mandated management (status 1) to permanent protection subject to extractive uses (status 3). GAP status 4 is defined as no known restrictions on land conversion to anthropogenic habitat types, but we included this designation in our calculations as these areas may provide some level of protection (e.g., conservation easements, resource management areas, state parks). Given that the extent to which these areas provide effective biodiversity protection is unknown, our analysis most likely overestimates the true level of protection. Finally, we conducted an initial screening of Great Lakes impaired areas (classified as Areas of Concern [AOCs]; epa.gov/great-lakes-aocs), defined as geographic areas with significant impairment of beneficial uses due to human activities at the local level. We calculated the average rankings within AOCs by intersecting the prioritization rank raster with the AOC boundaries to identify AOCs that are potentially suitable for restoration or delisting. We provide the results and discussion of the AOC analysis in Appendix A (see Analysis of impaired areas section) as it is a related, but tangential, decision support framework for wetland restoration.

3. Results

3.1. Species-habitat modeling

Relative abundance models for five marsh bird species (Common Gallinule, Marsh Wren, Pied-billed Grebe, Sedge Wren, Swamp Sparrow) met the criterion for inclusion in the prioritization. Average abundances estimated at surveyed grid cells for these five species ranged from 0.37 ± 0.03 (mean ± SE; Sedge Wren) to 1.18 ± 0.04 (Swamp Sparrow; Supplementary Table A.1). The relative abundance models for the remaining nine species (American Bittern, Black-crowned Night Heron, Black Tern, Blue-winged Teal, Least Bittern, Osprey, Sandhill Crane, Sora, and Virginia Rail) did not meet the criterion for inclusion, so instead we used the occurrence models to represent these species in the prioritization. Fit of species-habitat models varied among species and response type (occurrence vs. abundance), but each predictor generally explained 10–30% of the variation in the data after cross-validation. For occurrence models, cross-validated AUC averaged 0.78 (range: 0.67–0.86) and deviance explained averaged 0.47 (range: 0.15–0.84 Supplementary Table A.2). For abundance models, deviance explained averaged 0.65 (range: 0.42–0.88; Supplementary Table A.2). All Moran's I values were ≤ 0.06, indicating that there was no residual spatial autocorrelation in the data (Supplementary Table A.2).

Across species, the proportion of open water explained the most variation in occurrence on average (mean ± SE: 16.62 ± 5.00%), followed by latitude (15.19 ± 4.26%) and longitude (15.17 ± 3.82%; Fig. 2A). Mean impervious surface explained the most variation in abundance averaged across species (21.35 ± 9.88%), followed by the proportion of herbaceous vegetation (17.71 ± 5.89%) and water levels (11.71 ± 5.22%; Fig. 2B). The year covariate explained the least variation in occurrence and the second least in abundance of marsh bird species on average (Fig. 2). The relative importance of variables for both occurrence and abundance models differed substantially among species (Figs. 3 & 4; see Supplementary Figs. A.1–A.14 for plots of predictor variable relationships with occurrence/abundance for each species). For example, proportion of open water explained > 30% of

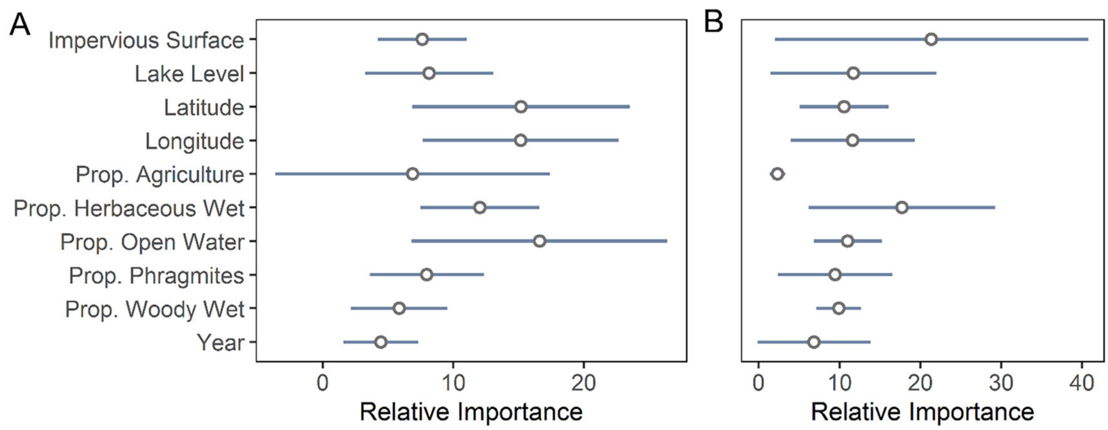

Fig. 2. Mean relative variable importance (gray circles) and 95% confidence intervals (blue horizontal lines) for 10 variables used as predictors of species (A) occurrence ($n = 9$ species) and (B) abundance ($n = 5$ species) in boosted regression tree models for a total of 14 marsh bird species across U.S. Great Lakes coastal wetlands during 2011–2017. Variables are listed on the *y*-axis in alphabetical order: mean impervious surface; annual Great Lakes water levels; latitude; longitude; proportions of agriculture (within 400 m radius of survey point), herbaceous wetland, open water, large *Phragmites australis* stands, and woody wetland; and year. See main text for full descriptions of covariates. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

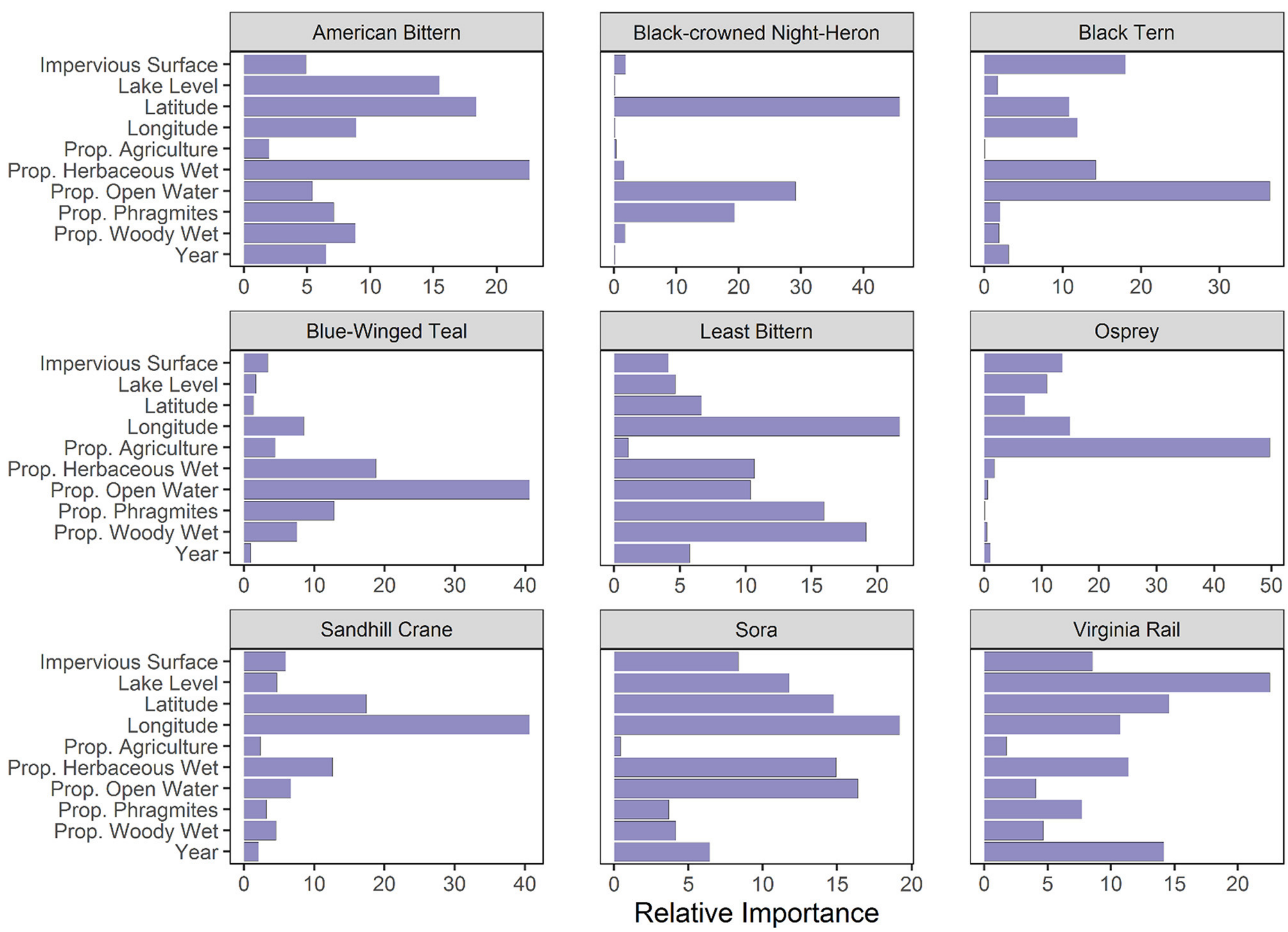

Fig. 3. Species-specific relative variable importance for 10 covariates used as predictors of marsh bird occurrence across U.S. Great Lakes coastal wetlands during 2011–2017. Results are shown for nine species for which the occurrence model was used in the coastal wetland prioritization. Variables are listed on the *y*-axis in alphabetical order: mean impervious surface; annual Great Lakes water levels; latitude; longitude; proportions of agriculture, herbaceous wetland, open water, large *Phragmites australis* stands, and woody wetland; and year. See Appendix A for partial dependence plots of the predictor variables in the species-specific occurrence models.

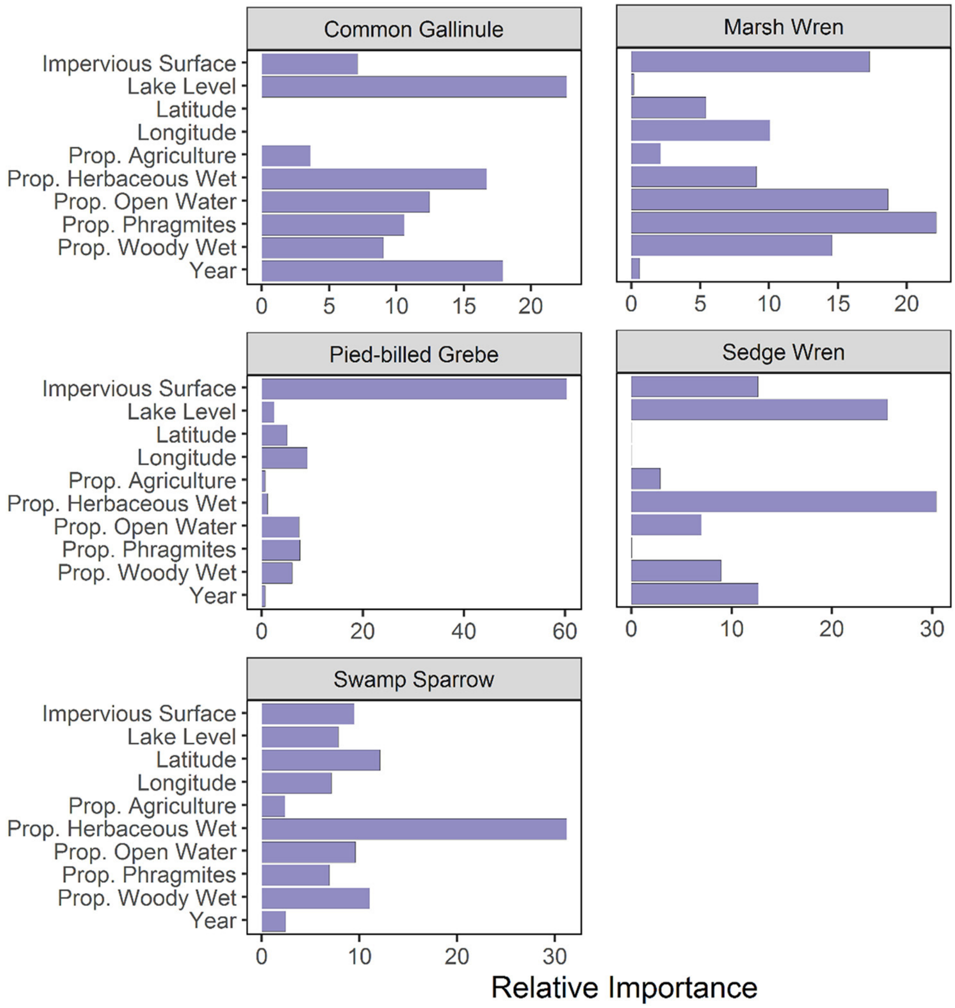

Fig. 4. Species-specific relative variable importance for 10 covariates used as predictors of marsh bird abundance across U.S. Great Lakes coastal wetlands during 2011–2017. Results are shown for five species for which the relative abundance model was used in the coastal wetland prioritization. Variables are listed on the *y*-axis in alphabetical order: mean impervious surface; annual Great Lakes water levels; latitude; longitude; proportions of agriculture, herbaceous wetland, open water, large *Phragmites australis* stands, and woody wetland; and year. Latitude and longitude were excluded for Common Gallinule and Sedge Wren. See Appendix A for partial dependence plots of the predictor variables in the species-specific abundance models.

the variation in Black Tern occurrence (Fig. 3), while herbaceous vegetation explained approximately 30% of the variation in Sedge Wren and Swamp Sparrow abundances (Fig. 4).

3.2. Coastal wetland prioritization

A total of 239,499 ha of coastal wetlands were ranked in the top 20% (i.e., high priority) across the U.S. Great Lakes. Overall, wetlands along lakes Ontario (median: 0.84), Erie/St. Clair (0.81), and Huron (0.73) had higher priority rankings, whereas lakes Michigan (0.51) and Superior (0.37) had lower rankings (boxplots in Fig. 5). There was considerable variation in rankings of wetlands across the shorelines of each lake (boxplots in Fig. 5), and a relatively strong spatial pattern basin-wide (e.g., highly ranked wetlands along northern and western U.S. shorelines; Fig. 6). High-priority areas tended to be concentrated within or near river mouths, bays, and estuaries (e.g., Chequamegon Bay in Wisconsin and St. Louis River Estuary near Duluth, Minnesota; Fig. 6). Wetlands along the northern shores of lakes Michigan and Huron were consistently ranked high, as were wetlands within Saginaw Bay in Michigan and eastern Lake Ontario in New York (Fig. 6). Several high-priority areas were in close proximity to human development (e.g., Green Bay, Wisconsin and Detroit, Michigan; Fig. 6).

Basin-wide, 42% of high-priority wetlands are currently under some level of protection (i.e., GAP status 1–4). The lakes with the greatest proportion of total wetland area ranked as high priority were Lake Ontario with 50% (47,679 ha, 25% of which are protected) and lakes Erie and St. Clair combined with 45% (37,029 ha, 50% of which are protected). Lakes Huron, Michigan, and Superior had 38% (71,233 ha, 41% of which are protected), 15% (69,960 ha, 48% of which are protected), and 4% (13,598 ha, 57% of which are protected) of coastal wetlands designated as high priority, respectively (Fig. 5). The lowest ranked grid cells were located along the shorelines of Lake Superior and southern Lake Michigan (darker shading in Fig. 6).

4. Discussion

Our study harnesses the power of a unique, long-term dataset that provides valuable information on the distribution and abundance of marsh birds. Because CWMP surveys were conducted across a broad geographic range and within a wide variety of wetland types and landscape conditions, these data provide critical decision support for marsh bird conservation in the U.S. Great Lakes basin. Our five-step approach allowed us to (1) identify high-priority wetlands for multiple species, including those in areas that are under-sampled by the CWMP; (2) reveal a spatial mismatch between ecological value and protection status across the basin; and (3) provide recommendations for conservation action in a region where wetland loss and degradation continue to threaten marsh bird populations.

4.1. Marsh bird-habitat associations

The amount of impervious surface in the surrounding landscape and availability of open water and herbaceous wetland were the most important predictors of marsh bird occurrence and abundance, on average, across species. The influence of impervious surfaces on abundance was highly variable among species (Fig. 2). In particular,

Fig. 5. Proportions of the total coastal wetland area along the five Great Lakes (U.S. only) that were designated as high-priority (i.e., ranked within the top 20%; shown in green) from the spatial prioritization (acreage shown in green text). Remaining coastal wetland acreages (i.e., 'Other'; those outside of the top 20%) are shown in gray for each lake. The boxplots (bottom right panel) show the median (solid black lines), interquartile range (bounds of boxes), and minimum/maximum (bottom and top of whiskers) of priority ranks for the wetland grid cells along each of the Great Lakes. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

mean impervious surface was a relatively strong predictor of Marsh Wren and Pied-billed Grebe abundances (with positive and negative influences, respectively; Figs. 4, A.7 & A.9). These results are in agreement with recent work that demonstrated a significant negative response of Pied-billed Grebe to the amount of surrounding developed land, in contrast to a positive Marsh Wren response (Saunders et al., 2019). Marsh Wren are known to inhabit wetlands dominated by invasive species such as *Typha* and *Phragmites* (Kroodsma and Verner, 2013), which are more likely to be near developed areas (Werner and Zedler, 2002), possibly producing this positive relationship with impervious surfaces (but see Panci et al., 2017).

The proportion of surrounding agriculture was highly variable in its importance in predicting species occurrence (Fig. 2), but was consistently unimportant in determining species abundance, which may, in part, be due to the scarcity of agricultural land within 400 m of sampled wetlands. This variation in explaining occurrence was a product of the relationship between Osprey and agriculture, a variable that explained 49.7% of the variation in Osprey occurrence, compared to < 10% for other species. Although Osprey mainly consume fish, recent evidence from an Osprey population in Germany suggests that individuals are becoming acclimated to agriculturally-dominated landscapes, and even preferentially nest in the open (i.e., near crop fields) because of higher breeding success near agricultural land (Bai et al., 2009). Thus, the importance of agriculture in predicting Osprey occurrence in the Great Lakes region may arise from higher resource availability within agriculturally-dominated areas, as suggested by the strong, positive relationship with this predictor (Fig. A.8).

Species-specific differences in the importance of open water and herbaceous wetland availability were also consistent with differences among focal species' marsh habitat structure and area requirements. For example, open water was generally preferred by wetland species that nest on or forage in deep water, such as Black Tern which builds nests on floating vegetation mats (Heath et al., 2009), and Black-crowned Night-Heron and Common Gallinule that primarily feed on small fish, amphibians, and aquatic vegetation in deeper marshes (Bannor and Kiviat, 2002, Hothem et al., 2010; all three relationships were positive, Figs. A.2–A.3 & A.5). American Bittern, Sedge Wren, Sora, and Swamp Sparrow are typically found in marshes characterized by an even mix of open water and emergent vegetation, and all had positive associations with herbaceous wetlands (Figs. A.1, A.11–A.13). Habitat features that might contribute to these associations include the availability of singing perches and nesting cover (wrens and sparrows), wetland plant seed abundance (e.g., Sora; Melvin and Gibbs, 2012), and high densities of macroinvertebrates (e.g., American Bittern; Lowther et al., 2009).

Spatial variation in the hydrology and productivity of Great Lakes coastal wetlands (Albert et al., 2005), as well as in focal species'

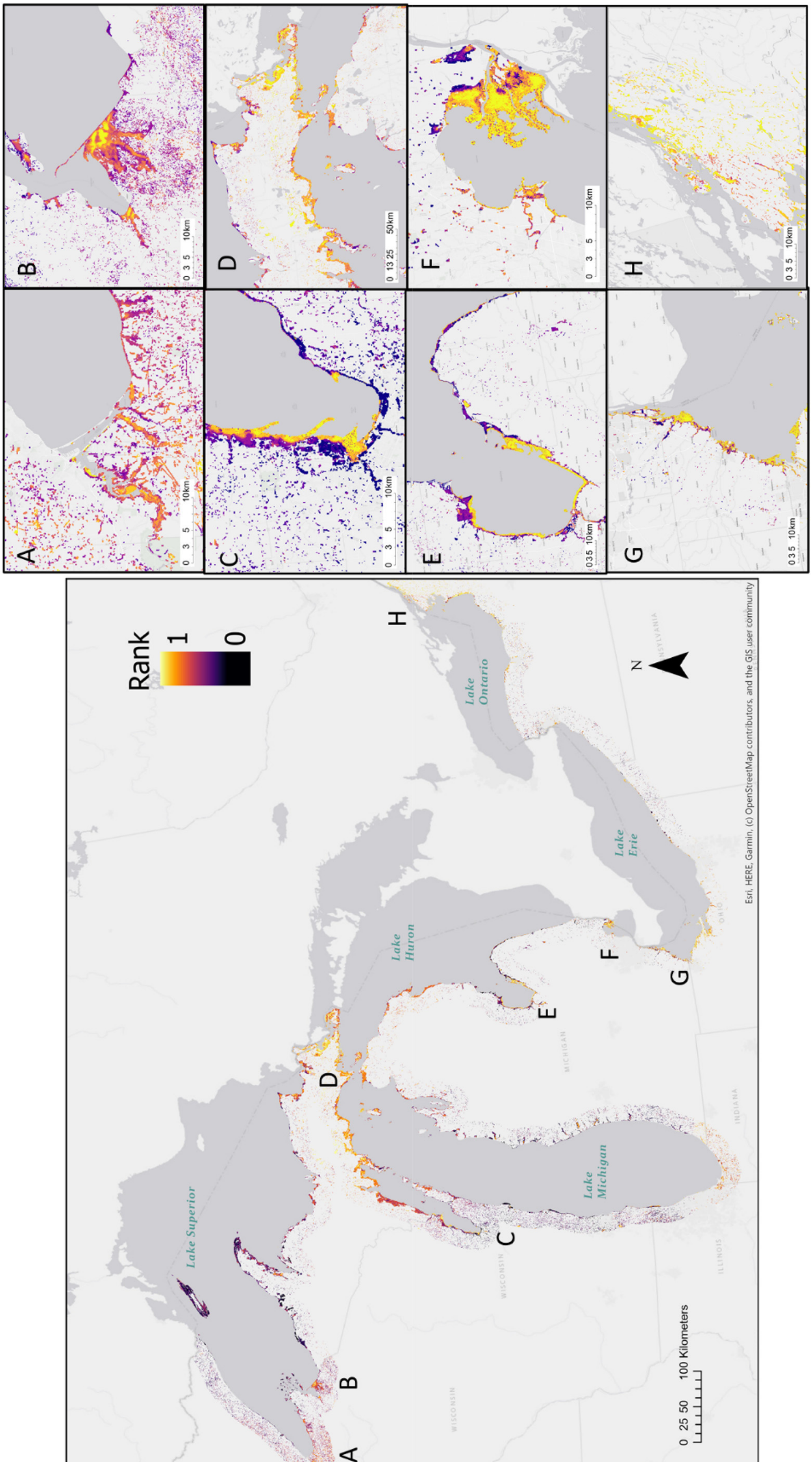

Fig. 6. Prioritization ranks of U.S. Great Lakes coastal wetlands from the Zonation optimization scaled from 0 to 1 (the analysis excluded coastal wetlands in Canada). The basin-wide results are shown on the left, and insets on the right show a sample of high-priority areas in greater detail: (A) St. Louis River Estuary in the Duluth-Superior harbor, Minnesota & Wisconsin; (B) Chequamegon Bay, Wisconsin; (C) Green Bay, Wisconsin; (D) northern Lakes Michigan and Huron, Michigan; (E) Saginaw Bay, Michigan; (F) Lake St. Clair, Michigan; (G) western Lake Erie, Ohio; and (H) eastern Lake Ontario, New York.

breeding ranges, likely accounts for the importance of latitude/longitude in predicting marsh bird occurrence across the basin. Specifically, we found that occurrence of Black-crowned Night-Heron, a species whose current breeding range is largely restricted to the southern portion of the Great Lakes (i.e., Erie, Ontario, and lower Michigan), had a strong, negative association with latitude (Fig. A.2). In contrast, Least Bittern, Sandhill Crane, and Sora occurrences were better predicted by longitude (with varying directions of that relationship; Figs. A.6, A.10, A.12), which may be a result of several different factors, including lake-specific differences in surrounding landscape features, regional climate, or anthropogenic stressors (Danz et al., 2005, 2007; Hanowski et al., 2007).

Although annual Great Lakes water levels generally were not important in predicting species occurrence or abundance, three focal species were particularly sensitive to this covariate. Occurrence and/or abundance of Virginia Rail, Common Gallinule, and Sedge Wren were well-predicted by lake level, suggesting that these species are more responsive to temporally-varying environmental conditions compared to other species. Previous work identified Virginia Rail and Common Gallinule as species that showed a strong response to seasonal hydrological conditions, given that individuals often build nests within emergent vegetation that is either shallowly flooded (Virginia Rail) or over open water (Common Gallinule; Desgranges et al., 2006, Gnass Giese et al., 2018). Similarly, Sedge Wren habitats are typified by vegetation and soils that are highly susceptible to drying or flooding caused by annual and seasonal variation in rainfall, as well as lake-level fluctuations if wetlands are hydrologically connected to the Great Lakes (Herkert et al., 2001). With more pronounced variability predicted for Great Lakes water levels under climate change (Music et al., 2015), these three species may be increasingly threatened by habitat loss due to unprecedented frequencies of extreme flooding and drying periods.

4.2. Priority coastal wetlands

Lake Ontario and Lake Erie/St. Clair had the largest proportions of high-priority areas for the marsh birds evaluated here (Fig. 5). Recent work corroborates our findings, in which calculation of bird-based indicators of coastal wetland quality yielded primarily high values for wetlands along the lower Great Lakes (see Uzarski et al., 2017b: Fig. 10). We found that high-priority wetland areas were generally concentrated along estuaries and bays (e.g., Chequamegon Bay, Green Bay, Saginaw Bay, Sandusky Bay), where wetland functions and productivity are enhanced at the interface with the lakes (Herdendorf, 1992; Gehring et al., 2020). High-priority wetlands were also concentrated along the western shore of Lake Erie, one of the most biologically productive areas in the basin due to its shallow depth and warm temperature. Grid cells along the northern shores of lakes Michigan and Huron (in Michigan's Upper Peninsula) were ranked consistently high within small wetlands far from shore, large wetland complexes close to shore, and on near-shore islands (Fig. 6D). Importantly, this high-priority area comprised ~50 km of contiguous wetlands that were under-sampled by the CWMP (mainly due to access issues); this finding suggests that survey efforts should be enhanced within this area where possible. Although management of expansive wetland complexes and those that are logistically difficult to access (e.g., offshore) presents a challenge, our results illustrate the heavy use of these areas by marsh birds and thus the likely maximization of return on conservation investments.

4.3. Wetland conservation potential

Our findings demonstrate ample opportunities to advance freshwater wetland conservation across the Great Lakes region. Less than half (42%) of high-priority coastal wetlands across the basin are currently under some level of protection, with Lake Superior's high-priority wetlands being afforded the most protection (57%) despite having the lowest proportion of priority areas along that lake. Lake Ontario had the largest proportion of high-priority wetlands, but these priority wetlands are currently the least protected (25%). Agriculture, industrial activity, and urbanization continue to dominate the Lake Ontario watershed (especially along the southeastern shoreline; Danz et al., 2007), threatening the integrity of the lake's unprotected, high-priority wetlands.

It is important to note that our bird observation data were collected only at wetlands > 4 ha in size that are hydrologically connected to a Great Lake, yet we applied our species-habitat models to our entire study area. Hence, we assume that the demonstrated relationships carry over to smaller wetlands and those lacking a direct connection to a Great Lake. In the future, integration of marsh bird survey data collected at a wider variety of wetland sizes and locations will help refine our results, especially in cases where prioritization of small wetlands or wetlands located further from the shoreline are of interest. Additionally, previous studies have evaluated multiple taxa as indicators of coastal wetland conditions (Brazner et al., 2007a, 2007b); future basin-wide prioritizations could be based on all taxa sampled by the CWMP to gain a better understanding of the importance of Great Lakes coastal wetlands for maintaining freshwater biodiversity as a whole.

5. Conclusions

The spatial mismatch between ecological value and protection status is an opportunity to improve the conservation of marsh birds in a region where wetland loss and degradation remain high. We recommend that areas identified as high-priority but currently lacking protection be considered in future conservation efforts. For example, it might be cost-effective to protect areas identified as high value for marsh birds with low land-use conflict, such as wetlands along the northern shore of Lake Michigan. On the other hand, restoration and land-sharing strategies (Triviño et al., 2018) could be directed towards areas with high conservation value that are threatened by intensive anthropogenic activity, including those wetlands close to urban centers such as Green Bay, Wisconsin and Detroit, Michigan. Overall, our findings provide insights into species-specific habitat associations, decision support for regional wetland conservation planning, and a generalizable approach for prioritizing coastal wetlands for marsh bird population persistence, and hence, the maintenance of valuable ecosystem services for the benefit of coastal communities.

Credit author statement

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Sarah P. Saunders: Methodology, Software, Formal analysis, Writing - Original Draft, Writing - Review & Editing, Visualization, Project administration, Supervision

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Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Acknowledgements

We are grateful to D. Wilcox, J. Bateman, B. Mudrzynski, and G. Lawrence for logistical support, as well as numerous Great Lakes Coastal Wetland Monitoring Program field technicians. We thank members of the Scientific Advisory Committee of Birds Canada's Long Point Waterfowl and Wetlands Research Program for comments that improved the paper. Support for this research was provided by the Great Lakes National Program Office of the U.S. Environmental Protection Agency (grant numbers GL-00E00612 and GL-00E00623), Birds Canada, S.C. Johnson, and The Bluff's Hunting Club.

Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.biocon.2020.108708.

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