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Ecologically Scaled Responses of Marsh Birds to Invasive *Phragmites* Expansion and Water-Level Fluctuations

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Abstract.—We examined effects of *Phragmites australis* on four marsh-dependent birds [Least Bittern (*Ixobrychus exilis*), Marsh Wren (*Cistothorus palustris*), Sora (*Porzana carolina*), Virginia Rail (*Rallus limicola*)] during water-level fluctuations within Saginaw Bay, Michigan. During 2002–2004 (pre-*Phragmites* expansion), 2008–2010 (*Phragmites* expansion), and 2014–2015 (increasing water levels-decreasing *Phragmites* coverage), we measured area of native vegetation, area of *Phragmites,* and distance between native vegetation patches at 21 coastal wetlands. We calculated ecologically scaled landscape indices (ESLIs) to determine changes in carrying capacity and connectivity for each species in the wetland landscape through time. Carrying capacity and connectivity values were greatest for all species during 2002–2004, likely due to the limited influence of *Phragmites* on the landscape during that period. By 2008-2010, expansion of *Phragmites* severely reduced marsh bird habitat carrying capacity and connectivity of wetland landscapes. Rising water levels, associated with reduced *Phragmites* cover, resulted in further slight reductions in connectivity and slight increases in amount of wetland habitat. Data from a subset of focal sites in Saginaw Bay suggested that marsh birds responded positively to increasing water levels. Our study demonstrates utility of ESLIs as a conservation tool for identifying key factors that impact landscape structure and avian community composition over time. *Received 7 Apr 2021, accepted 9 Nov 2022.*

Key Words.—climate change, ecologically scaled landscape indices, ESLI, Great Lakes coastal wetland, habitat fragmentation, habitat loss, invasive species, marsh birds, *Phragmites australis*, water-level fluctuations

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Multiple stressors affecting coastal wetland habitat have contributed to the decline of many marsh-obligate species (Crewe *et al.* 2006). These species contend with anthropogenic and natural disturbances that can alter habitat quality and quantity. Primary anthropogenic stressors include agricultural and urban development and the introduction of invasive species, which impact the size and quality of coastal wetland habitat (Niemi and McDonald 2004). Agricultural ditches and channels, for example, increase fragmentation of coastal wetlands and alter biological communities (Harding *et al.* 1999; Relyea 2005; Schock *et al.* 2014). Numerous factors influence the presence and abundance of marsh birds, including wetland size (Brown and Dinsmore 1986; Quesnelle *et al.* 2013), wetland isolation (Brown and Dinsmore 1986; Smith and Chow-Fraser 2010), and degree of water-vegetation interspersion in wetlands (Rehm and Baldassarre 2007; Hohman *et al.* 2021).

The exotic strain of common reed (*Phragmites australis*; hereafter: *Phragmites*) is a non-native plant species that has been introduced to the Laurentian Great Lakes (Great Lakes) region. Since the mid-1990s, this species has expanded its range and further fragmented many Great Lakes coastal wetlands (Tulbure and Johnston 2010; Wilcox 2012), sometimes creating impenetrable barriers that limit the ability of wildlife to find potential habitat (League *et al.* 2007). Previous studies show horizontal expansion rates by *Phragmites* of up to 3 m per growing season (Warren *et al.* 2001; Howard and Turluck 2013; Fussel *et al.* 2015), highlighting the potential for rapid onset of negative effects on ecosystems and biotic communities. Especially when water levels remain low, *Phragmites* tends to rapidly expand through coastal wetlands (Wilcox *et al.* 2003; Wilcox and Nichols 2008). This expansion can be promoted by anthropogenic reductions to natural water level fluctuations (Frieswyk and Zedler 2007).

Water fluctuations have historically facilitated a shifting temporal mosaic of wetland types (Keddy and Reznicek 1986; Herdendorf 1992; Wilcox 1995; Wilcox and Nichols 2008). Despite the beneficial effect of creating a diversity of habitat types temporally, naturally fluctuating water levels can cause loss and fragmentation of existing coastal wetland habitat patches (Gilbert *et al.* 2010). Marsh-obligate species are presumably adapted to this natural variability, although to varying degrees (Timmermans *et al.* 2008; Hohman *et al.* 2021). Appropriate water levels are a key requirement for supporting marsh birds (Murkin *et al.* 1997; Tozer *et al.* 2010). Both water levels and water extent at the maxima of natural fluctuations are generally positively correlated with marsh bird abundance in the Great Lakes region (Timmermans *et al.* 2008; Chin *et al.* 2014; Tozer *et al.* 2016; Gnass Giese *et al.* 2018; Hohman *et al.* 2021). Increasing water levels can also be a habitat modifier and reduce the extent of *Phragmites* over time (Wilcox and Nichols 2008).

Previous studies have attempted to determine the impact of invasive, non-native plants, including *Phragmites*, on marsh birds. Expansion of invasive *Spartina* spp. was associated with reduced numbers of waterbirds in estuarine wetlands (Daehler and Strong 1996; Gan *et al.* 2009, Liu *et al.* 2010), and total abundance of marsh nesting bird species was greater in meadow marsh habitat compared to *Phragmites* stands (Meyer *et al.* 2010). At least one marsh bird species, the Marsh Wren (*Cistothorus palustris*), may benefit as a result of *Phragmites* expansion due to a net gain in vertical vegetative structure (Benoit and Askins 1999). When *Phragmites* stands were used by marsh nesting species, edges were selected (Meyer *et al.* 2010; Robichaud and Rooney 2017) and high-water levels appeared to increase suitability of *Phragmites* stands as habitat (Robichaud and Rooney 2017). The dry conditions and dense vegetative structure generally found in *Phragmites* stands may reduce foraging efficiency (Benoit and Askins 1999) and nest site availability (Meyer *et al.* 2010) therein.

Individual area requirements, body size, and mobility play pivotal roles in determining how a species may uniquely perceive and respond to fragmentation (e.g., due to expansion of *Phragmites* or fluctuating water levels) and how that species identifies suitable habitat (Vos *et al.* 2001; Gehring and Swihart 2003). Ecologically-scaled landscape indices (ESLIs) allow one to examine distribution patterns and compare responses of different species to fragmentation within the same landscape (Verboom *et al.* 2001; Vos *et al.* 2001; Gehring and Swihart 2003; Opdam and Wascher 2004; Opdam *et al.* 2008). Compared to traditional landscape metrics, ESLIs explicitly account for ecological processes underlying metapopulation persistence and accurately interpret how landscape structure and the ecological profile of organisms influence metapopulation persistence (Rattis *et al.* 2018; Allen *et al.* 2019).

Herein, we apply an ESLI approach to determine the impacts of *Phragmites* expansion on marsh bird habitat and populations in Great Lakes coastal wetlands over a time period of fluctuating water levels. Rising water levels reduce *Phragmites* cover, therefore our analysis examines the effect of increasing *Phragmites* cover and the subsequent effect of increasing water levels. In particular, the application of a landscape approach and ESLIs to coastal systems remains novel (Torio and Chmura 2015). Both abiotic (Pearson and Dawson 2003; Benton 2009) and biotic (Van der Putten *et al.* 2010; Lewis *et al.* 2017) factors can influence the geographic distribution of a species and its habitat, with effects of invasive species likely observed across local to global scales (Mack *et al.* 2000). Given the ability of *Phragmites* to remain temporally viable in the seedbank and rapidly expand its spatial extent with changing water levels (Wilcox 2012), we predicted that, as an invasive biotic factor, *Phragmites* would be a dominant, broad scale factor shaping wetland habitat. To understand variation in response to these factors, we chose four marsh-obligate bird species (hereafter marsh birds) from three taxonomic orders as focal species: Least Bittern (*Ixobrychus exilis*; Pelicaniformes), Marsh Wren (Passeriformes), Sora (*Porzana carolina*; Gruiformes), and Virginia Rail (*Rallus limicola*; Gruiformes). These species represented the range of area requirements and dispersal abilities for marsh birds in our system. These species rely on the vegetative cover of wetlands to provide adequate foraging, breeding, and nesting habitat and rarely use the landscape matrix surrounding wetlands. Extensive loss of wetland habitat (Dahl and Allord 1996) has been implicated in population declines for these species (Conway *et al.* 1994; Moore *et al.* 2009, Quesnelle *et al.* 2013). However, explicit modelling of how temporal variation in habitat availability and connectivity affects the viability of marsh bird populations is still lacking. This information would help land managers identify particularly vulnerable marsh bird species and determine the required management response to *Phragmites* and/or water level fluctuations. We demonstrate how ESLIs can be used to determine species-specific sensitivities to habitat loss and fragmentation, which is needed for landscape planning and management, and to parse the effects of range expansion by an invasive species as a primary factor influencing carrying capacity, connectivity, and persistence of marsh bird populations.

METHODS

Our study occurred in Saginaw Bay, Michigan on the coast of Lake Huron (Fig. 1). Study sites were characterized by open coastal wetlands and sandy soils, which created ideal habitat for *Phragmites* expansion (Tulbure and Johnston 2010). In 1997, receding water levels in the Great Lakes region resulted in rapid *Phragmites* expansion (Tulbure and Johnston 2010; Wilcox and Nichols 2008; Wilcox 2012). *Phragmites* coverage at plots in Saginaw Bay that were initially studied between 2001 and 2003 increased by a weighted mean factor of 4.9 by 2005 and became established throughout Saginaw Bay in large monocultures by 2010 (Tulbure and Johnston 2010). Between 2002 and 2014, Lakes Huron and Michigan water levels were below average levels (Fig. 2). In 2014-2015, higher than average water levels occurred (NOAA, Great Lakes Environmental Research Laboratory; Fig. 2). Water levels increased 0.47 m in depth in Lakes Huron and Michigan between 2002 (i.e., when water levels were 0.32 m below historic average water levels) and 2015 (i.e., when water levels were 0.15 m above historic average water levels, Smith *et al.* 2016; Fig. 2). Our focal wetlands were a subset of those monitored for the Great Lakes Coastal Wetland Monitoring Program (CWMP; Uzarski *et al.* 2017; Uzarski *et al.* 2019; Hohman *et al.* 2021). The CWMP utilized a stratified random design (by Great Lake and hydrogeomorphic type) to identify which wetlands were monitored, with the condition that each wetland was ≥ 4 ha

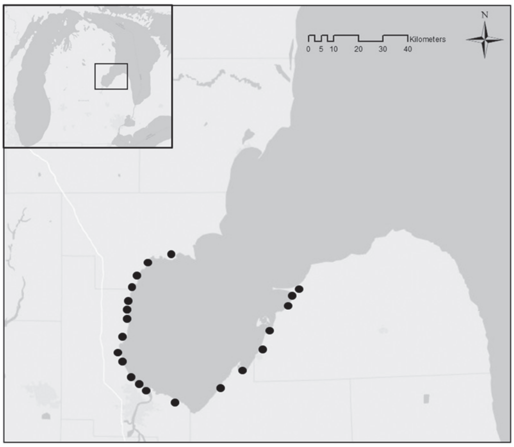

Figure 1. Location of lacustrine wetland sites in Saginaw Bay, Michigan examined during 2002–2015.

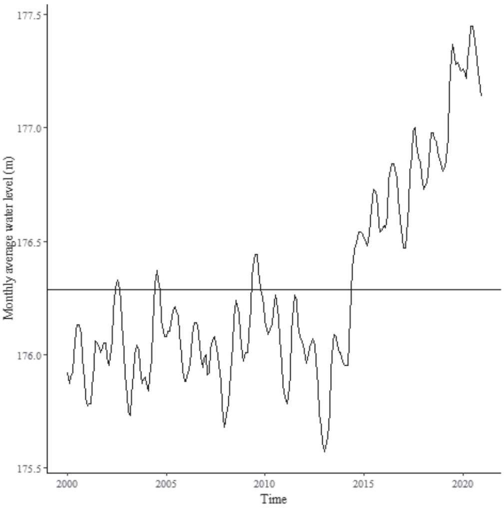

Figure 2. Mean monthly water level (m, IGLD85) for Lake Huron-Michigan from National Oceanic Atmospheric Association's (NOAA) Great Lakes Water Level Dashboard for Jan 2000 to Dec 2020. The horizontal line is the average water level during 2000–2020. NOAA's Great Lakes Water Level Dashboard was accessed on 19 March 2021 at https://www.gleri.noaa.gov/data/dashboard/G:D_HTML5.html

in size and had a surface water connection to a Great Lake. For our study, we randomly selected 21 CWMP lacustrine coastal wetlands along Saginaw Bay's coastline, which spanned 125 km (Fig. 1).

We used ArcMap 10.6 (ESRI, Redlands, California) to create wetland patch polygons based on vegetation characteristics and water extent from 3 time periods: 2002–2004 (pre-*Phragmites* basin-wide expansion), 2008–2010 (*Phragmites* basin-wide expansion), and 2014–2015 (increasing water levels above historic average water levels and decreasing *Phragmites* coverage). Expansion of *Phragmites* among sites in Saginaw Bay had occurred within 2–4 years of low-water levels (Tulbure and Johnston 2010), while distinct plant assemblages, including *Phragmites*, were maintained for 3 years as lake levels rose (Wilcox and Nichols 2008). In our system, increasing water level also was a factor in reducing the extent of *Phragmites* (Wilcox and Nichols 2008) with total *Phragmites* extent across our sample of wetlands declining from 52% in 2008–2010 to 30% in 2014–2015. Thus, our time periods corresponded with biologically-relevant and distinct changes in coastal wetlands in the study area and provided a foundation from which to attribute underlying causes in marsh bird habitat change across time. We identified the area of wetland vegetation suitable as marsh bird habitat (emergent, herbaceous vegetation that was not *Phragmites*) using CASI hyperspectral imagery and LiDAR imagery between 2002–2004 (Becker *et al.* 2007) and PALSAR imagery from 2008–2010 and 2014–2015 (Bourgeau-Chavez *et al.* 2013). Previous studies have shown that the edges of *Phragmites* stands were sometimes used by marsh birds (e.g., Lazaran *et al.* 2013), although the interior of large stands were rarely used (Meyer *et al.* 2010). Also, the interface between open water and wetland vegetation is known to be selected by marsh birds (Rehm and Baldassarre 2007). Thus, our polygons included a 10-m buffer around suitable wetland habitat patches into adjacent *Phragmites* stands and open water to acknowledge use by marsh birds.

Following Vos *et al.* (2001), we calculated ESLIs for each focal marsh bird species to determine average patch carrying capacity (ESLI_K) and average connectivity (ESLI_C) among the 21 wetland sites. We considered birds at these sites to be part of the same metapopulation, and ESLIs provided an assessment to compare wetlands across the study area. We conducted literature reviews for each species to obtain a priori estimates of individual area requirements and mobility rates (Table 1). We calculated ESLI_K for each species as:

$$\sum_{i=1}^{n} \frac{K_{si}}{n},$$

where n was number of patches and K_{si} represented the number of individuals of species s that could occupy patch i at any given time, which was a function of patch area divided by individual area requirement (territory size) of species (Vos *et al.* 2001; Table 1). We calculated ESLI_C for each species as:

$$\sum_{i=1}^{n} \frac{C_{si}}{n},$$

where C_{si} represented the connectivity for species s in patch i, which was a summation of patch area and exponential relationship between a species-specific dispersal ability and distance between patches (Vos *et al.* 2001; Table 1). In this formulation, dispersal ability corresponded to the relative magnitude of movements (i.e., parameterized as α-values; Vos *et al.* 2001), and marsh birds during the nesting season exhibited predominantly local-scale movements within a wetland patch (e.g., Bogner and Baldassare 2002; Table 1). We log-transformed all ESLI values for plots and analysis.

We performed multi-response randomized block procedures (MRBP; Mielke and Berry 2001) in PC-ORD 6.22 (MjM, Glenden Beach, Oregon) to compare the extent of habitat changes for each species across the three time periods. Since the MRBP required a balanced design, we omitted 2 of 21 wetland sites because they lacked the full range of temporal data. With the remaining 19 wetlands, we created blocks based on time period for each wetland and compared ESLI_K and ESLI_C values for each wetland and species across the three time periods. For each time period, we calculated percent change in habitat carrying capacity and connectivity and in Euclidean distance measurements between ESLI outputs for each species to identify if the largest change was associated with *Phragmites* expansion or the reduction of *Phragmites* with increasing water levels.

Table 1. Average home-range size and dispersal distance of focal marsh bird species used to calculate ecologically scaled landscape indices (ESLIs) in Saginaw Bay, Michigan coastal wetlands during 2002–2015. Alpha values are relative dispersal distance coefficients from Vos et al. (2001) and correspond to limited movement patterns these marsh birds exhibit during the nesting season.

Species	Average Home Range (ha)	Dispersal Distance (km)	α_s	Reference
Least Bittern	9.70	1–3	1.67	Bogner and Baldassare (2002); Lor and Malecki (2006)
Marsh Wren	0.15	1–3	1.67	Kale (1965); Leonard and Picman (1987)
Sora	0.21	0.1–1	5	Johnson and Dinsmore (1985); Lor and Malecki (2006)
Virginia Rail	0.20	0.1–1	5	Johnson and Dinsmore (1985); Lor and Malecki (2006)

To determine if our analyses predicted observed trends in marsh bird abundance in Saginaw Bay, we analyzed CWMP data that were collected at the 21 focal wetlands. Data were not available for the pre-*Phragmites* expansion time period, so we were only able to explore the influence of rising water levels and related decreasing extent of *Phragmites* on marsh bird abundance. For 12 of the wetlands, 15 min marsh bird surveys (5 min passive, 5 min of marsh bird playback including all focal species, 5 min passive) were conducted at least at one point during multiple years between 2011 and 2019. Each sample point was visited twice with visits at least 10-15 days apart and surveys were conducted between late May and early July (Tozer *et al.* 2017). Surveys occurred between 0.5 hr before sunrise and 4 hr after sunrise or between 4 hr before sunset and 0.5 hr after sunset (Tozer *et al.* 2017; Uzarski *et al.* 2017). Abundance and detectability for our focal species was not influenced by year (Tozer *et al.* 2017), so we did not include any detectability corrections. For these 12 CWMP sites, we compared the total number of focal species counted during the two survey dates between the first sampling year (2011 to 2014—below average water levels) and the last sampling year (2016 to 2019—water levels higher than our 2014–2015 ESLI dataset and above historic average water levels). We also compared the sums of individuals counted for each species during the two annual survey dates at each site between the first and last year sampled.

RESULTS

We identified 878 wetland patches of suitable marsh bird habitat across the 3 time periods, including 271 patches (31% of total) in 2002–2004, 345 patches (39%) in 2008–2010, and 262 patches (30%) in 2014–2015. Habitat area declined 24% from the beginning to the end of the study period. Namely, there were 3,122 ha of suitable habitat patches in 2002–2004, 1,985 ha in 2008–2010, and 2,367 ha in 2014–2015. Average habitat patch size decreased from 11.52 ha (SE = 1.48) in 2002–2004 to 6.86 ha (SE = 0.71) in 2008–2010 and then increased to 7.58 ha (SE = 0.76) in 2014–2015 (Fig. 3).

For each species, we found that ESLI scores changed between each of the three time periods, reflecting changes in both carrying capacity and patch connectivity in Saginaw Bay coastal wetlands (Table 2; Fig. 4a). For all species, the 2002–2004 period (pre-*Phragmites* basin-wide expansion) exhibited the highest level of connectivity ($ESLI_C$) and greatest carrying capacity ($ESLI_K$) compared to the other periods (Fig. 4b and 4c). Connectivity levels declined, with the largest (i.e., 12–14%) decrease due to *Phragmites* expansion, in each successive period for all species (Table 2; Fig. 4b). Carrying capacity ($ESLI_K$) declined 19–39% for all species with *Phragmites* expansion between 2002–2004 and 2008–2010, then increased 4–10% between 2010 and 2015 as water levels began to rise and *Phragmites* coverage began declining (Table 2; Fig. 4c). Within

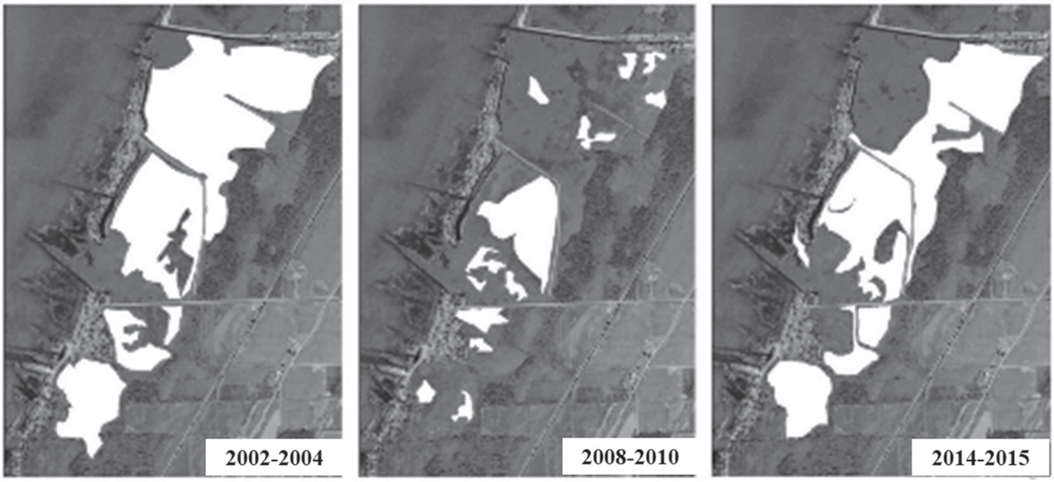

Figure 3. Suitable habitat patches (white polygons) were mapped for Saginaw Bay, Michigan coastal wetlands across 3 time periods: pre-*Phragmites* basin-wide expansion = 2002–2004 (left image); *Phragmites* basin-wide expansion = 2008–2010 (center image); increasing lake levels with subsequent decrease in *Phragmites* cover = 2014–2015 (right image).

Table 2. Multi-response randomized block permutation test results and magnitude of changes in ESLI scores for marsh birds in Saginaw Bay, Michigan coastal wetlands during 2002–2004 (pre-*Phragmites* basin-wide expansion), 2008–2010 (*Phragmites* basin-wide expansion), and 2014–2015 (increasing water levels). $ESLI_C$ is average patch connectivity and $ESLI_K$ is average patch carrying capacity.

Species		T[a]	A[b]	*P*-value[c]	% Change 2002–2010	% Change 2010–2015
Least Bittern	$ESLI_C$	4.14	0.02	0.001	12%	5%
	$ESLI_K$	4.90	0.03	< 0.001	39%	10%
Marsh Wren	$ESLI_C$	4.10	0.02	0.001	12%	5%
	$ESLI_K$	4.82	0.03	< 0.001	19%	4%
Sora	$ESLI_C$	2.79	0.01	0.010	14%	5%
	$ESLI_K$	4.73	0.03	< 0.001	21%	4%
Virginia Rail	$ESLI_C$	2.79	0.01	0.010	14%	5%
	$ESLI_K$	4.82	0.03	< 0.001	21%	4%

[a] MRBP test statistic indicating the separation between groups (i.e., time periods)
[b] chance-corrected within-group agreement compared to random expectation
[c] $P < 0.05$ indicated ESLI scores were different among time periods

and among years, Marsh Wrens always had the largest carrying capacity, whereas Least Bitterns had the smallest (Fig. 4c). Marsh Wrens and Least Bitterns had identical connectivity values (Fig. 4b). Soras and Virginia Rails always had connectivity values lower than the other two species within years and had identical connectivity values (Fig. 4b). Virginia Rails and Soras also had virtually identical carrying capacity values (always within 0.02 units) each period. For all species, we found a 3.5-fold change in ESLI scores with *Phragmites* expansion into the system compared with a 1.2-fold change in ESLI scores with rising water levels and *Phragmites* decline (Fig. 4a).

Of the 12 CWMP sites sampled in Saginaw Bay, focal species richness increased at six sites (50%), decreased at two sites (17%), and remained unchanged at four sites (33%) between 2011 and 2019. Sora and Virginia Rail counts increased between the first and last year sampled at two sites (17%) and remained the same for 10 sites (83%), with nine sites that remained the same having no Soras detected either year and 10 sites having no Virginia Rails detected either year. Marsh Wren counts increased at nine sites (75%) between 2011 and 2019, decreased at two sites (17%), and remained the same at one site (8%). Marsh Wrens occurred at all sites. Least Bitterns decreased at one site (8%) and remained absent at 11 sites (92%).

DISCUSSION

When water levels are low, *Phragmites* colonizes wetlands quickly and can replace resident wetland vegetation with expansive monocultures (Trebitz and Taylor 2007; Tulbure and Johnston 2010; Judd and Francoeur 2019). High water levels can reduce *Phragmites* coverage and have been associated with high relative abundance of many wetland species (Timmermans *et al.* 2008; Gnass Giese *et al.* 2018), but may result in a degree of inundation and coastal squeeze (Torio and Chmura 2015) that marsh birds cannot tolerate. Accordingly, during time periods which experienced increasing *Phragmites* coverage followed by rising water levels, we found that marsh bird habitat available in Saginaw Bay coastal wetlands was fragmented. However, *Phragmites* expansion most severely reduced the amount and connectivity of wetland habitat. Rising water levels, which were associated with reduced *Phragmites* cover, resulted in further slight reductions in wetland connectivity and slight increases in amount of wetland habitat. Wetland average carrying capacity actually increased with rising water levels, presumably due to a successional setback of *Phragmites.* Although they did not address fluctuating water levels, Daehler and Strong (1996) and Gan *et al.* (2009) also found that non-native invasive plant expansion (i.e., *Spartina* spp.) reduced available habitat and waterbird abundance in

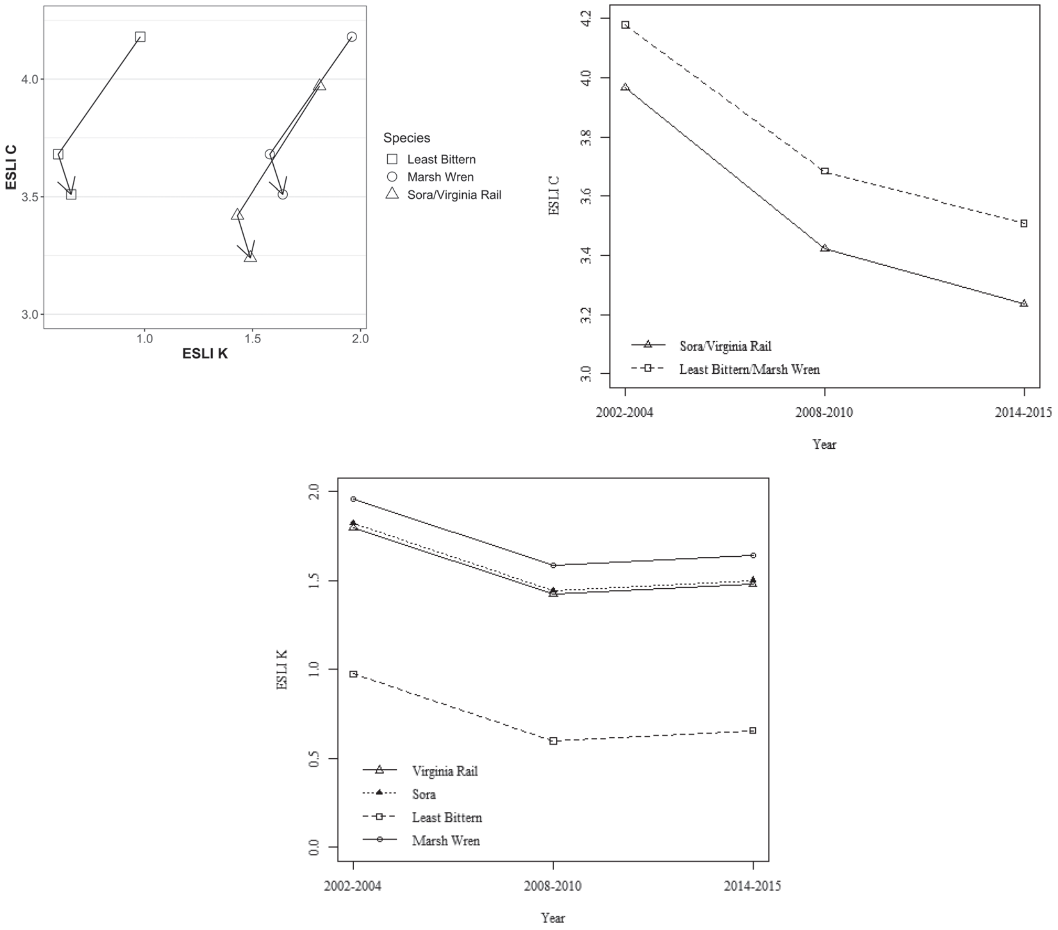

Figure 4. Carrying capacity (ESLI$_K$) and patch connectivity (ESLI$_C$) values plotted for marsh birds during three time periods: pre-*Phragmites* basin-wide expansion = 2002–2004; *Phragmites* basin-wide expansion = 2008–2010; increasing lake levels with subsequent decrease in *Phragmites* cover = 2014–2015 for coastal wetlands in Saginaw Bay, Michigan. ESLI$_C$ vs. ESLI$_K$ plot (A) with ESLI coordinate points for each species connected with an arrow that follows the sequential changes across the three time periods, with the arrow beginning in 2002–2004 and ending in 2014–2015. ESLI$_C$ vs. year plot (B) demonstrating change in landscape connectivity over the three time periods. ESLI$_K$ vs. year plot (C) demonstrating change in landscape carrying capacity over the three time periods. Note that Sora and Virginia Rail are represented by the same symbols in ESLI$_C$ plots given their identical values.

estuarine wetlands. Water levels during our study periods were below or slightly above the average water level since 2000 (Fig. 2). There is likely a high-water threshold beyond which marsh bird habitat may be negatively impacted.

Different ecological profiles among species, and therefore differences in population responses to habitat changes, should be considered prior to implementing management actions (Zacchei *et al.* 2011). Smaller habitat patches result in lower densities, lower breeding success, and higher probabilities of extinction for marsh birds (Brown and Dinsmore 1986; Winter and Faaborg 1999). A combination of a reduction in habitat area and reduced connectivity of habitat patches (Fig. 4a) likely negatively affects populations of our focal species at a regional scale. Though ESLI$_C$ and ESLI$_K$ values followed similar trajectories for each species through time (Fig. 4b, 4c), Least Bitterns appeared most vulnerable due to the lower carrying capacity within the landscape (Fig. 4c), which is supported by population viability analysis we conducted and presented elsewhere (Dinehart 2019). This is consistent with Verboom *et al.* (2001) who found that larger heron-sized marsh birds, defined as a 'bittern group' in their study, needed substantially larger networks of habitat patches for sustaining populations. ESLIs can help managers identify how species differ with respect to patch connectivity and/or carrying capacity in the landscape (Vos *et al.* 2001). As such, decisions about which species most need management action can be better informed.

Field data from Saginaw Bay suggested that between the initial site surveys conducted during 2011–2014 (i.e., when we analyzed habitat availability) and site surveys conducted during 2016–2019 (i.e., when we didn't analyze habitat availability but water levels increased further) most sites experienced increased or static focal species richness. Our site survey results partially agreed with ESLI projections during 2002–2015, especially ESLIs linked to carrying capacity (Fig. 4c). For example, Marsh Wrens appeared to increase across study sites, while Least Bitterns appeared to decline across sites. Tozer and Mackenzie (2019) found that marsh bird species richness and abundance increased following control of *Phragmites* in wetlands. Timmermans *et al.* (2008) found that relative abundance of Least Bitterns, Marsh Wrens, Soras, and Virginia Rails correlated positively with changing water levels. We found increasing water levels (NOAA, Great Lakes Environmental Research Laboratory; Fig. 2) which occurred between the initial site survey dates and the last site surveys dates tended to benefit Marsh Wrens, and may benefit other focal marsh bird species if *Phragmites* cover is further reduced with rising water levels (Timmermans *et al.* 2008). Hohman *et al.* (2021) found increases in water extent and interspersion in Great Lakes coastal wetlands during 2013-2018 which corresponded with increased marsh-obligate bird richness and increased abundance of Least Bitterns, Marsh Wrens, Soras, and Virginia Rails and other marsh-obligate birds. Marsh Wrens were detected at all sites, which is consistent with ESLIs suggesting carrying capacity and connectivity was highest for Marsh Wrens in this landscape. Least Bitterns were rare across all sites and detected at only one of 12 sites. Although we didn't have pre-*Phragmites* abundance data for Least Bitterns, loss of habitat due *Phragmites* expansion may have contributed to their current rarity in our system since this species may be particularly vulnerable to *Phragmites* expansion (Robichaud and Rooney 2017). Other than American Coots (*Fulica americana*), Least Bitterns were the least abundant marsh bird detected throughout coastal wetlands in the Great Lakes basin (Tozer *et al.* 2017). Discrepancies between our ESLI predictions and surveys may be due to individuals still settling into their summer breeding territories during our initial surveys each year (Hansen 2019; Kane *et al.* 2019).

If the focal marsh bird species use *Phragmites* stands more extensively than we modelled (i.e., >10 m into stands), then we likely underestimated carrying capacity in the landscape, although our conclusion about the relative importance of the influence of *Phragmites* expansion would remain unchanged. In our system, *Phragmites* extent was confounded by water level (Wilcox and Nichols 2008), thus application of ESLIs in a system with stable water levels would aid in further parsing out the importance of biotic vs. abiotic factors in shaping avian communities (Godsoe *et al.* 2017; Daniel and Rooney 2021). The use of an ESLI approach could also be incorporated into study designs that explore the influences of surrounding land use (Panci *et al.* 2017) and conspecific and heterospecific attraction with changing population abundances (Field and Gehring 2015) since these factors may be important to focal species. Our estimates of dispersal capabilities might be low, despite being based on available literature, however, the use of dispersal coefficients makes the ESLI approach robust (Vos *et al.* 2001), and our novel application of the ESLI approach remains an important extension of its utility. Due to the heterogeneity of marsh habitat availability among years, it is likely that marsh birds are able to find suitable habitat away from locations where they have bred in the past and may shift to use inland sites if coastal areas become unsuitable (Hohman *et al.* 2021). Applying ESLIs to inland sites would be beneficial in long-term management of these local population shifts since amount and connectivity of habitat would be universally important.

Our demonstrated use of ESLIs in a dynamic system could serve as a model for identifying conservation needs and isolating key factors driving fragmentation of habitat in a variety of ecological systems. The results of our study may prove especially useful to managers of marsh birds at locations experiencing *Phragmites* or other non-native plant species expansion and/or water level fluctuation. Particularly within local wetlands and wetland landscapes which feature Least Bitterns and other species that have large area requirements, keeping *Phragmites* from expanding should be a management priority. Despite continued rising water levels in the Great Lakes since 2014, the effective displacement of *Phragmites* is temporary (Davis *et al.* 2000; Wilcox 2012). Furthermore, water level averages are projected to decline in the future due to climate change (Gronewold *et al.* 2013), and the projected decline may promote further expansion of *Phragmites* and necessitate management activities to reduce its spread (Wilcox 2012; Carlson Mazur *et al.* 2014). Management action could be targeted based on results of ESLIs that identify and prioritize which species most urgently require conservation efforts (Opdam and Wascher 2004), perhaps identifying thresholds of *Phragmites* removal required for different species, and aid in refining strategies for promoting wetland integrity and wetland bird communities (Zou *et al.* 2016; Grand *et al.* 2020).

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