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Diversity of herpetofauna at restored cranberry bogs: A comparative survey of herpetofaunal diversity at a restored wetland in comparison to a retired cranberry bog to assess the restoration success

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Wetlands perform critical ecological functions and provide wildlife habitats. Yet, wetland degradation continues at a global scale. In Massachusetts, USA, wetland restoration has reached remarkable heights, partly promoted by the retirement of cranberry bogs. In this study, to assess the effectiveness of cranberry-farm restoration for conservation of native herpetofauna, we surveyed both retired and restored cranberry bogs in south-eastern Massachusetts. Using both visual encounter surveys and baited aquatic traps, we documented herpetofaunal species and their relative abundance. Both survey methods combined, the cumulative herpetofaunal species richness at the restored bogs (16) exceeded that of the retired bogs (11). Our trap surveys indicated that the amphibian species richness at the retired bog was significantly greater than that of the restored bog. In contrast, reptilian species richness as well as the relative abundance of both amphibians and reptiles were significantly greater at the restored bog compared to the retired bog. Subsequent analyses we performed identified that greater habitat heterogeneity emerging from active restoration intervention was the underlying driver of elevated richness and abundance. Most frequently encountered herpetofauna at the restored versus retired bogs were habitat generalists with broader geographic ranges and are not of conservation concern. Our findings suggest that the restored bog we monitored is still in the early-recovery phase after active intervention. We urge the need for long-term herpetofaunal inventories via systematic, standard surveys to assess restoration success.

Keywords: restoration, wetlands, herpetofauna, conservation, community, cranberry bogs

INTRODUCTION

Wetlands are among the world's most productive ecosystems and sustain a myriad of ecosystem functions (Gibbs, 2000; Dudgeon et al., 2006). Despite limited global spatial extent (~6 % of the Earth's land area), wetlands are disproportionately high in biodiversity, hence considered keystone ecosystems (Reis et al., 2017; Gardner & Finlayson, 2018; Figel et al., 2019). Wetlands support a multitude of life-history needs of native fauna and flora. For example, as many as 9.5 % of animal species, including one-third of all vertebrate species, depend on wetlands for at least part of their life cycles (Balian et al., 2007). Despite the multifaceted ecological values, wetlands are among the most threatened habitats (Gibbs, 2000; Dudgeon et al., 2006; Keddy et al., 2009). In the US, draining and filling of wetlands has occurred since the 17th century (Dahl, 1990; Dahl et al., 1991; Gardner & Finlayson, 2018).

Given high conservation potential and functional attributes (stormwater retention, nutrient assimilation, groundwater recharge, and carbon sequestration), wetlands are crucial for global environmental sustainability and resilience (Zedler, 2000; Zedler & Kercher, 2005; Keddy et al., 2009). Therefore, wetland restoration is essential to preserve both wetland biodiversity and ecosystem functions. New sustainability policies and advancements in conservation research have led to commendable efforts in wetland restoration (Postel & Thompson Jr, 2005; Hoekstra et al., 2020). Ecological restoration is a process that recreates, initiates, assists, or accelerates the recovery of a degraded, damaged, or modified ecosystem with respect to environmental health, structural and functional integrity, and ecological sustainability (Ehrenfeld, 2000; Zedler, 2000). The restored state can either resemble the historic community structure and ecosystem processes or an alternative stable state (Suding et al., 2004; Martin, 2017).

While wetland restoration is widely practiced, post-restoration biological monitoring is either largely neglected or limited to opportunistic inventories. Post-restoration appraisals enable critical, comparative evaluation of restoration techniques (Downs & Kondolf,

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2002; Skinner et al., 2008), guide future management decisions, and help reduce uncertainties in contemporary applications (Michener, 1997; Skinner et al., 2008; Loflen et al., 2016). Monitoring is required to track progress along the recovery trajectory, implement corrective actions, and provide feedback on ecosystem state and restoration interventions, thereby inform future actions (Choi, 2004; Klemas, 2013). Although plant communities have been the overwhelming foci in wetland monitoring (Matthews & Spyreas, 2010), floristic diversity alone cannot be considered a universal biodiversity surrogate; thus faunal surveys may provide complementary insights for post-restoration assessments (Lewandowski et al., 2010). Herpetofauna are recognised for their heightened sensitivity to overall environmental quality, and therefore are widely regarded as an indicator of habitat status (Hager, 1998; Welsh Jr & Droege, 2001; Waddle, 2006; Welsh Jr & Hodgson, 2008). Given their shorter generation cycles compared to other tetrapods, herpetofauna can elicit rapid ecological responses to restoration. Many amphibians and reptiles exhibit both ontogenetic and seasonal shifts in habitat associations, thus their community composition can reflect emergent properties of the overall restored wetland complex (Gibbons et al., 2000; Davic & Welsh, 2004). Additionally, in North America, herpetofauna account for a substantial biomass across a wide array of wetlands (Russell et al., 2002a; Russell et al., 2002b; Balcombe et al., 2005). These attributes make monitoring herpetofauna a prudent approach to monitor biological outcomes of wetland restoration.

In this study, we conducted a comparative survey on herpetofauna across two wetland habitat types in south-eastern Massachusetts: an unrestored, retired cranberry bog (hereafter, referred to as the “retired bog”) and a former cranberry bog recently restored into a freshwater wetland complex (hereafter, referred to as the “restored bog”). The specific objectives of our study were to (1) compare species richness, (2) overall abundance, and (3) community structure of herpetofauna between retired and restored wetland systems. Our study will elucidate how restoration of retired cranberry bogs into self-sustaining wetlands aid biodiversity conservation.

Study area

Located in south-eastern Massachusetts (Fig. 1) of the North-eastern Coastal ecoregion, our study area abuts Cape Code Pine Barrens, Narragansett and Bristol Lowlands, and southern New England Coastal Plains and Hills. The specific sites we surveyed included (1) Tidmarsh Wildlife Sanctuary, a recently restored (2016) 481-acre freshwater wetland complex (TWS), managed by Mass Audubon, and (2) Foothills Preserve (FP), a 42-acre retired cranberry bog complex, located north-west of TWS and owned by the Town of Plymouth. Both sites were former commercial-scale cranberry farms that operated in unison for over a century. Both TWS and FP are similar in land-use histories, geographical context, and elevation and are in proximity to each other, hence any biological differences are attributable to restoration. Nearly 200 acres of TWS were restored into a mosaic of wetland, aquatic, and upland habitat types (Ballantine et al., 2020). This included: dam removal and partially or completely plugging irrigation canals while reconstructing the meandering lotic systems to reconnect stream channels with floodplains (Norriss, 2018). Introduction of large dead wood and reformation of riffle-pool mesohabitat sequences restored the structural diversity of stream habitats. Additionally, to enhance spatial heterogeneity across the floodplain, a pit-and-mound microtopography was formed throughout the former bogs. Creation of open-water lentic systems also enhanced the habitat diversity across the wetland complex whereas introduction of native trees and shrubs (Atlantic white cedar in particular) assisted in accelerating wetland recovery. The entire restoration process was a collaborative venture between Massachusetts Division of Ecological Restoration, Tidmarsh Living Observatory (a network of academic research institutes), and Mass Audubon. In contrast, FP is neither actively restored nor has been managed as a commercially productive bog since 2010 (by the conclusion of fieldwork); thus, it has underdone secondary succession in the absence of major extrinsic disturbances. As such, the retention ponds, dams, irrigation channels, perimeter ditches, channelised stream flow, and sand layers remained still intact, thus, FP is heavily influenced by farming legacies. In contrast to TWS, no microtopographic complexity exists at FP. TWS contains greater habitat diversity than FP, which is attributable to the restoration process since the pre-restoration habitat stricture at TWS and FP were the same.

METHODS

We conducted our survey from mid-May 2019 to mid-November 2019 and used two standard techniques to adequately survey all habitat types at both TWS and FP, including open waters, wetlands, and uplands: (1) deployment and overnight recovery of non-lethal standard, baited aquatic traps and (2) visual encounter surveys (VES). These techniques have been successfully employed in similar habitats for the same focal taxa elsewhere (Adams et al., 1997; Fellers, 1997; O'Donnell et al., 2007; da Silva, 2010). We conducted sampling between May and August with three consecutive trap nights per week. Our sampling period corresponded with the increased activity of herpetofauna during the growing season. In each trap, we recorded the species, sex (for sexually dimorphic species), age class (adult or juvenile/ larvae), and relative abundance of each species. After proper identification, we released all captured animals back to the capture site. In successive deployments, we replaced the bait.

Trap types we used included: (1) funnel traps, (2) minnow traps (large and small Promar Collapsible Traps, Cabela’s LLC), and crab traps (Memphis Nets & Twine Co, Inc) placed in shallow water environments, and (3) hoop traps (Memphis Nets & Twine Co, Inc) suspended with stakes and floats, and placed in deeper and open-water habitats of ponds. Upon deployment, we ensured that at least a third of the trap height was above water. Funnel,

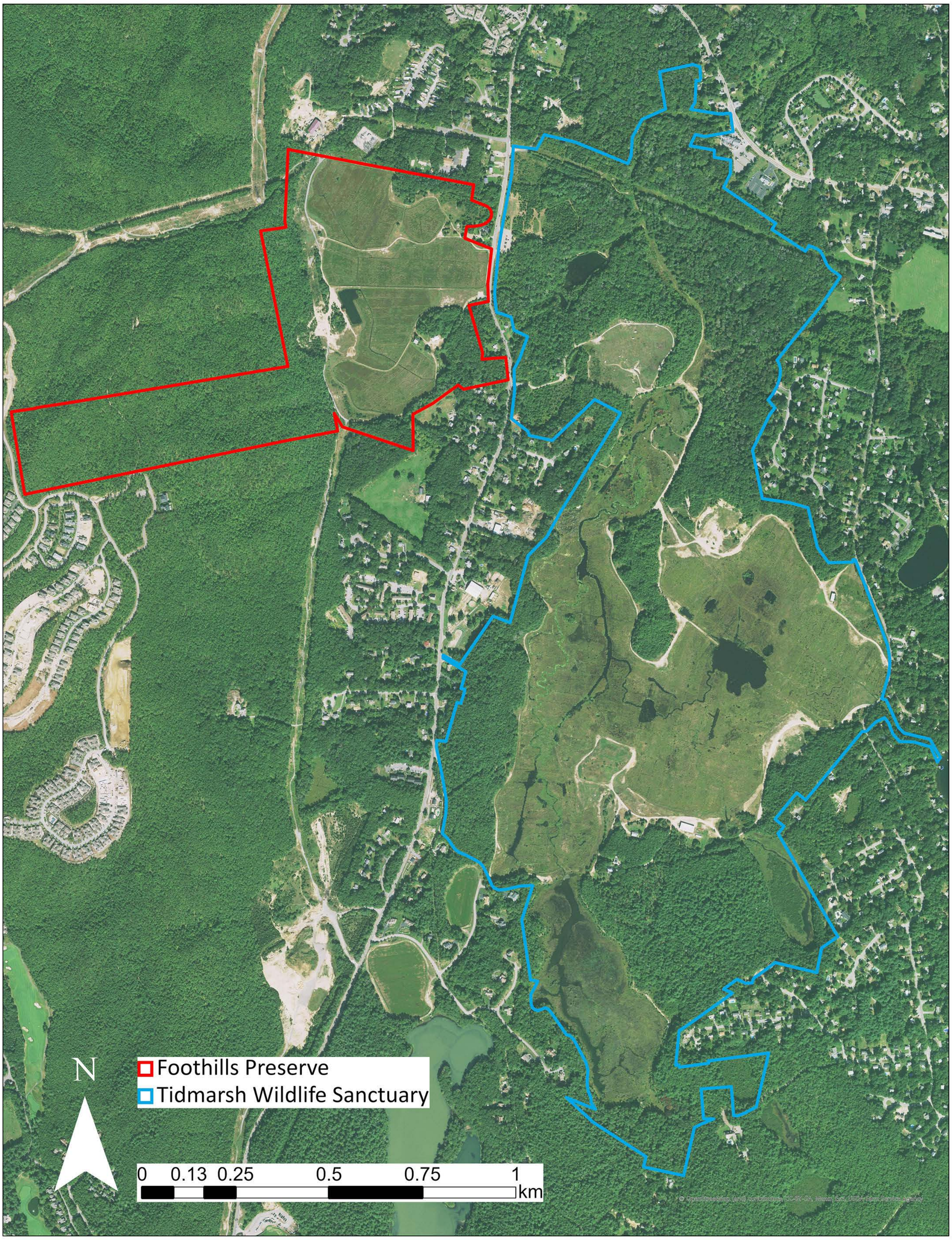

Figure 1. Study sites: Mass Audubon Tidmarsh Wildlife Sanctuary (TWS), a 481-acre restored wetland complex (Blue), and Foothills Preserve (FP), a 42-acre unrestored, retired cranberry bog (Red). Both are located in Plymouth, Massachusetts. Data sources: ESRI World Imagery, ESRI World Street Map.

hoop, and crab traps were baited interchangeably with either oil-immersed sardines or wet cat food whereas minnow traps were baited with dry, beef-based dog food. Use of these trapping methods and baits have been successful in similar research (Adams et al., 1997; Willson & Dorcas, 2004).

Between the restored and retired sites, the number of traps deployed varied as a function of availability of habitat types (Fig. 2), spatial extents, and spatial arrangement. The retired cranberry bog only had two

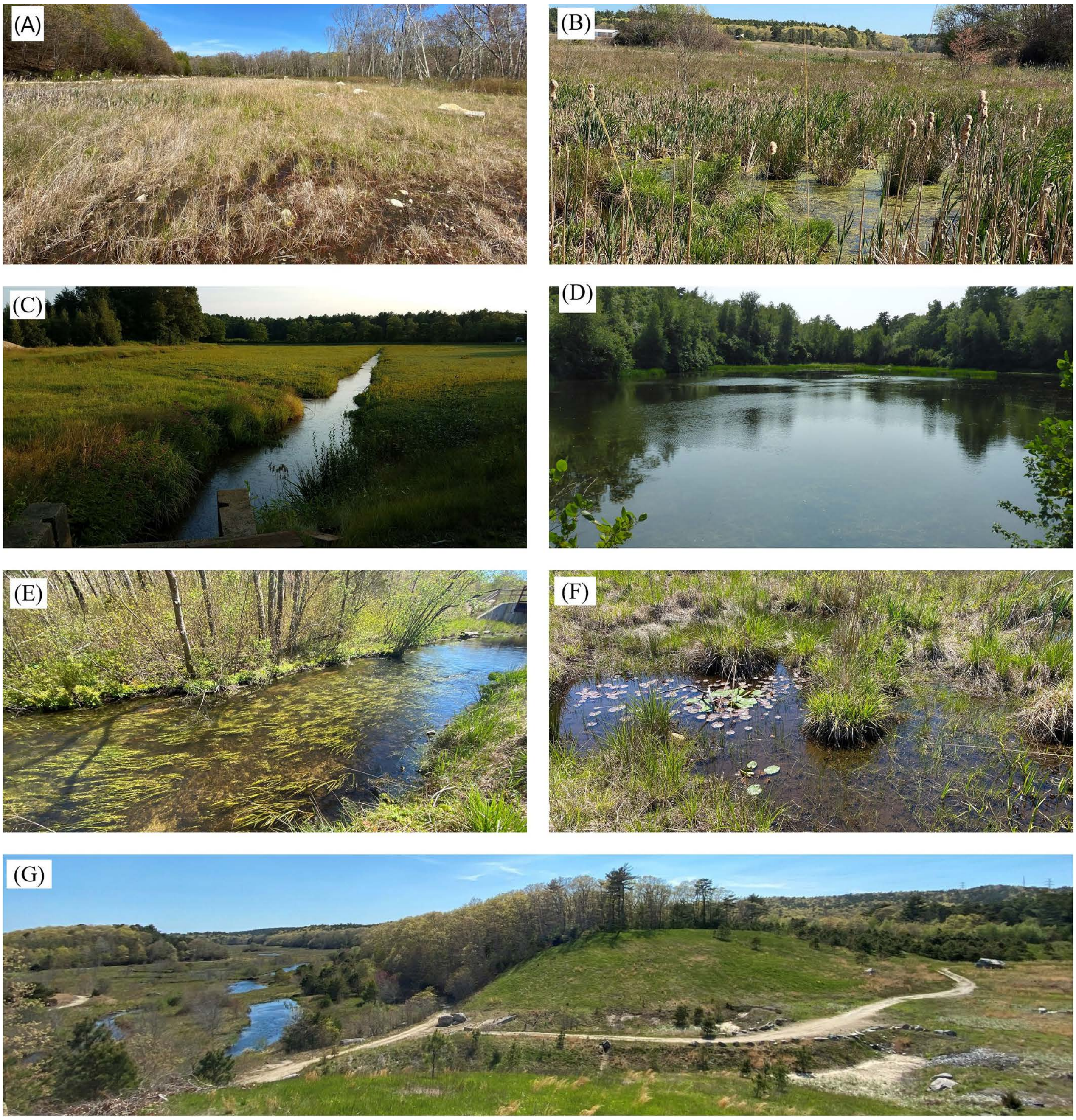

Figure 2. (A-G): Images of the restored bog and unrestored habitat types at the retired cranberry bog: **(A)** floodplain, **(B)** mesic prairie, **(C)** irrigation canal, **(D)** holding pond, **(E)** stream channel, **(F)** ephemeral pool, and **(G)** xeric uplands. All A-G are restored locations. Only C-D are the unrestored habitats.

habitat types that summed to eight distinct trapping sites: irrigation canals (both perimeter and lateral ditches) as lotic systems and holding (retention) ponds as lentic systems. We deployed 2-3 funnel traps and one minnow trap at each retention pond and 1-2 funnel traps per irrigation canal. The restored bog had three different habitat types: freshwater marshes (floodplains, mesic prairies, wet meadows), dugout open-water ponds (lentic systems), and reengineered, meandering streams (lotic systems). We deployed 2-3 funnel (when water levels are high) or 1-2 crab traps (when water levels are lower) within freshwater marshlands. We deployed 3-5 traps per dugout pond, which included 3-4 funnel traps, 2-3 minnow traps, and one hoop trap. At stream habitats, we deployed 2-3 funnel traps. We set traps at a total of 32 sites within the restored bog.

In addition to aquatic trapping, we conducted weekly VES to bolster detection of aquatic herpetofauna in upland habitats and to document semi-aquatic or terrestrial species. During VES, we actively searched throughout upland habitats and dip-netted in areas with standing water while visually scanning for surface-active individuals, and captured animals either manually or by nets. We recorded species identity, sex (if sexually dimorphic), and life-history stage (adult, juvenile/larvae) for all herpetofauna found during VES. If egg masses were found, we also attempted to identify them to the finest taxonomic resolution. The VES varied in person hours and area covered (45-120 mins with 2-6 people) across different habitats. The VES were non-systematic, therefore, only used to document species presence.

Since the response variables (relative abundance and species richness) did not fit into a Gaussian distribution, had high levels of heteroscedasticity, and our sampling efforts being unevenly distributed between restored versus retired bogs, we opted for non-parametric tests in our statistical analyses. To account for dissimilar trapping efforts among different sampling locations, we calculated the catch per unit effort as number of individuals or species captured per trap night per deployment site to standardise trap data across different habitat types.

$$\textbf{Species richness} = \frac{\textbf{Total number of species captured per trapping site per night}}{\textbf{Number of traps deployed at the site}}$$

$$\textbf{Relative abundance} = \frac{\textbf{Total number of individuals captured for a given species per trapping site per night}}{\textbf{Number of traps deployed at the site}}$$

To account for seasonality and temporal effects of captures, we used the sampling month as covariates. To examine significant differences between the restored and retired sites for herpetofaunal species richness and total abundance, we ran an approximative Wilcoxon-Mann-Whitney (WMW) test where the species richness or relative abundance were considered as the response variables and binary restoration status (actively restored or retired with no active restoration efforts) as the predictor variable. To account for temporal effects, we blocked for the sampling month and ran the same test without blocks.

We ran Permutational Analyses of Univariate Variance (PermANOVA) for modeling species richness and abundance of reptiles, amphibians, and total herpetofauna from trap data (Freeman-Lane algorithm with 5,000 permutations). We also ran Permutational Multivariate Analyses of Variance (PerMANOVA) for modeling overall community structure of herpetofauna from trap data considering the sampling month as a covariate. To determine the environmental drivers of aquatic herpetofaunal community, we first calculated the Bray-Curtis matrix for the herpetofaunal community and considered the distance matrix as the response variable with Euclidified squareroot transformed dissimilarities. We treated sampling month, and restoration status as main effects, habitat type as a nested variable of restoration status and the specific site where the traps were deployed as a nested variable of habitat type. In addition, we included interactions between restoration status × month, habitat type × month, and trapping site × month. For unordered categorical predictor variables, sum contrasts were set-up where coefficients for each categorical variable were constrained to add up to zero while polynomial contrasts were set for ordered categorical predictors (such as sampling months). We used R statistical programme and RStudio Intergraded Development Environment for all statistical analyses (RStudio Team, 2020; R Core Team, 2021).

RESULTS

Combing both VES and trap surveys, we recorded a total 10 and eight amphibian species and four and six reptile species at the restored and retired bogs, respectively (Table 1). Among amphibians, all but spotted salamanders (*Ambystoma maculatum*) and northern leopard frogs (*Lithobates pipiens*) were documented as adults. The spotted salamander was documented based on a single cluster of egg masses found during our VES while the northern leopard frog was found as larvae during our trap surveys; both in marsh habitats of the restored bog. The rest of the anurans were documented as both larvae and adults (Table 1). For both the restored and retired bogs, American bullfrogs (*Lithobates catesbeianus*) and green frogs (*Lithobates clamitans*) were the most abundant amphibian, while Eastern painted turtles (*Chrysemys picta*) were the most abundant reptile. We only found a single non-native species, the red eared slider (*Trachemys scripta elegans*), an encounter limited to a single trap capture at an open-water lentic system at TWS (Table 1).

Herpetofaunal species richness and abundance between the restored versus retired bog

Based on trap surveys, amphibian species richness was significantly less at the restored bog than in the retired bog (WMW test: $z = -4.36$, $p < 0.0001$) even after controlling for the temporal effects (WMW test: $z = -3.99$, $p < 0.0001$) (Fig. 3). In contrast, reptile species richness was significantly greater in the restored bog than in the retired bog (WMW test: $z = 3.54$, $p = 0.0001$), even when accounted for temporal effects (WMW test: $z = 3.63$, $p = 0.0001$) (Fig. 3). Likewise, overall herpetofaunal species richness from trap surveys was significantly greater in the restored bog than in the retired bog (WMW test: $z = -2.76$, $p = 0.003$), even when controlled for the temporal effects (WMW test: $Z = -2.60$, $P = 0.0057$) (Fig. 3). Overall abundance of both amphibians (WMW test: $z = -6.96$, $p < 0.0001$) and reptiles (WMW test: $z = -3.36$, $p < 0.0003$) as well as for all herpetofauna combined (WMW test: $z = -6.35$, $p < 0.0001$) was significantly lower for the retried cranberry bog than the restored bog. These inferences remained unaffected even when controlled for temporal variability (amphibians: $z = -6.98$, $p < 0.0001$; reptiles: $Z = -3.65$, $p = 0.0002$; herpetofauna: $z = -6.42$, $p < 0.0001$).

Drivers of herpetofaunal richness and abundance

Habitat type, specific trapping site, and the interaction terms between habitat type × month as well as trapping site × month were the significant drivers of amphibian species richness (PermANOVA, Table 2). The trapping site × month interaction was the only significant driver for amphibian abundance. Among significant predictor variables, trapping site × month interaction had the strongest influence on amphibian species richness. Neither amphibian richness nor abundance varied significantly as a function of time alone, yet, space × time interaction appeared significant in driving amphibian diversity metrics. Similarly, the restoration status alone (i.e., whether a restored or a retired bog) had no influence on amphibian richness or abundance. Rather, specific

Table 1. The presence or absence of all documented amphibian and reptile species in restored wetlands and retired cranberry bogs as well as different habitat types nested therein. Presence or absence was determined using both trapping and Visual Encounter Survey (VES) data combined. Restored vs retired column indicates where each species was found: restored wetlands only (RS), retired cranberry bogs only (RT); or both (B). Life-history stage column states what life-history stages were found for each species: adult (A), juvenile (J), larval (L), or egg-masses (E).

Scientific Name	Vernacular name	Restored vs retired	Freshwater marshes & floodplains	Irrigation canal	Lentic system	Lotic system	Ephemeral pools	Xeric upland	Life- history stage
Ambystoma maculatum	Spotted salamander	RS			x		x		E
Anaxyrus americanus	American toad	B	x	x	x	x	x	x	A, J
Anaxyrus fowleri	Fowler's toad	B	x	x	x		x	x	A, L
Dryophytes versicolor	Gray treefrog	B	x	x	x				A, L
Lithobates catesbeianus	American bullfrog	B	x	x	x	x			A, L
Lithobates clamitans	Green frog	B	x	x	x	x	x		A, L
Lithobates palustris	Pickerel frog	B	x	x	x				A, L
Lithobates pipiens	Northern leopard frog	RS			x	x			L
Lithobates sylvaticus	Wood frog	B	x			x			A
Pseudacris crucifer	Spring peeper	B			x				A, L
Reptiles									
Chelydra serpentina	Common snapping turtle	B	x	x	x	x		x	A, J
Chrysemys picta	Eastern painted turtle	B	x	x	x	x		x	A, J
Sternotherus odoratus	Eastern musk turtle	RS			x	x			A, J
Storeria occipitomacu-lata	Northern red-bellied snake	RT		x					A, J
Thamnophis sirtalis	Common garter snake	B	x						A, J
Thamnophis sauritus	Eastern ribbon snake	RS	x			x			A, J
Trachemys scripta elegans	Red-eared Slider	RS			X				A

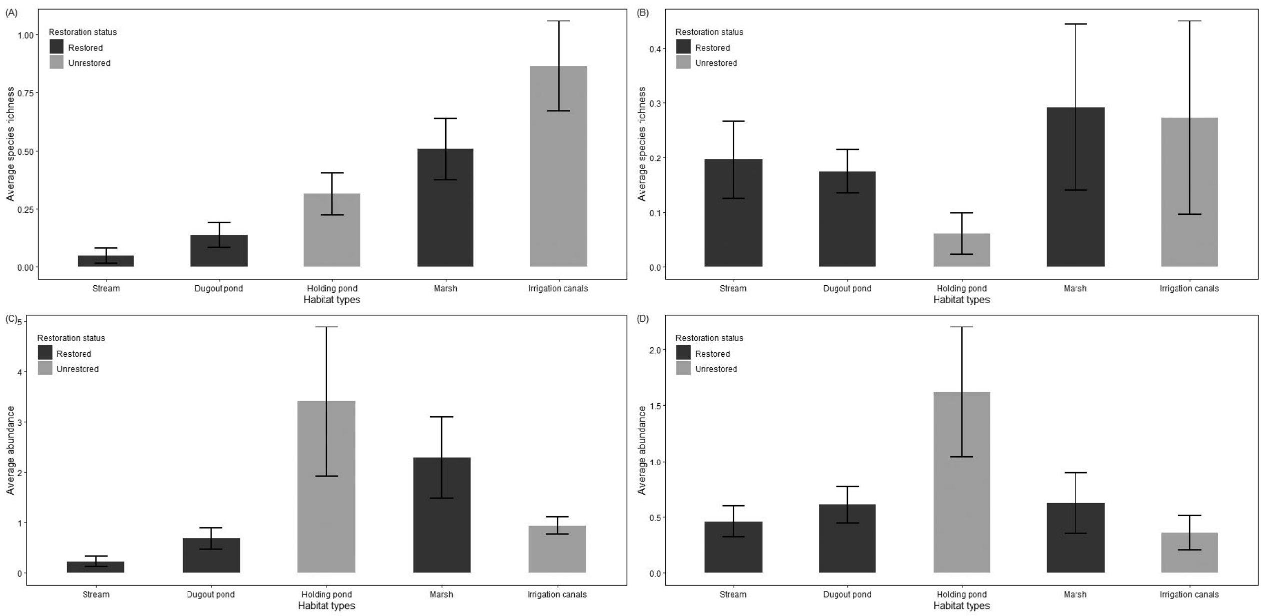

Figure 3. Diversity metrics of herpetofauna from surveys at the restored bog (Mass Audubon's Tidmarsh Wildlife Sanctuary, TWS) and the retired bog (Foothills Preserve, FP). Species richness of amphibians **(A)** and reptiles **(B)** and total abundance of amphibians **(C)** and reptiles **(D)**.

Table 2. (A-F): Results of the Permutational Analyses of Variance (PermANOVA) for modeling species richness and total abundance of both amphibians (A, B) and reptiles (C, D). Species richness and total abundance were included as response variables. Main effects are trap type, restoration status (restored or unrestored), and date of sampling. Habitat type nested within restoration status and trap location nested within habitat type are also included as predictor variables. Interactions include habitat type × sampling month and trap location × month. 0<'***'> 0.001 <'**'> 0.01 <'*'>0.05

Predictor variable	Amphibians						Reptiles					
	(A) Species richness			(B) Abundance			(C) Species richness			(D) Abundance		
	SS	F	p	SS	F	p	SS	F	p	SS	F	p
Trap type	0.43	0.781	0.496	77.902	0.739	0.442	0.537	2.544	0.058	31.456	3.993	0.025*
Restoration status: restored wetlands or retried bogs	0.013	0.072	0.281	53.976	1.536	0.441	0.066	0.932	0.744	0.764	0.290	0.164
Month of survey	0.004	0.019	0.889	9.074	0.258	0.611	0.539	7.667	0.006**	0.070	0.027	0.873
Habitat type	1.539	1.383	0.025*	186.352	0.884	0.165	0.281	0.667	0.604	2.979	0.189	0.102
Trapping site	8.027	0.676	0.001**	1650.651	0.734	0.123	1.494	0.332	0.028*	101.293	0.603	0.214
Habitat type × month	5.491	1.480	0.029*	369.213	0.525	0.136	1.762	1.252	0.824	72.978	1.390	0.209
Trapping site × month	13.564	0.914	0.023*	2672.976	0.950	0.038*	6.835	1.215	0.000***	455.067	2.166	0.021*

Table 3. Permutational Multivariate Analysis of Variance (PerMANOVA) of the overall community structure of herpetofauna from trap surveys. The Bray-Curtis distance matrix was used as the multivariate response variable, restoration status (retired bog or restored wetland), habitat types, trap type, and the interactions between the above main effects were used as predictors while the date of the surveys as a covariate to correct for the temporal effects. Significant codes: 0< '***' >0.001 <'**'> 0.01 <'*'>0.05

	Herpetofauna Community Structure				
	SS	MS	F	R^2	Pr(>F)
Restoration status: restored wetlands or retried bogs	0.1981	0.198085	20.5315	0.0342	0.001***
Date of survey	0.0933	0.018659	1.934	0.01611	0.043*
Habitat type	0.2786	0.092873	9.6262	0.0481	0.001***
Trapping site	0.206	0.017169	1.7795	0.03557	0.014*
Habitat type × month	0.1363	0.010482	1.0865	0.02352	0.048*
Trapping site × month	0.3732	0.008482	0.8791	0.06443	0.609
Trapping site × month	13.564	0.914	0.023*	2672.976	0.950

habitat types that have emerged due to restoration and bog retirement were the drivers of the amphibian assemblage (PermANOVA, Table 2). All traps used seemed to be equally successful in capturing amphibians as trap type had no significant effects on amphibian diversity metrics.

Significant predictors of reptile species richness included: trapping site × month interaction, trapping site, and the survey month while trapping site × month interaction was the only significant environmental predictor of reptile abundance (PermANOVA, Table 2). The trapping site × month interaction was the most influential variable for both abundance and richness of reptiles. This indicated that amphibian species richness varied inconsistently among different habitat types as well as trapping sites across the sampling season, which underpinned the importance of seasonality in structuring the herpetofaunal assemblages. The catch per unit effort seemed to have also varied among different trap types as evident by significance of the trap type as a predictor of reptile abundance. Like amphibians, the restoration status alone influenced neither the reptile richness nor abundance. Rather, specific locations and habitat types that emerged in response to restoration and bog retirement were the drivers of the reptile assemblage (PermANOVA, Table 2).

Drivers of the herpetofaunal community structure and composition

The overall variation in species composition in the entire herpetofaunal assemblage was significantly driven by restoration status, survey month, habitat type, and trapping site while the restoration status accounted for the greatest variation in species composition (PerMANOVA, Table 3). The habitat type × month interaction was also significant, which further underpinned the seasonality effect on structuring the herpetofaunal community.

DISCUSSION

The species inventory we complied for both the restored and retired bogs— VES and traps combined— included 17 species of herpetofauna. Among these, 16 were recorded from the restored bog at TWS, whereas 11 species were recorded from the retired bog (Table 1) at FP. Eleven species were shared between the restored and retired bogs. Five species were unique to the restored bog although only a single species was exclusive to the retired bogs. Ecological responses of amphibians and reptiles to wetland restoration were different as revealed by our analyses.

Aquatic amphibian communities at the retired bog were significantly greater than that of the restored bog while the opposite was true for aquatic reptiles. Nonetheless, the overall abundance of all herpetofauna in the restored bog exceeded that of retired bogs. The amphibian community at both the restored and retired bogs were dominated by Ranids. Throughout the northern temperate zone, Ranids have been successful at colonising waterbodies in industrial agroecological systems as well as other artificial wetlands (stormwater ponds, cattle ponds, millponds) despite high degrees of nutrient pollution (Homan et al., 2004; Brand & Snodgrass, 2010). Relatively large, hydrologically stable constructed wetlands (such as farm reservoirs) in our study area can support both amphibian reproduction and a greater biomass than smaller ephemeral wetlands (Pechmann et al., 1989; Baber et al., 2004). The reservoirs in the retired bog are larger in size (both surface area and volume) than the restored open-water habitats (Parris, 2006). Therefore, the former offers more niche space and other critical resources for amphibians than the latter. Consequently, the retired bog can accommodate a diverse assemblage of amphibians.

The larval development of large, North-American Ranids usually takes multiple years, therefore, their fitness increases in perennial water bodies such as those found in farmlands (Paton & Crouch III, 2002; Shulse et al., 2010). The reservoirs of retired bogs are comparable to those of farmlands— perennial, nutrient-rich, homogenous in habitat structure, and fish occupied— thus are more suitable for widely distributed Ranids such as bullfrogs and green frogs (Paton & Crouch III, 2002). These Ranids have anti-predatory adaptations (distasteful larvae, avoidance behaviour, or rapid growth), therefore fish presence has no tangible impacts on their survival (Shulse et al., 2010). Further, without active farming, standing water in the retired bog is limited to irrigation canals and reservoirs, which act as refugia for aquatic obligates. This can inflate the amphibian richness in sites we sampled. The agricultural history and homogenised habitat structure at the retired bog can be less suitable for amphibian predators. Anthropocentric landscapes— industrial agroecosystems in particular— undergo biotic homogenisation where human commensals and generalists are accrued at the expense of rare species and habitat specialists (McKinney & Lockwood, 1999; McKinney & Lockwood, 2001; Baeten et al., 2012). Recruitment of tolerant species can elevate absolute species richness in human-modified habitats though such species assemblages are unlikely to include range-restricted and unique species or species of conservation concern (Baber et al., 2004).

The active interventions in restored habitats— pit-and-mound microtopography, reengineered meandering stream channels, ephemeral wetlands with variable hydroperiods, addition of woody debris, and introduction of native flora— have contributed to a much greater structural diversity and overall habitat heterogeneity while increasing the overall wetland acreage (Dimino et al., 2018; McCanty & Christian, 2018). As such, the restored bog provides optimal niche dimensions for a range of life-history functions such as foraging, reproduction, nursing, hibernation, aestivation, and growth (Zedler, 2000; Funk et al., 2013). Importance of niche breadth for herpetofaunal assemblages and other aquatic communities have been substantiated across different geographies (Krzysik, 1979; Behangana & Luiselli, 2008; Marino et al., 2019). Consequently, as predicted by niche diversification and habitat-area concepts, reptile species richness as well as overall abundance of both amphibians and reptiles were greater at the restored bog. The acreage of restored bog is much larger than that of the retired bog, therefore, the former offers a broader resource base, which elevates both the carrying capacity and intrinsic growth rate of herptile populations (Griffen & Drake, 2008). Given the greater habitat area, the restored bog is less burdened with edge effects and more resilient to anthropogenic disturbances emerging from the suburban landscape matrix (Harper et al., 2005). Hence, habitat size can be an important driver of differential herpetofaunal richness and abundance between restored verses retired bogs.

The restored and retired bogs we studied were managed together for commercial cranberry farming for centuries using the same management strategies. When in active production, the restored (TWS) and retired bogs (FP) in our study had comparable habitat structures including cultivated cranberry beds, reservoirs, irrigation channels, perimeter ditches, and surrounding woodlands. Given geographic proximity, both FP and TWS likely have the same source populations and equally accessible by dispersing herpetofauna. Thus, pre-restoration and pre-retirement habitat conditions as well as the original herpetofaunal community structure at TWS and FP are likely similar. Therefore, the observed biological differences can be attributed reliably to wetland restoration. The availability of new habitats and enhanced habitat heterogeneity resulting from restoration can be the primary divers of greater reptile richness and overall herpetofaunal abundance at the restored bog.

Unexpectedly lower amphibian richness at the restored bog can be attributable to several mechanisms. The restoration interventions in wetland environments create a single, prolonged, intensive, pulse disturbance, which includes dramatic changes in the surface topography, hydrologic processes, and nutrient dynamics (McCanty & Christian, 2018; Hoekstra et al., 2020). For instance, dam removal and sand excavation resuspend copious volumes of nutrients into the water column and alters the fluvial processes while microtopographic modifications alter the subterranean microhabitats as well as surface cover structure. These major disturbances in the physical habitat structure, aquatic biochemistry, and hydrology can result in mortality, shrinking the species richness of remnant, post-restoration biological communities (Middleton, 1999; Petranka et al., 2007).

Amphibians are sensitive to environmental perturbations (Blaustein et al., 1994). Restoration actions can act as a pulse disturbance, which may delay colonisation of disturbance-intolerant amphibians. Amphibians are patchily distributed across their breeding habitats, highly philopatric, and have low vagility (Davic & Welsh, 2004). Therefore, amphibian community in restored habitats may remain species depauperate in early stages of post-restoration (Lehtinen & Galatowitsch, 2001). Particularly given limited home ranges and dispersal and dependency on habitat connectivity, saturation of amphibian richness in the restored bog may take multiple years (Burbrink et al., 1998; Hager, 1998; Grant et al., 2010). Nested in a suburban landscape (Walberg, 2013; Norriss, 2018), TWS may not have sufficient old-growth forest cover to support adult life-history needs of amphibians (Semlitsch, 2002; Petranka et al., 2007; Blomquist & Hunter, 2009). In early phases of colonisation, selection processes favor species with high mobility and generalist traits while species with specialised niche requirements and limited spatial distributions take longer to colonise novel habitats (Mierzwa, 2000; Petranka et al., 2007). Locally abundant, regionally widespread "core species" can readily access and colonise suitable habitats in the landscape (Hanski, 1982; Cadotte & Lovett-Doust, 2007). In contrast, colonisation by satellite species takes longer as they are constrained by landscape permeability, proximity to source habitats, and smaller navigation ranges (Mierzwa, 2000; Lehtinen & Galatowitsch, 2001; Petranka et al., 2007). This explains the greater abundance of generalist species as well as scarcity of rare species and specialists in the restored bog.

All herpetofauna we documented are regionally abundant, habitat generalists with a broad geographic distribution. Herpetofauna we inventoried are listed in neither the US/ Massachusetts Engendered Species Acts nor the IUCN Global Red List. However, the northern leopard frog we recorded at the restored bog has undergone local and regional population declines across a few localities in New England (Gilbert et al., 1994; Pope et al., 2000; Blomquist & Hunter, 2009). Although limited in incidences, presence of northern leopard frogs in the restored bog is noteworthy.

Agricultural legacies and the impacts of the disturbance history are known to persist in aquatic and wetland environments (Harding et al., 1998; Scott, 2006; Ballantine et al., 2017). Hence, century-long farming history is the likely driver of species depauperation at the retired bog. Given the recent restoration intervention, the physical habitat template of the restored bog is temporally dynamic. For instance, the channel geomorphology, streambed heterogeneity, and stream velocity at TWS have undergone dramatic shifts within the first few years of restoration (McCanty, 2020). Similarly, the vegetation structure, composition, and above ground biomass have not reached a stable state at TWS. Since TWS is still passaging through early recovery trajectory, the habitat structure is undergoing dramatic changes. Such environments are better suited for high-plasticity traits and opportunist strategies in contrast to highly specialised life-histories (Russell et al., 2002b; Petranka et al., 2007). Consequently, herpetofauna we found at the restored bogs were largely comprised of generalist species. With sufficient time past the active restoration interventions, as the restored bog reaches a stable state alongside a stable physical habitat structure, taxonomic and trait composition of the herpetofaunal community is likely to diversify (Mierzwa, 2000; Lehtinen & Galatowitsch, 2001; Petranka et al., 2007). Our study also showed tangible influences from short-term temporal covariates on the herpetofaunal community as well. For instance, the significance of month x habitat and month x trapping site interactions on diversity metrics and species composition suggested non-trivial within-season species turnover in the herpetofaunal community.

Evidence for pond-breeding amphibians— such as wood frogs (*Lithobates sylvaticus*) and mole salamanders (*Ambystoma* sp) regardless of their life-history stages— were infrequently found at both restored and retired bogs. Forested vernal pools and small, fishless ephemeral wetlands with small-to-moderate hydroperiods are the primary breeding habitats for these pond-breeding specialists (Cormier et al., 2013). Ephemeral wetlands in the retired bog are limited to tire ruts with unpredictable hydroperiods. Ephemeral marshland depressions in the restored bogs are intermittently connected to perennial waters, thus accessible by predatory fish, which negatively impacts pond-breeding amphibians (Pechmann et al., 1989; Semlitsch, 2002; Petranka et al., 2007). Thus, neither restored nor retired bogs provide ideal habitats for pond-breeding amphibians to sustain long-term viability.

Both richness and abundance of reptiles were greater in the restored bog compared to the retired bog. Restoration efforts at TWS produced a variety of wetlands, meandering stream channels, and semi-perennial ponds. Along with the forest buffers, TWS has morphed into a spatially heterogeneous upland-wetland-aquatic habitat complex forming multiple ecotones, which further enhances both habitat and resource availability for herpetofauna (Norriss, 2018; Ballantine et al., 2020). The process-based restoration has also yielded a diverse range of wetlands with variable flow dynamics, hydrologic features, and vegetation structure, which reinforces the biologically critical resource base at TWS (Briggs et al., 2016; Harvey et al., 2019). In addition, dam removal reconnected the flow-through systems back to the watershed reforming migratory pathways for herpetofauna to navigate through stream networks (Grant et al., 2010). Moreover, reformed stream sinuosity rekindled channel-floodplain interactions, which has widened the resource base (such as foraging opportunities) for freshwater-dependent herpetofauna. In contrast, impoundments and channelised streams of the retired bog not only impede species immigration from source populations but also restricts movement of remnant populations. Restored hydrologic processes— flood pulse between the channel and the floodplain, groundwater discharge that moderates the thermal environment, and watershed-wide stream connectivity— is fundamental to maintain the habitat heterogeneity and to hasten post-restoration trajectory at TWS (Harvey et al., 2019; Ballantine et al., 2020; McCanty, 2020).

Our preliminary findings indicated that restoration was critical for providing habitats for native herpetofaunal communities at a shorter time scale after restoration, at least for those communities that are locally common and regionally abundant. Without active intervention, retired bogs are unlikely to transform into wetlands although the perimeter ditches, irrigation canals, and holding reservoirs can become herpetofaunal refugia. As showed in our study, these refugia offer opportunity for highly resilient human-commensal herpetofauna. Given the underlying sand layers, retried cranberry bogs are likely to undergo upland successions resulting in plant communities dominated by scrub oak, pitch pine, or white pine (Mylecraine et al., 2003; Klee et al., 2019). Retired bogs are also susceptible to exotic invasions, and secondary metabolites released by these invasive plants can result in reduced larval growth and survival (Maerz et al., 2004).

Temporal scale of wetland recovery after active restoration is highly variable. Though wetlands can recover partial functionality within a few years following restoration, regaining full complement of functions requires 5-10 years for low-stress systems whereas diversity-rich or specialised systems take much longer (20-100 years) (Zedler & Callaway, 1999; Matthews & Spyreas, 2010). Further, high latitude, temperate systems that are frequently disturbed by climatic extremities (such as north-eastern US) and stochastic events will require decades to reach the climax community. Hereto, we underscore the need for continued monitoring at TWS to provide further insights into occupancy of rare and conservation-dependent species. Long-term ecological monitoring also opens opportunities for a thorough evaluation of temporal community turnover in restored wetlands. Short-term assessments of biological responses to restoration, such as our study, can help strategise site-specific adaptive habitat management actions, such as headstarting, upland revegetation, and invasive-species management (Kentula, 2000; Zedler et al., 2012). Moreover, long-term, continuous monitoring of retired bogs in comparison to bogs restored following variable designs and trajectories are crucial to determine the most effective restoration procedures.

Unexpected and undesirable developments have been reported in wetland restoration, particularly in high-stress systems (wetlands embedded in dramatically modified river basins) and wetlands with disturbance legacies (Kentula, 2000; Klötzli & Grootjans, 2001). The re-assembly of floral, faunal, and microbial communities to quasi-natural or desired levels at a restored wetland depends on biotic constraints (presence of source populations, metacommunity dynamics), evolutionary histories (phylogenetic constraints and local adaptations), community interactions (competition, trophic dynamics), structural diversity at local scale, landscape-scale processes and connectivity, and current and historical disturbance regimes (land-cover change and hydrological modifications) (Klötzli & Grootjans, 2001; Walker et al., 2004; Klimkowska et al., 2010). Consequently, if the regional species pool is impoverished, local source communities are dispersal limited, or there are impediments to landscape-scale connectivity (outside the restored bog), the restored habitat will have vacant niches, leading to establishment of exotic species. Historical, long-term agricultural land-uses may render some habitats resilient to restoration. In such cases, instead of moving towards the intended trajectory, restored habitats revert to pre-restoration status, as evident from temperate grasslands and middle-to-high order streams of south-eastern US (Harding, 1997; Harding et al., 1998). In our study, evidence for invasive herpetofauna was limited to a single event of capturing a female red-eared slider, a freshwater turtle native to south-eastern US that is competitively superior to those of the north-eastern US. However, this isolated incidence does not suggest any undesirable outcomes. Although both the restored and retired bogs we surveyed shared 10 herptile species in common, since restored sites were significantly greater in herptile abundance and reptile richness, there is no evidence implying resilience or resistance to restoration at TWS.

Conclusive Remarks

The retired bog had been left unmanaged for close to a decade before our survey. Despite lack of active farming for nearly a decade, no rare, threatened, unique species or habitat specialists have colonised therein. As such, retirement from commercial production and subsequent passive restoration alone are insufficient to bolster herptile diversity in retired bogs. Although our observations on unique or conservation-dependent herpetofauna at TWS are infrequent, reptile species richness and herpetofaunal abundance at TWS was greater than that of FP. As TWS continues to recuperate from both century-long framing legacies and pulse disturbance induced via active restoration, exploring turnover in the herpetofaunal community is imperative to determine the suitability for conservation-dependent species. Cranberry farms constitute a critical element in the landscapes of south-eastern Massachusetts. A multitude of economic, ecological, and logistic constraints have led to abandonment of cranberry bogs in Massachusetts. Cranberry bogs taken out of commercial production generate opportunities for wetland restoration. Hereto, our study can serve as a blueprint to develop community-wide surveys to assess biological responses to wetland restoration. Such studies will formulate a scientifically robust knowledgebase that reinforces decision-making in wetland restoration, management, and conservation policies.

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