ECOSYSTEM FUNCTIONING OF GREAT SALT LAKE WETLANDS

by

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A thesis submitted in partial fulfillment
of the requirements for the degree

of

MASTER OF SCIENCE

in

Ecology

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UTAH STATE UNIVERSITY
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2019

ABSTRACT

Ecosystem Functioning of Great Salt Lake Wetlands

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Utah State University, 2019

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Great Salt Lake (GSL) wetlands account for ~80% of Utah wetlands and are critical habitat for birds migrating along the Pacific and Central Flyways. Like many wetlands worldwide, natural GSL wetlands have been declining because of anthropogenic effects and the spread of invasive species. The functioning of GSL wetland habitats and the services they provide, however, have not been well documented. This knowledge gap hinders our ability to predict the effects of species loss and our ability to undertake science-based restoration and revegetation practices.

To better understand how the loss of different habitat types in GSL wetlands affects the provisioning of ecosystem services, we quantified and compared eight ecosystem functions and multifunctionality across seven primary wetland habitat types (*Bolboschoenus maritimus, Schoenoplectus acutus, S. americanus, Typha latifolia, Salicornia rubra, Phragmites australis*—or unvegetated playa) within the Bear River Migratory Bird Refuge (BRMBR) and The Nature Conservancy Great Salt Lake Shorelands Preserve. Specifically, I studied eight ecosystem functions that support important ecosystem services such as climate mitigation, water quality, primary production, and habitat provisioning for wildlife. I quantified individual functions and modeled the relationship between habitat types and functions using linear mixed effects models as well as created two different measurements of multifunctionality.

In this study, I show that maintaining habitat diversity will be critical for maintaining multifunctionality in GSL wetlands. In general, habitats varied greatly in their ability to perform functions at a high level, and no single habitat type could support all eight functions even at the 20% threshold. I found that *Typha latifolia* and *Schoenoplectus acutus* had the highest functional values of any native species. In addition, I found that despite being an invasive species, *P. australis* also had high functional levels, although it performed poorly for providing bird habitat. Despite that *T. latifolia*, *S. acutus* and *P. australis* had high functioning, we found that a diversity of habitats are required to maintain multiple ecosystem services This study supports the idea that habitat heterogeneity is critical in supporting a multifunctional environment and diversity loss may cause a reduction in functioning and the ecosystem services provided by GSL wetlands.

(65 pages)

PUBLIC ABSTRACT

Ecosystem Function of Great Salt Lake Wetlands

Maya Pendleton

The Great Salt Lake (GSL) wetlands account for ~75% of all Utah wetlands and provide not only critical habitat for millions of migratory birds, but also provide valuable ecosystem functions and services as well as economic benefits to Utahns. However, these wetlands are facing an aggressive invader, *Phragmites australis*, that has spreading across the GSL wetlands and replacing native wetland habitats. Wetland managers have spent countless resources and time trying to control the spread of *P. australis* and restore GSL wetlands. However, we do not fully understand how these wetlands functions and services are being altered with this habitat homogenization because functional data for our wetland species have not been well documented. This lack of knowledge may hinder wetland restoration efforts.

To create baseline functional data for the GSL wetland species and better understand how the spread of *P. australis* might be affecting the overall health of the system, I measured eight individual ecosystem functions for seven dominant habitat types found across the GSL wetlands. I compared these individual functions across habitat types as well as created two different multifunctionality indices using an averaging and a thresholds approach. With these comparisons, I was able to determine the distinct functional strengths of different wetland habitat types and their overall functional abilities.

I found that functional abilities varied greatly by habitat type and that not one single habitat could support every function even at the lowest threshold measured. I found that *Typha latifolia, Schoenoplectus acutus,* and *P. australis,* had the highest multifunctional values. However, I also found that some habitats offered unique functions, such as *Salicornia rubra* and playa, and that these functions were lacking in other habitats, including the most multifunctional habitats. These findings suggest that maintaining habitat heterogeneity will be critical in ensuring a fully functioning wetland system that can provide a multitude of ecosystems services that benefit both humans and wildlife. The findings of this study will supply wetland managers with a better understanding of the functional strengths of different wetland habitats. This data will aid in ongoing restoration efforts by enabling managers to target certain functions and create more efficient and effective management plans.

ACKNOWLEDGMENTS

I would like to thank the Bear River Migratory Bird Refuge and The Nature Conservancy for supporting my research and for being fantastic and cooperative people to work with. I would also like to thank Utah State University’s Extension Program and The Ecology Center for supplying partial funding for this project.

I would like to thank my fantastic major advisor Dr. Trisha Atwood. She funded most of this project and has been incredibly patient, supportive, and enthusiastic about this project and with me. I have learned so much from her and she has greatly strengthened both my ecological research abilities and my character. I would also like to thank my committee members Drs. Karin Kettenring and Kim Sullivan for their vast knowledge and expertise. I would also like to thank Drs. Edd Hammill, Will Pearse, and Frank Howe for the extra guidance they gave me and Shane Sterner for selflessly helping me clean seeds for my project, a very daunting task.

I want to thank all of my volunteers, friends, undergraduate researcher Sam Sedgewick, and Adam Brewerton. They were courageous enough to come out into the field with me even though it meant being sunburned, bug-bitten, scrapped up, and water-logged. I could not have accomplished any of this without you all. I want to thank my family who has supported me through my entire educational career. It has been a hard journey, but they have supported me through every moment. Finally, I would like to thank my father. His wisdom and memory have helped make this project a reality.

Maya Cassidy Pendleton

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INTRODUCTION

Ecosystem functioning can be defined as the collective activities of plants, animals, and microbes and the effects these activities have on different biotic, chemical, and physical conditions in the environment (Naeem et al., 1999). These activities allow an ecosystem to perform various functions such as nutrient cycling and sequestration, primary production, soil retention, and habitat provisioning. Furthermore, many of these functions have been deemed valuable to humans (i.e., ecosystem services) providing services such as climate mitigation and water purification (Wall & Nielsen, 2012). As humans impact the environment through land development, climate change, habitat degradation, and the introduction of invasive species, there have been several changes and losses in ecosystem functioning, and thus the ability of ecosystems to provide ecosystem services (Naeem et al., 1999). Restoring and understanding ecosystem functioning has become increasingly important as we develop our understanding of the importance of natural systems for human wellbeing (Cardinale et al., 2012).

Research has suggested that biodiversity is positively related to ecosystem functioning (Hector & Bagchi, 2007; Maestre et al., 2012; Lefcheck et al., 2015a; Alsterberg et al., 2017). There are two main mechanisms driving the effect of increased biodiversity on higher functioning—complementarity and a sampling effect. The complementarity effect suggests that species occupy different niche spaces and that species can facilitate each other in ways that enhance functioning more than what would be expected for a monoculture (Loreau & Hector, 2001; Cardinale et al., 2007). The sampling effect states that ecosystem functions may be provided by one or a couple of dominant species within the community and that this dominance arises from certain factors like interspecific competition, species interactions, and resource use (Tilman, Lehman, & Thomson, 1997; Loreau & Hector, 2001). Higher diversity (often quantified as species richness or functional diversity) in an area increases the probability of these functionally dominant species being present (Huston, 1997; Wardle, 1999; Loreau & Hector, 2001). However, it is also known that sampling effects and complementarity are not necessarily independent and their relative importance may be dependent on the spatial scale that diversity is being measured (Fargione & Tilman, 2005; Zhu et al., 2015). Furthering our understanding of how complementarity and sampling effects influence biodiversity and ecosystem functioning will allow us to better determine the types of management and conservation strategies we need to incorporate into our landscapes.

Most of the research on biodiversity-ecosystem functioning has been focused on a single function such as primary productivity. However, this focus does not take into account important trade-offs and synergies between species and functions (Byrnes et al., 2014). Also, few ecosystems are managed for a single ecosystem function or service. Rather, society often values an ecosystem for multiple, sometimes conflicting ecosystem functions and services (Cardinale et al., 2012). As a result, recent biodiversity-ecosystem functioning research has focused on the relationship between biodiversity and multifunctionality, or the ability of an ecosystem to support different functions and services simultaneously (Manning et al., 2018).

Multifunctionality, like individual functions, is thought to be positively related to biodiversity because of dynamic interactions between species that drive ecosystem processes (Maestre et al., 2012a; Lefcheck et al., 2015). Studies that focused on individual functions found that although biodiversity had an overall positive effect on the function being measured, the effects became saturated at a certain level of species richness (Hooper et al., 2005). When considering multiple functions, however, higher levels of biodiversity were needed compared to individual functions, and there was no saturation point. Multiple studies across different taxa, functions, and ecosystems (Maestre et al., 2012a; Gamfeldt et al., 2013; Lefcheck et al., 2015) have found that increased levels of species richness allows for the provisioning of more functions (Hector & Bagchi, 2007; Gamfeldt, Hillebrand, & Jonsson, 2008; Zavaleta et al., 2010; Byrnes et al., 2014). Maintaining higher biodiversity is thought to be important for maintaining multiple functions because it is unlikely that one species can maximize all functions (Gamfeldt & Roger, 2017). Species may have functional trade-offs or synergies that allow them to excel in some functions while lacking in others (Zavaleta et al., 2010; Gamfeldt et al., 2013). This means that in order to maintain many functions at high levels across an ecosystem, a diversity of species that provide various functions need to be present (Hector & Bagchi, 2007; Isbell et al., 2011; Meyer et al., 2018).

Not only has most of the biodiversity-ecosystem functioning literature focused on the effects of this relationship on single ecosystem functions, but most of the studies, even multifunctionality studies, have also been conducted at small spatial scales (e.g., 1 m^2 plot-level) (Hector & Bagchi, 2007; Zavaleta et al., 2010; Isbell et al., 2011). Although landscape-level multifunctionality studies are rare, those that exist have found that maintaining habitat and community level biodiversity increases a landscapes multifunctionality (Pasari et al., 2013; Alsterberg et al., 2017; Hautier et al., 2018). Looking at functions across a landscape and across different ecosystems may alter the significance of complementarity and sampling effects. As the scale of an area increases, complementarity may have less of an effect upon ecosystem function because the distance between species may be so great that facilitation is not possible. For example, the presence of a nitrogen-fixing plant will increase nitrogen availability for species in the direct vicinity of the nitrogen-fixer, but it is unlikely to increase nitrogen availability for plants that are kilometers away. Landscape-level diversity may be especially important in systems that contain large monotypic stands of species, such as wetlands and heavily managed landscapes. A recent study found that for heavily managed forests in Europe, maintaining landscape-level diversity was critical for providing multifunctionality (Van der Plas et al., 2016). Different forestry species performed certain functions and higher landscape diversity ensured that the different functions were present in at least one area across the landscape (Van der Plas et al., 2016). Results from this study and others suggest that at the landscape-scale, the inclusion of multiple functional dominants (i.e. sampling effect) is important for increasing multifunctionality, especially in landscapes that typically contain monotypic stands. However, further research is needed to understand how the relationship between biodiversity and ecosystem functioning is affected by spatial scale and the number of functions studied.

CHAPTER INTRODUCTION

Wetlands cover only ~ 5% of the earth, yet they contribute nearly 40% of the ecosystem services and functions provided by natural lands (Zedler & Kercher, 2005). Despite their importance to society, wetlands are some of the most endangered ecosystems. We have lost at least 50% of wetlands worldwide, and most of this loss is attributed to either urbanization or agriculture (Zedler & Kercher, 2005). This loss paired with the economic and functional value of wetlands inspired the U.S Government to create a no-net-loss of wetlands policy under the Bush administration, as well as a global wetland protection treaty at the Ramsar Convention (Mitsch & Gosselink, 2000). However, current wetland restoration and mitigation practices often fail to produce wetlands that provide functions and services similar to natural wetlands (Zedler & Callaway 1999; Moreno-Mateos, et al., 2012). Our inability to mimic or maintain natural levels of wetland functioning may be because we do not fully understand how biodiversity influences functions (Zedler, 2000; Meli et al., 2014). This lack of understanding may hinder successful wetland restoration.

The Great Salt Lake (GSL) and its wetlands are both internationally and locally important ecosystems. Each year millions of birds traveling along the Pacific and Central flyways use the GSL wetlands for resting, foraging, and breeding (Paul & Manning, 2002; Aldrich & Paul, 2002). In addition, GSL wetlands may help mitigate climate through carbon storage and sequester heavy metals and nutrients from runoff (Zedler & Kercher, 2003; Rai, 2008). Overall, the ecosystem services provided by the GSL bring in millions of dollars for the state annually (Bioeconomics, I. 2012). However, the functions and services of these wetlands may be threatened. In 1983, flooding of the GSL disturbed the native wetland vegetation and caused *Phragmites australis,* an aggressive invasive species from Eurasia, to spread across the landscape (Kettenring, de Blois, & Hauber, 2012). *Phragmites australis* differs from native GSL wetland plants because of its broader environmental tolerance such that it can grow in a diversity of physiochemical conditions (salinity, hydrology) (Lissner &Schierup, 1997; Ailstock & Center, 2000). In comparison, native plants grow in stratified monotypic stands according to their physiological tolerance, creating high habitat-level diversity. *P. australis* already covers ~ 92 km^2 of GSL (Long et al., 2017) and its ability to out-compete native plants is homogenizing the landscape, which in turn is greatly reducing habitat-level biodiversity (Chambers, Meyerson, & Saltonstall, 1999).

Over the past decade, the eastern United States and the Intermountain West have spent significant resources trying to control the spread of *P. australis* and to restore native vegetation (Rohal et al., 2018). However, many of these restoration projects, especially along the GSL, have seen low success rates. Low success rates have been linked to limited recolonization of native communities following the removal of *P. australis* (Rohal, Cranney, & Kettenring, 2019). Revegetation of native species after the removal of invasive species is now considered extremely important for the successful restoration of these wetlands (Kettenring & Adams, 2011; Rohal et al., 2018). Despite the multitude of other wetland plants, revegetation efforts in GSL wetlands have almost solely focused on three native species of bulrush (*Bolboschoenus maritimus*, *Schoenoplectus acutus*, and *S. americanus*) due to manager preference (Rohal et al., 2018). This focus on bulrushes has largely been attributed to the fact that these species are perceived to be the primary provider of cover, nesting sites, and food resources for avian species of recreational interest (Olson, Lindsey, & Hirschboeck, 2004; Petrie, Vest, & Smith, 2013; Roberts, 2013; Manning et al., 2018). However, this focus does not take into account the multitude of other functions that should be considered during revegetation efforts and the role that other dominant habitat types may be playing in supporting important ecosystem functions at a landscape level.

Revegetation efforts may do well to focus on a variety of plant species because over the past few decades, research has suggested that there is a positive relationship between biodiversity (species, genetic, and habitat) and ecosystem functioning (Hector & Bagchi, 2007; Maestre et al., 2012a; Lefcheck et al., 2015; Alsterberg et al., 2017). Furthermore, Lefcheck et al., (2015) and many others have found that higher biodiversity also supports ecosystem multifunctionality or the ability of an ecosystem to simultaneously provide multiple functions and services. These studies suggest that habitat diversity in the GSL may be important for the provisioning of critical ecosystem functions that underlie ecosystem services. To date, however, no studies have compared the provisioning of different functions across GSL's dominant wetland plant species. Thus, we do not understand how ecosystem functioning may be changing because of the invasion of *P. australis* and management efforts to control it.

This study aimed to further our understanding of GSL wetlands and the provisioning of ecosystem functions by different habitat types by addressing the following objectives: 1) Determine how independent ecosystem functions vary across different wetland habitat types within the GSL. 2) Determine how multifunctionality, as measured by a multifunctionality index (MI), varies across different wetland habitat types. To meet these objectives, we chose to focus on eight ecosystem functions that support ecosystem services of climate mitigation, water quality, primary production, and habitat provisioning for wildlife (Table 1). These functions include below- and above-ground carbon storage, below- and above-ground nitrogen storage, above-ground biomass (a proxy for primary production), heavy metal accumulation, seed nutritional value, and avian diversity, richness, and presence/absence.

METHODS

Study Area

This study focused on wetlands in the Bear River Migratory Bird Refuge (BRMBR) and The Nature Conservancy Great Salt Lake Shorelands Preserve (GSLSP) both located on the eastern side of the GSL (Fig. 1). The BRMBR lies at the mouth of the Bear River and contains nearly 323 km^2 of habitat. It is part of the federal National Wildlife Refuge system and because of its extreme hemispheric importance to avian species, it has been designated as a Western Hemisphere Shorebird Reserve Network site (Western Hemisphere Shorebird Reserve Network, 2018). The BRMBR is a heavily managed refuge that is impounded in many areas and contains a variety of upland and wetland habitats (Downard, Endter-Wada, & Kettenring, 2014). The GSLSP property was purchased by The Nature Conservancy in 1994 and covers roughly 18 km^2. GSLSP actively manages the vegetation and avian species on the preserve; however, these wetlands lack the impoundments found within the BRMBR location. BRMBR and GSLSP were selected for this study because they contain large stands of both native and non-native wetland plants. Within these two locations, we characterized ecosystem functions on five native vegetated habitat types: broad-leaf cattail (*Typha latifolia*), alkali bulrush (*B. maritimus*), three-square bulrush (*S. americanus*), hardstem bulrush (*S. acutus*), and pickleweed (*Salicornia rubra*), one non-native vegetated habitat type (*P. australis*), and one unvegetated habitat type (playa). These represent some of the most dominant habitat types across the GSL wetland landscape (Downard et al., 2017).

Using field surveys, we identified areas > 400 m^2 of continuous, unmixed vegetation for each for the seven habitat types. This plot size was selected to reduce any interactive effects on functions from neighboring plant species. In total we had 68 plots: *T. latifolia* (8 plots), *B. maritimus* (10 plots), *S. americanus* (10 plots), *S. acutus* (9 plots), *S. rubra* (10 plots), *P. australis* (10 plots), and playa (11 plots).

Individual Function Measurements

Below-ground carbon and nitrogen storage

Below-ground carbon and nitrogen stocks were quantified using methods from Howard et al., (2014). We collected one, 30 cm composite soil core from the center of each plot and transported them to the lab in an upright position (to reduce nutrient mixing within the core) where they were immediately processed or frozen. Because of different soil types and soil moisture we used two types of corers to extract sediments: a PVC push corer (5 cm diameter * 30 cm height) and an AMS brand push corer (2.2 cm * 30 cm height). When possible, soil samples were taken to a depth of 30 cm. However, several playa *S. rubra* sites had a shallower soil matrix. In these sites, soil cores were taken to the maximum depth possible (0-15 cm). Soils were subsampled from each core at 5 cm intervals, dried to a constant weight, and homogenized into a fine powder. Soil samples were analyzed for percent carbon and nitrogen content at the University of Hawaii at Hilo's analytical lab using a Costech elemental analyzer.

We calculated below-ground carbon and nitrogen stocks by combining percent content with bulk density. To calculate bulk density, we multiplied the sample dry weight by the core volume. We used the following equation to calculate below-ground carbon and nitrogen stocks for each plot: Mg carbon ha^{-1} or Mg nitrogen ha^{-1} = 10,000* subsection thickness (m)*bulk density*(% carbon or nitrogen/100). All subsections within each plot were summed to determine the total carbon/nitrogen stock per hectare of habitat. Carbon and nitrogen stocks were standardized to 30 cm or the maximum core depth for sites with more shallow soil matrixes.

Above-ground biomass and above-ground carbon and nitrogen storage

We collected plant biomass as a proxy for primary production (above-ground biomass production m^{-2}). We collected plant biomass using established methods for herbaceous wetland species (Howard et al., 2014). Plant biomass samples were collected during August and September 2018, when biomass had reached its peak. Within each vegetated plot, we randomly established three, 0.5 m^2 subplots using a PVC frame. Within each subplot, we destructively harvested all rooted material (i.e. not wrack) that was both living and dead by cutting the plant at the soil-atmosphere interface. Plant samples were dried to a constant weight at 60^o C and weighed.

We used subsamples from our above-ground biomass samples to analyze the percent carbon and nitrogen of stems and leaves. Samples were dried at 60^o C to a constant weight (~ 72 hours) and homogenized to a fine powder. Percent carbon and nitrogen were analyzed at the University of Hawaii at Hilo's analytical lab using a Costech elemental analyzer. The percent carbon and nitrogen content for each species were averaged across plots to develop a carbon and nitrogen conversion factor for each species (Table A1). Above-ground carbon and nitrogen stocks were calculated by multiplying the carbon or nitrogen content by the above-ground biomass estimates (see methods above) for each plot.

Heavy metal accumulation in above-ground biomass

An undergraduate researcher who ran a project concurrently with my thesis work collected data on heavy metal accumulation by plants in all my vegetated plots. Within each vegetated plot, we collected 5 grams of stem biomass. We chose stems because *S. rubra* has highly modified leaves and the leaves of *S. americanus* and *S. acutus* are often highly reduced and we wanted to standardize the structure of the plant that was collected as heavy metal distributions within plant structures can vary (Stoltz & Greger, 2002). Plant samples were dried to a constant weight, ground to a fine powder, and analyzed for copper, arsenic, selenium, lead, mercury, and cadmium at the University of Hawaii at Hilo's analytical lab using a Vairan Vista MPX ICP-OES Spectrometer. Heavy metal extractions were done using methods from Hu et al. (2000). Heavy metal uptake by each plant species per m^2 was calculated by multiplying the concentration of each metal by the plot above-ground biomass (see methods above).

Seed nutritive value

We calculated the amount of seed nutrition per m^2 by multiplying seed mass by the seed nutrition for each plant species. Seeds were collected from our plots after seeds had ripened: June–July for *S. acutus* and *S. americanus,* late August–September for *B. maritimus,* September for *T. latifolia,* late September–October for *P. australis,* and October for *S. rubra.* Following this collection, we used slightly different methods to determine seed densities for the bulrush species *P. australis, T. latifolia,* and *S. rubra*. For the bulrushes, we first counted the total number of seed heads in each subplot. We then collected 3 seed heads from each subplot for a total of 90 seed heads from each species of bulrush. In the lab, we counted the number of seeds in 15-20 seed heads and developed an allometric equation that described the species-specific relationship between seed head weight and the number of seeds per seed head (Table A2). We then weighed our remaining seed heads, applied the allometric equation to each head that was not hand-counted, and then averaged all 90 seed heads to determine the average number of seeds per seed head. To calculate the seed density in each subplot, we multiplied the average number of seeds per head by the total number of seed heads counted in each subplot. Finally, we calculated the total dry mass of seeds per plot for each species by multiplying the seed density by the average dry weight of an individual seed. For *P. australis* and *T. latifolia*, because counting the total number of seeds per seed head was not practical due to the thousands of seeds, we made three subsections of each seed head and counted the number of seeds per subsection. We then developed species-specific allometric equations that described the relationship between seed abundance and seed head weight (Table A2) and used this equation to estimate the number of seeds per seed head for *P. australis* and *T. latifolia*. We then used the same methods as for the bulrush species to calculated total seed density and total dry seed mass for each plot of *P. australis* and *T. latifolia*. *S. rubra* does not produce easily identifiable flowering heads and the seeds germinate within the parent plant. Because no established methods for collecting seeds from *S. rubra* exist and several species of birds are known to consume the fleshy tips of *S.* rubra (Zedler, 1982), we estimated the nutritional value by weighing the entire stem-free above-ground biomass within each subplot.

To complete nutritional analysis of the seeds, mass amounts of each seed type was collected from 5 plots for each species. Seeds were cleaned to ~95% pure seed. In the case of *S. rubra*, where seeds were not collected, the tips of the plants were used for nutritional analyses. Seeds and *S. rubra* tips were sent to the Bar Diamond Lab in Parma, Idaho for analysis of apparent metabolizable energy (AME) for waterfowl. AME was used instead of TME (true metabolizable energy) because TME calculations involve lengthy feeding trials with live birds which were resources we did not have. Also, AME has been widely used in quantifying the energy of feed stuffs for birds (Miller & Reinecke, 1984). In addition to AME, the lab also provided information on crude protein, crude fat, ash, acid detergent fiber, neutral detergent fiber, and gross energy which are available in Table A3. Total AME per m^2 of habitat (kcal/m^2) was calculated by multiplying the average AME for each seed species by the total dry seed biomass or stem-free above-ground biomass for *S. rubra* for each plot.

Avian diversity, richness and presence/absence

We calculated seasonal and overall bird diversity (Shannon-Weiner diversity), species richness, and species presence/absence for each habitat type using point counts. Point counts were conducted from the center point of each plot. Point counts were chosen because they have been used in other wetland surveys to link avian species with habitat use and are effective in dense vegetation such as *P. australis* and *T. latifolia* (Benoit & Askins, 1999). Surveys started at sunrise and were concluded 3 hours after sunrise. Surveys were conducted during Spring, Summer, and Fall of 2018 to capture the diversity of bird communities across the year. Surveys within each plot lasted 5 minutes. All birds seen and heard up to a maximum distance of 300 m from the center of the plot were counted. However, we excluded fly-overs that were not specifically using a habitat type. Birds that were flushed from the area when approaching the point were also counted.

Following the five-minute counting period, we played the calls of two secretive marsh birds, the Virginia Rail, and the Sora, to detect their possible presence.

Diversity data were compiled in two ways. First, we grouped all bird sightings purely by habitat type, which we called “compiled bird data” or CBD. For example, if we were standing in a *B. maritimus* plot doing a survey, we may have also recorded a bird that was in a neighboring *T. latifolia* stand and that observation would have been included in the *T. latifolia* diversity analysis, even though it was not directly attached to a plot. This method gave us a single diversity and richness metric across seasons, as well as an annual metric for each habitat type which is a common method used in other bird habitat studies (Harris, Milligan, & Fewless, 1983; Bibi & Ali, 2013). For multifunctionality (see below for methods) and presence/absence analysis, we needed to retain a plot level structure so that we could have replicates for each habitat type, this data structure is referred to as “truncated bird data” or TBD throughout the rest of the thesis. In this data structure, only birds occupying that specific habitat plot were counted and recorded, and all bird observations outside of the plot were disregarded. We calculated avian species richness by using the maximum number of species observed in each habitat type. Shannon-Weiner diversity scores and avian richness were calculated using the “vegan” package in R version 3.4.4. To supplement this study further, we also investigated the presence/absence of specific functional guilds of birds in each habitat type. Here we used the TBD and pooled our observations across the seasons. For this analysis, we grouped all birds into 5 functional guilds: shorebirds (American Avocets, White-faced Ibis, etc.), marsh birds (Virginia Rail, American Bittern, etc.), waterfowl

(Cinnamon Teal, Mallard, etc.), songbirds (Common Yellow-throat, Red-Winged Blackbirds, etc.), and water birds (Double-crested Cormorant, Forster’s Tern, etc.).

Multifunctionality Measurements

To evaluate the level of multifunctionality within each habitat type, we used two methods. The first is known as the "averaging" approach (Byrnes et al., 2014). Using the individual functional data collected, we developed a multifunctionality index (MI) for each of the seven habitat types. We calculated an MI by first taking the mean and standard deviation of each ecosystem function to create a Z-score (standardized deviate) for each observation of that function (Maestre et al., 2012). For functions that were measured in subplots, the values were averaged together to create one value per plot, which was then Z-transformed. Z-scores are a common method for standardizing functions that have been measured in different, non-comparable units (Byrnes et al., 2014). We weighted all functions equally by adjusting the Z-scores of functions that contained multiple independent measures of that function. For example, heavy metal accumulation is a single function, however, we measured the accumulation of six different metals, which would up-weight this function if we included a Z-score for each metal independently in our MI. To equally weight our functions, we calculated a Z-score for each independent measure of that function and then took the average Z-score as the final score. To calculate the overall MI of each plot, we averaged the weighted Z-scores for all the functions (Byrnes et al., 2014), with a higher MI indicating a higher level of multifunctionality.

In addition to the average MI, we also evaluated multifunctionality performance using the "threshold" approach (Byrnes et al., 2014). This approach allowed for the investigation of how many functions are being maintained above a set of desired thresholds (Byrnes et al., 2014; Gamfeldt, Hillebrand & Jonsson, 2008; Zavaleta et al., 2010). For this approach, the threshold was based upon the averaged maximum observed value for each function. This maximum observed value was calculated by averaging the top eight scores [this averaging number was determined by using the smallest sample size of the functions measured (Byrnes et al., 2014)]. For bird diversity, we used only the overall annual Shannon-Weiner diversity index as opposed to individual season indices. Since habitat types varied in their ability to store different metals, we included each independent metal in our threshold approach. Because we did not combine the metals, we indicated the average number of metals contributing to each habitat's threshold score (Fig. 9) to visualize if metal accumulation was driving high threshold scores.

After calculating maximum values for each function, we used a sensitivity analysis by setting thresholds at 20%, 40%, 60%, and 80% of the calculated maximum value for each function to determine functional performance. The number of functions reaching each threshold was summed for each plot, with a higher sum indicating that more functions were being provided at that threshold.

Data Analysis

We investigated the effect of habitat type on below-ground carbon and nitrogen stocks, using an analysis of variance (ANOVA). Differences among habitat types for below-ground carbon and nitrogen stocks were analyzed using Tukey's post-hoc test. All analyses were done using the "stats" "lme4" and "multcomp" packages in R version 3.4.4. To determine the effect of habitat type on above-ground carbon and nitrogen stocks, heavy metal accumulation, plant biomass, seed AME, MI and MI thresholds, we used a linear mixed-effect model (LME) with subplots as the random effect. An LME was chosen over a linear model to account for the variation that may have occurred among the subplots. All analyses were done using the “lme4” and “multcomp” packages in R version 3.4.4. Differences between habitat types for all ecosystem functions were further analyzed using Tukey’s post-hoc test.

To examine the effect of habitat type on avian presence/absence, a bias reduced binomial-response generalized linear model using the R package “brglm” was used. A Chi-test between the model and a null model was used to determine overall model significance. An uncorrected Tukey’s post-hoc test was done to determine differences between habitat types.

RESULTS

Carbon storage

There was a significant difference between habitat types in below-ground carbon stocks (Fig. 2a; $P < 0.001$). Post-hoc Tukey’s analyses indicated that playa and *S. rubra* had significantly lower below-ground carbon stocks, 32-46% less, compared to *B. maritimus*, *T. latifolia*, and *S. acutus*, but was not significantly different from *S. americanus* and *P. australis.* There was no significant difference in below-ground carbon stocks between *B. maritimus*, *T. latifolia*, *S. acutus*, *S. rubra*, *S. americanus*, and *P. australis* (all $P > 0.05$).

Similar to below-ground carbon stocks, there was a significant difference between habitat types in above-ground carbon stocks. Tukey’s tests indicated that *P. australis* and *T. latifolia* stored significantly more above-ground carbon than the other habitat types (P

< 0.01) with the exception of *S. acutus* which was not significantly different from *T. latifolia* (P = 0.89) but was less than *P. australis* (P = 0.007). *B. maritimus*, *S. rubra*, and *S. americanus* had significantly lower above-ground carbon stocks compared to all other habitat types (P < 0.01) and stored 66-96% less above-ground carbon than *P. australis* and *T. latifolia* but were not significantly different than one another (Fig. 2b).

Nitrogen storage

We found a significant difference among habitat type and below-ground nitrogen stocks (Fig. 3a; P < 0.001). *T. latifolia, S. acutus*, and *S. americanus* all stored significantly more below-ground nitrogen than the other habitats (all P < 0.001). *P. australis* stored an intermediate amount of below-ground nitrogen and was not significantly different from *B. maritimus* or *T. latifolia* (Fig. 3a). *B. maritimus, S. rubra*, and playa had significantly lower below-ground nitrogen stocks compared to all the other habitat types, with 57-74% less nitrogen than the highest storing species, *T. latifolia, S. acutus,* and *S. americanus*.

Above-ground nitrogen stocks also significantly differed among habitat types (Fig. 3b; P < 0.001). However, the patterns in above-ground nitrogen stocks varied greatly from below-ground nitrogen stocks. *P. australis* stored significantly more above-ground nitrogen than all other habitat types (P < 0.01). *S. acutus* stored the second most above-ground nitrogen and was significantly different from all other habitat types (all P < 0.01). *B. maritimus, S. rubra, T. latifolia,* and *S. americanus* stored 77-97% less above-ground nitrogen than *P. australis* but were not significantly different from each other (Fig. 3b).

Above-ground biomass

Our results indicate that *P. australis* had significantly more above-ground biomass than all other habitat types (Fig. 4; all $P < 0.001$), with the exception of *T. latifolia* ($P = 0.09$). *S. acutus* was not significantly different than *T. latifolia* ($P = 0.92$). *B. maritimus*, *S. rubra*, and *S. americanus* had 66-93% less biomass than *P. australis*, *T. latifolia*, and *S. acutus*, but were not significantly different from each other.

Heavy metal accumulation in above-ground biomass

With the exception of arsenic (Fig. 5b; $P = 0.052$), metal accumulation differed significantly among habitat types (all $P < 0.05$). However, the patterns in metal accumulation among the different habitat types varied depending on the metal analyzed. For copper, *P. australis* stored significantly more copper than the other habitats (Fig. 5a; $P < 0.05$) with the exception of *T. latifolia* and *S. americanus*. However, *T. latifolia* and *S. americanus* did not differ significantly from *B. maritimus*, *S. rubra*, or *S. acutus* (all $P > 0.05$). *P. australis* also stored significantly more mercury compared to the other habitat types (Fig. 5e; all $P < 0.05$). *S. acutus* stored significantly more selenium (up to 67% more) and lead (up to 70% more) compared to any other habitat type (Figs 5c and 5d; all $P < 0.01$). None of the other habitat types significantly differed from one another in selenium or lead storage (all $P > 0.05$). Finally, *S. rubra* stored up to 90% more cadmium than any other habitat types (Fig. 5f; all $P < 0.001$). *T. latifolia, S. americanus, P. australis, and S. acutus* did not differ from one another in cadmium storage (all $P > 0.05$).

Seed nutritional value

We found a significant difference in seed nutritional value among habitat types (Fig. 6; $P < 0.001$). A post-hoc Tukey's analysis revealed that *T. latifolia* greatly exceeded (> 60%) the nutritional value per area compared to all other species ($P < 0.001$). No other habitats were significantly different from each other.

Avian species diversity

The Shannon-Weiner diversity indices (DI) for habitat type varied by season (Table 2). *S. acutus* had the highest diversity index score in spring (DI = 2.472463), *T. latifolia* had the highest index score in fall (DI = 2.079416), and *B. maritimus* had the highest score in summer, as well as the combined season score (DI = 2.021678; DI = 2.582014). *P. australis* had the lowest diversity scores across all categories with the exception of fall.

Avian species richness

Bird species richness (R) also varied by season (Table 2). *S. rubra* has the highest richness in the spring (R = 19), *T. latifolia* had the highest richness in the fall (R = 14), and *B. maritimus* had the highest richness in the summer, as well as combined across the seasons (R = 21; R = 29). *S. americanus* had the lowest richness across all categories.

Avian guild presence/absence

There was a significant difference in the occurrences of shorebirds in the different habitat types (Fig. 7a; $P < 0.001$). There were significantly more shorebirds observed in *B. maritimus* than in any other habitat ($P < 0.05$) with the exception of *S. rubra* ($P = 0.1$) and playa ($P = 0.08$), which did not significantly differ from *B. maritimus*. We also observed significantly more shorebirds in *S. rubra* and playa compared to *P. australis* (both P < 0.05). Although we did not observe any shorebirds in *P. australis,* the occurrence of shorebirds in *P. australis* did not significantly differ from *S. acutus*, *T. latifolia*, or *S. americanus* (all P > 0.05).

We also found a significant difference in the occurrences of marsh birds among the different habitat types (Fig. 7b; P = 0.0003). Significantly more marsh birds were observed in *T. latifolia* compared to playa, *S. rubra*, *S. americanus, B. maritimus,* and *S. acutus* (all P < 0.05). However*, S. acutus* and *P. australis* were not significantly different from *T. latifolia* (P = 0.12 and P = 0.28, respectively) and were not significantly different from each other (P= 0.54) or from *B. maritimus* and *S. americanus* (all P > 0.1). We observed more marsh birds in *P. australis* compared to *S. rubra* and playa (P < 0.05). *S. rubra,* playa, *S. americanus, B. maritimus,* and *S. acutus* were not significantly different from each other, despite that no marsh birds were observed in playa.

There was a significant difference in the occurrences of songbirds among the different habitat types (Fig. 7d; P < 0.0001). Significantly fewer songbirds were observed in playa (P < 0.05). We found no other significant differences between the habitat types.

There was also a significant difference in the occurrence of water birds among the different habitats (Fig. 7e; P < 0.006). We observed significantly more water birds in *S. rubra* and playa compared to *S. americanus* (P = 0.02 and P = 0.03, respectively) and *P. australis* (P = 0.05). No other significant differences were observed between the habitats for water birds (all P > 0.05). Finally, we found no significant differences in the occurrences of waterfowl (Fig. 7c; all P = 0.2446).

Multifunctionality averaging approach

There was a significant difference in the multifunctionality of the different habitat types when analyzed using the standardized averaging approach (Fig. 8; $P < 0.001$). *T. latifolia*, *P. australis*, and *S. acutus* all had a multifunctionality index 1.5-2X higher than all other habitats ($P < 0.001$) but were not significantly different from each other. *B. maritimus*, *S. rubra*, and playa were not significantly different from each other. *S. americanus*, while not significantly different from *B. maritimus* or playa, was significantly higher than *S. rubra* ($P = 0.018$).

Thresholds approach

We found a significant difference between habitat multifunctionality at all four (20%, 40%, 60% and 80%) functional thresholds (all $P < 0.001$; Fig. 9). *Typha latifolia, P. australis*, and *S. acutus* could maintain more functions at the 20%, 40%, and 60% thresholds compared to the other habitats (all $P < 0.001$), with the exception of *S. americanus* which was not significantly different from the three habitats at the 20% threshold. *Typha latifolia, P. australis*, and *S. acutus* still maintained more than *B. maritimus*, *S. rubra*, *S. americanus*, and playa (all $P < 0.05$) at every threshold. Finally, at the 80% threshold, *S. acutus and P. australis* maintained the greatest number of functions (~3). *Typha latifolia* could perform ~2 functions about the 80% threshold and was not significantly different from any habitat type while the remaining habitats were only capable of maintaining a single function at 80% of the maximum and were significantly different from *S. acutus and P. australis* ($P < 0.05$).

CHAPTER DISCUSSION

In this study, we tested the ability of different GSL wetland habitat types to provide a variety of independent ecosystem functions, as well as multiple ecosystem functions simultaneously relating to carbon storage, nitrogen storage, primary production, heavy metal accumulation, and avian habitat. We found that the different habitat types varied in their abilities to support independent ecosystem functions and multifunctionality. Considering that wetland plants along the GSL and elsewhere grow in large monotypic stands, our results indicate that habitat-level diversity is important for maintaining a wide range of ecosystem functions. Our results are consistent with another study that focused on multifunctionality at a landscape-level within highly managed, monotypic stands of forests (van der Plas et al., 2016), and those from smaller-scale studies (Pasari et al., 2013; van der Plas et al., 2016).

We found that no single wetland species can support all eight of the ecosystem functions measured. In fact, not a single species can support all eight functions even at the 20% threshold. Of all the habitat types, in terms of individual functions, *T. latifolia* performed the best (Table 3), supporting the highest level of functioning for seven of the functions measured (including all six metals as their own function). *T. latifolia* did particularly well for functions related to carbon and nitrogen storage, primary production, and some aspects of bird habitat provisioning. The invasive plant, *P. australis* was the second-best performing species (Table 3), with high levels of functioning for functions related to above-ground biomass, such as primary production, above-ground nitrogen, and carbon storage. However, it performed poorly in terms of bird habitat, which is the primary focus of management efforts at BRMBR (Rohal et al., 2018). *Schoenoplectus acutus* came in third and performed well for sequestering below-ground carbon and nitrogen as well as selenium and lead (Table 3). The lowest performing habitats were playa and *S. rubra*, likely due to their lack of above-ground biomass, an important characteristic for many of the ecosystem functions we focused on in this study. Although *S. rubra* was also low scoring in most functions, it was the only habitat that accumulated the heavy metal cadmium. In fact, metal accumulation required the largest diversity of habitat types, with copper primarily accumulating in *S. americanus*, *P. australis,* and *T. latifolia*, selenium and lead primarily accumulating in *S. acutus*, mercury primarily accumulating in *P. australis*, cadmium primarily accumulating in *S. rubra*, and arsenic accumulating in all plant species equally. These results reinforce the idea that habitat heterogeneity is needed to support a diversity of ecosystem functions (Pasari et al., 2013; van der Plas et al., 2016; Alsterberg et al., 2017).

We investigated the ability of different GSL wetland habitat types to provide not only individual functions but also their multifunctional abilities. We found that the habitats differed in their multifunctional abilities, as well as their ability to perform multiple functions above certain thresholds. At the 80% threshold, only *S. acutus, T. latifolia* and *P. australis* were able to provide more than a single function, however *S. acutus's* high threshold score was largely the result of its ability to accumulate several types of metals. We also found that *T. latifolia, S. acutus* and *P. australis,* provided the highest level of multifunctionality through the averaging approach. The high levels of multifunctionality offered by *P. australis* suggests that this aggressive invasive is capable of supporting multiple services related to nutrient storage and heavy metal uptake, which supports its current use in many constructed wetlands for remediation (Calheiros, Rangel, & Castro, 2009) and a more nuanced view of this plant for its provisioning of ecosystem services more generally (Kiviat 2013). Unfortunately, *P. australis'* ability to support nutrient storage and heavy metal uptake appears to come at the cost of providing bird habitat for GSL avian fauna. However, native *T. latifolia* and *S. acutus* also had comparable multifunctional capabilities to *P. australis* and provide better bird habitat, suggesting that a trade-off between functions that support bird habitat and those that support nutrient and heavy metal accumulation may not be necessary.

The three bulrush species are the focus of most of the restoration efforts for the GSL (Marty, 2016; Marty & Kettenring, 2017; Rohal et al., 2018). *S. acutus* performed the most individual functions of the three bulrush species and had one of the highest multifunctionality indices of any wetland species. Specifically, *S. acutus* had high below-ground carbon and nitrogen storage, and also high lead and selenium accumulation. *B. maritimus* generally performed poorly for heavy metal accumulation and nutrient storage, with the exception of below-ground carbon, and it had one of the lowest multifunctionality indices. However, *B. maritimus* had some of the highest bird diversity of any of the habitats. *S. americanus* also had a low multifunctionality index but performed well for below-ground nitrogen storage. Despite that bulrush seeds are thought to be an important component of the diet of migrating waterfowl in GSL (Petrie et al., 2013), they had similar or lower AME compared to the other wetland species, particularly *T. latifolia*. However, the seeds of all these species tend to ripen at different times of the year and may be chosen by different types of birds (generalists vs. specialists) and may have different seasonal importance in avian diets throughout the year. Overall, these results suggest that in order to maintain a diversity of functions in the GSL, wetland restorations should focus on maintaining a high level of habitat diversity.

Although *T. latifolia* and *P. australis* showed high multifunctionality, a more thorough examination of these species and our results is warranted for wetland managers. First, it should be noted that both *T. latifolia* and *P. australis* are considered aggressive and spread rapidly. Planting these species or reducing the control of them in wetlands may cause further habitat degradation through habitat homogenization, which would be detrimental to the overall functioning and health of the ecosystem as functions unique to other habitats would be lost. For example, playa and *S. rubra,* and *B. maritimus* are critical habitat for migratory shorebirds (a major priority for BRMBR) and this function cannot be replaced or mitigated with other, more multifunctional, habitats such as *T. latifolia*. Second, although playa, *S. rubra,* and *B. maritimus* had low multifunctionality, this was in part due to the fact that the functions chosen to be measured in this study heavy relied on aboveground biomass. Playa, *S. rubra,* and *B. maritimus* had the lowest above-ground biomass which would naturally give them lower values for heavy metal accumulation, aboveground biomass, and primary production. Third, it is also important to remember that each species grows best in different physiological conditions (i.e. water levels and salinities) and these differences likely play into their unique functional roles in the ecosystem. When focusing on revegetating and restoring wetlands, different factors including unique functional abilities, multifunctionality, and growth characteristics of different habitats need to be considered and understood to best develop effective management plans.

Certain limitations arose from this study because the BRMBR and GSLSP are highly disturbed wetlands. Also, some aspects of wetland management techniques may have had an impact on our results. One large obstacle these wetlands face is a lack of senior water rights (Frank et al., 2016). Because these wetlands are located at the bottom of the watershed, they are not always supplied with adequate water to support plant growth (Downard et al., 2014). The water received is diverted and heavily controlled by wetland managers who decide which areas to flood or drain (Downard et al., 2014). This kind of water manipulation could have affected several of our ecosystem functions such as plant biomass and seed production. These wetland systems are also exposed to cattle grazing to remove *P. australis* (Duncan 2019). Although none of the areas were actively grazed during the collection of the ecosystem functions for this study, historical grazing could have resulted in legacy effects on some of our functions. It is well known that grazing can influence below-ground carbon stocks through compaction of the soil (Davidson et al., 2017). Finally, in some areas of BRMBR, *P. australis* was heavily treated with herbicides, which could have had legacy effects on its biomass and seed production. Although these limitations and disturbances may have affected the expression of our ecosystem functions, many wetlands across the USA and elsewhere are heavily managed and have similar management practices and disturbances to those in BRMBR and GSLSP (Brinson & Malvárez, 2002).

GSL wetlands are highly dynamic in nature and face many threats including invasive species, pollution, urban encroachment, and water loss (Kettenring et al., 2012; Downard et al., 2014; Wurtsbaugh et al., 2017; Li, Endter-Wada, & Li, 2019). By developing an understanding of the different functions offered by the different wetland habitats, we can make more informed decisions about restoration efforts. Our results suggest that if managers want to maintain a diversity of ecosystem functions relating to carbon storage, nitrogen storage, heavy metal accumulation, and bird habitat provisioning, they will need to incorporate a diversity of plant species into revegetation efforts. However, wetland managers are often targeting specific functions. In these cases, our results help managers identify potential functional synergies and trade-offs that may occur because of their management decisions. The results from this study also further our understanding of multifunctionality at a landscape-scale and the importance of maintaining diversity, in this case, habitat diversity, even in relatively species-poor ecosystems. Although our study supports the importance of habitat diversity for functioning, our focus was on a single wetland system in the GSL basin. To further our understanding of the dynamic and complex nature of wetland multifunctionality, future efforts should focus on different wetland systems in multiple settings. Understanding the interplay between landscape-level diversity and ecosystem functioning can give us the tools to better manage our wetland resources, plan for future needs, and meet restoration goals in the face of a changing planet (Zedler 2000, Zedler and Kercher 2005, Finlayson et al., 2018).

DISCUSSION

This thesis investigated the individual and multifunctional abilities of different GSL wetland habitat types. GSL wetlands face many disturbances and issues, most notably, habitat homogenization due to the aggressive invader *P. australis* (Kettenring, de Blois, & Hauber, 2012). There have been many efforts to remove *P. australis* and restore these wetlands to maintain bird habitat (Rohal et al., 2018). Despite their importance, very few studies have assessed the functional abilities and values of the different wetland habitat types in the GSL. This gap in knowledge hinders restoration efforts because we do not fully understand how ecosystem functions and services are changing across GSL because of *P. australis* and efforts to manage its spread. To fill this knowledge gap, we studied eight ecosystem functions that support climate mitigation, water quality, primary production, and habitat provisioning for wildlife across seven different habitat types. We found that there was no single habitat type that could perform every function at a high level. We also found that the habitats differed in their ability to provide multiple services simultaneously but again, no one habitat was able to support more than three functions at 80% of the maximum functioning levels. This suggests that even in relatively species-poor systems, species and habitat diversity are important for maintaining multiple functions.

The results of this study enhance our understanding of habitat diversity-multifunctionality relationships and support the theory that increased biodiversity is critical in maintaining a multi-functional ecosystem. However, our study was done in an ecosystem where species diversity happens at the habitat-scale because wetlands in the GSL form large monotypic stands of wetland species. Enhanced ecosystem functioning in our system as a result of increased diversity may be more related to sampling effect than complementarity because species are too far apart spatially to facilitate one another. This may suggest that the mechanisms governing the relationship between biodiversity and ecosystem functioning are scale dependent.

The findings of this study not only add to the growing field of biodiversity and ecosystem functioning research but also have large implications for stakeholders wishing to manage ecosystem functions across the GSL and other wetlands. Our results can help managers select wetland plant species that optimize specific individual functions or multifunctionality. In our study, we found that wetland managers may be missing out on an opportunity to enhance several individual functions by narrowly focusing revegetation efforts on only a few native species, and that such a management decision is likely to lead to the loss of overall functioning of a wetland. Also, *P. australis* provided a surprising array of ecosystem functions, despite its invasive nature; although it provided poor habitat provisioning for avian fauna. In addition, our results can help managers identify potential synergies and trade-offs among functions. For example, revegetation efforts that focus solely on *B. maritimus* because it supports high bird diversity may lead to negative effects such as eutrophication and enhanced heavy metal toxicity in wildlife because of this species poor ability to take up nitrogen and heavy metals. Understanding such trade-offs are important to ensure that management actions do not lead to future degradation of the system and that informed decisions are being made about the management of habitats that provide a diversity of ecosystem services to different end-users.

In conclusion, this study adds novel and valuable findings that further our understanding of the biodiversity and ecosystem functioning relationship and help support management decisions in GSL wetland. Our research findings underscore the importance of maintaining habitat diversity in the GSL wetlands if we are to sustain a multifunctional ecosystem. Furthermore, our research adds to the growing field of landscape multifunctionality research and emphasizes the importance of future studies to investigate ecosystem multifunctionality at large spatial scales. Ecosystems across the planet are facing many challenges and pressures such as habitat homogenization and climate change. To better protect and restore our valuable resources and the services they provide, it is critical that we more fully understand the dynamic relationship of biodiversity and functioning.

Table 1. The wetland ecosystem functions measured in this study paired with the ecosystem services they represent, and the methods used to measure them.

Ecosystem Function	**Ecosystem service**	**Measurement**
Regulatory	Climate Mitigation	Above & Below-ground Carbon Stocks (Mg/ha)
	Water Purification	Above & Below-ground Nitrogen Stocks (Mg/ha), Above-ground Heavy Metal Accumulation (ug/m^2)
Provisioning	Primary Productivity	Above-ground Biomass (g/m^2)
Habitat	Habitat Provisioning	Bird Diversity, Richness, Presence/Absence, Seed Nutrition

Table 2. Shannon-Weiner diversity index scores (DI) and richness (R) calculated among different Great Salt Lake wetland habitat types. Calculations were done for each season as well as combined. (BOMA= *Bolboshoenus maritimus*, PHAU= *Phragmites australis*, PLAYA= playa, SARU= *Salicornia rubra*, SCAC= *Schoenoplectus acutus*, SCAM= *S. americanus,* and TYLA= *Typha latifolia*,).

	Spring		**Summer**		**Fall**		**Combined**	
Habitat	**DI**	**R**	**DI**	**R**	**DI**	**R**	**DI**	**R**
BOMA	2.13	13	2.02	21	1.76	13	2.58	29
PHAU	1.68	11	0.49	11	1.10	7	1.14	16
PLAYA	2.14	13	1.82	9	1.16	8	2.38	23
SARU	2.14	19	1.61	10	1.02	9	2.38	27
SCAC	2.47	14	1.38	9	1.00	7	2.22	19
SCAM	1.81	10	1.03	5	0.97	5	1.99	14
TYLA	2.17	18	1.81	12	2.08	14	2.40	27

Table 3. A comparison of Great Salt Lake wetland habitat types and functions provided. Highlighted areas indicate the habitat type(s) that was the highest performer for that certain function. Function abbreviations: A-G C= above-ground carbon (Mg/ha), A-G N= above-ground nitrogen (Mg/ha), A-G Bio=above-ground biomass (g/m^2), B-G C= below-ground carbon (Mg/ha), B-G N= below-ground nitrogen (Mg/ha), Seed= apparent metabolic energy (kCal/m^2), Div= bird diversity across all seasons, Rich= bird richness across all seasons, Cu= above-ground copper accumulation (mg/m^2), As= above-ground arsenic accumulation (mg/m^2), Se= above-ground selenium accumulation (mg/m^2), Pb= above-ground lead accumulation (mg/m^2), Hg= above-ground mercury accumulation (mg/m^2), Cd= above-ground cadmium accumulation (mg/m^2). (BOMA= *Bolboshoenus maritimus*, PHAU= *Phragmites australis*, PLAYA= playa, SARU= *Salicornia rubra*, SCAC= *Schoenoplectus acutus*, SCAM= *S. americanus*, and TYLA= *Typha latifolia*,).

Function	**Habitat**						
	BOMA	**PHAU**	**PLAYA**	**SARU**	**SCAC**	**SCAM**	**TYLA**
A-G C		X					X
A-G N		X					
A-G Bio		X					X
B-G C	X				X		X
B-G N					X	X	X
Seed							X
Div	X						
Rich	X						
Cu		X				X	X
As	X	X		X	X	X	X
Se					X		
Pb					X		
Hg		X					
Cd				X			
Total	**4**	**6**		**2**	**5**	**3**	**7**

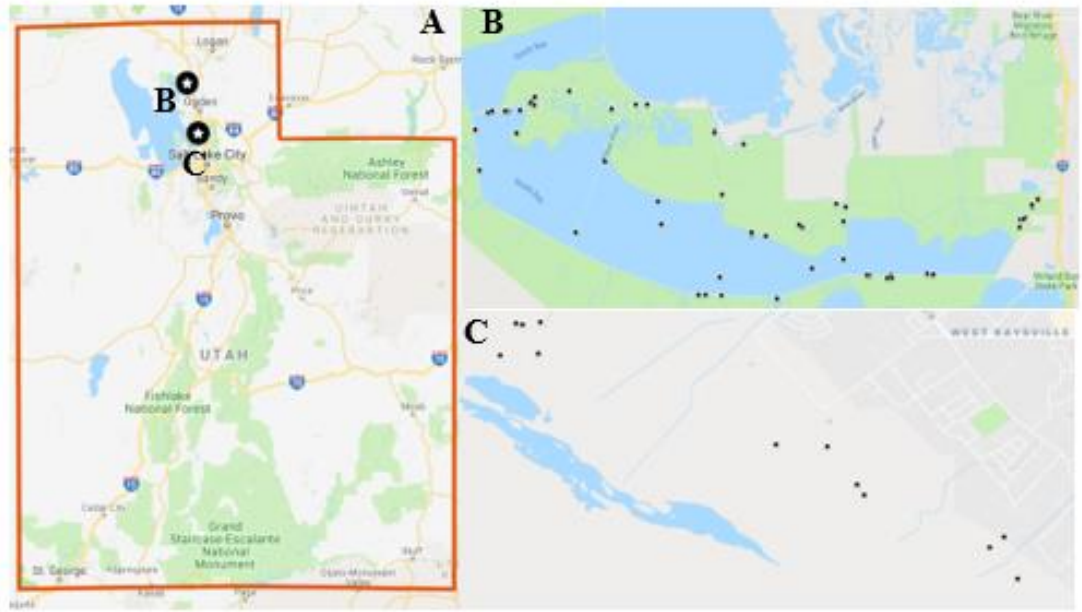

Fig. 1. Locations of plots in this study. All plots were located on the east side of the Great Salt Lake in Northern Utah within the Bear River Migratory Bird Refuge and The Nature Conservancy. Sites are identified with a star (A). Plot locations within the Bear River Migratory Bird Refuge (B). Plot locations within The Nature Conservancy Great Salt Lake Shorelands Preserve (C). Plots are identified with a black dot.

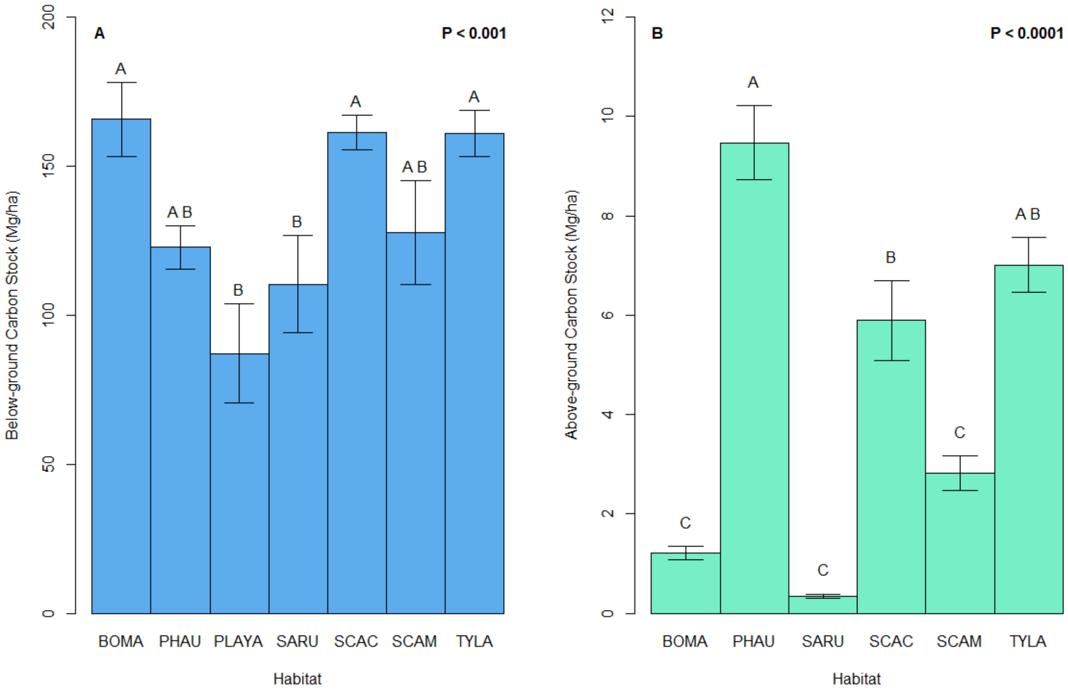

Fig. 2. Average (± s.e.) below-ground carbon stocks (Mg/ha) (A) and above-ground carbon stocks (Mg/ha) (B) among Great Salt Lake wetland habitat types. Letters above bars show significant differences between habitat types. (BOMA= *Bolboshoenus maritimus*, PHAU= *Phragmites australis*, PLAYA= playa, SARU= *Salicornia rubra*, SCAC= *Schoenoplectus acutus*, SCAM= *S. americanus*, and TYLA= *Typha latifolia*,).

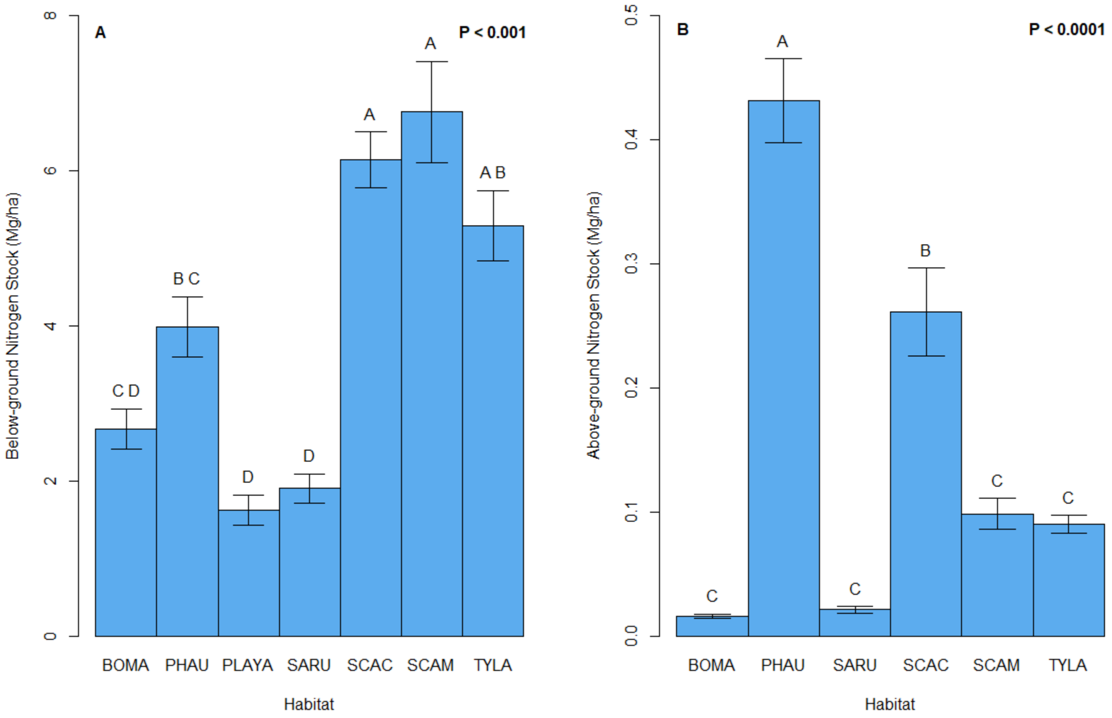

Fig. 3. Average (± s.e.) below-ground nitrogen stocks (Mg/ha) (A) and above-ground nitrogen stocks (Mg/ha) (B) among Great Salt Lake wetland habitat types. Letters above bars show significant differences between habitat types. (BOMA= *Bolboshoenus maritimus*, PHAU= *Phragmites australis*, PLAYA= playa, SARU= *Salicornia rubra*, SCAC= *Schoenoplectus acutus*, SCAM= *S. americanus*, and TYLA= *Typha latifolia*,).

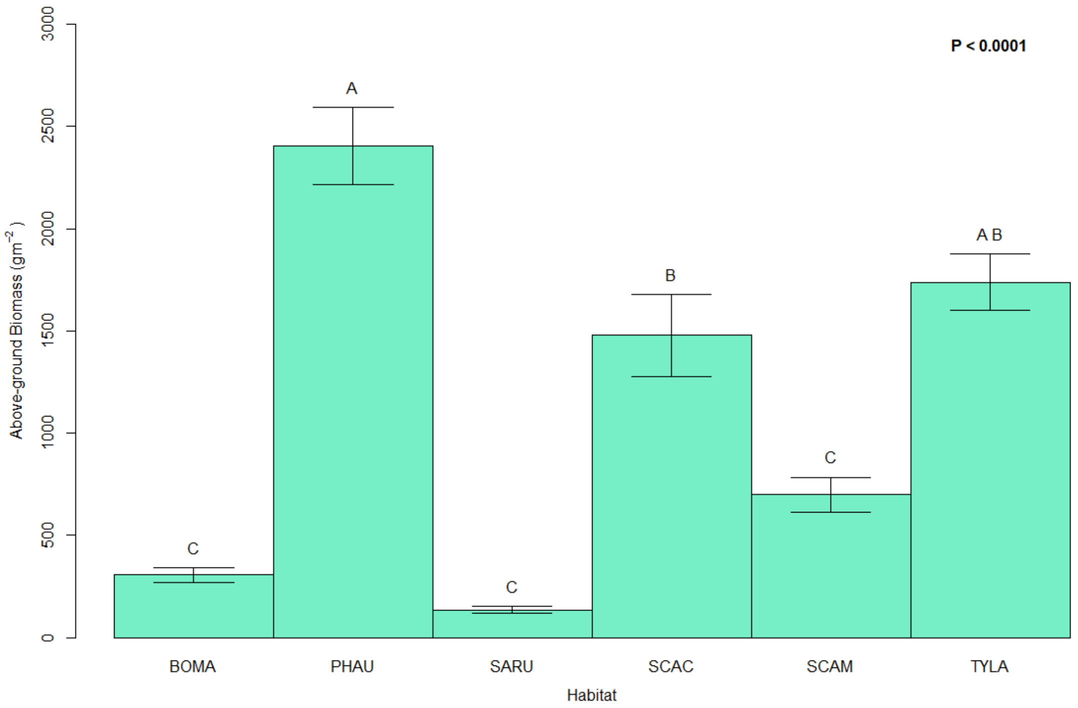

Fig. 4. Average (± s.e.) above-ground biomass (g m^{-2}) among Great Salt Lake wetland habitat types. Letters above bars show significant differences between habitat types. (BOMA= *Bolboshoenus maritimus*, PHAU= *Phragmites australis*, SARU= *Salicornia rubra*, SCAC= *Schoenoplectus acutus*, SCAM= *S. americanus*, and TYLA= *Typha latifolia*,).

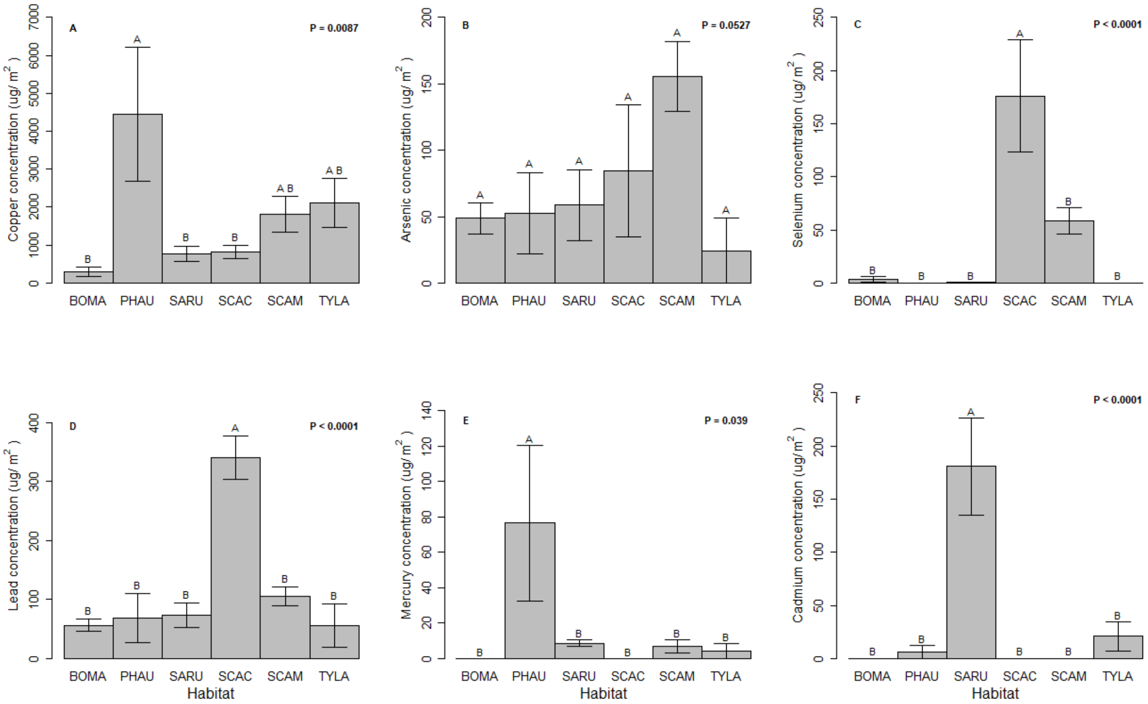

Fig. 5. Average (± s.e.) above-ground heavy metal accumulation (ug/m^2) in different Great Salt Lake wetland habitats: copper (A), arsenic (B), selenium (C), lead (D), mercury (E), and cadmium (F). Letters above bars show significant differences between habitat types. (BOMA= *Bolboshoenus maritimus*, PHAU= *Phragmites australis*, SARU= *Salicornia rubra*, SCAC= *Schoenoplectus acutus*, SCAM= *S. americanus*, and TYLA= *Typha latifolia*,).

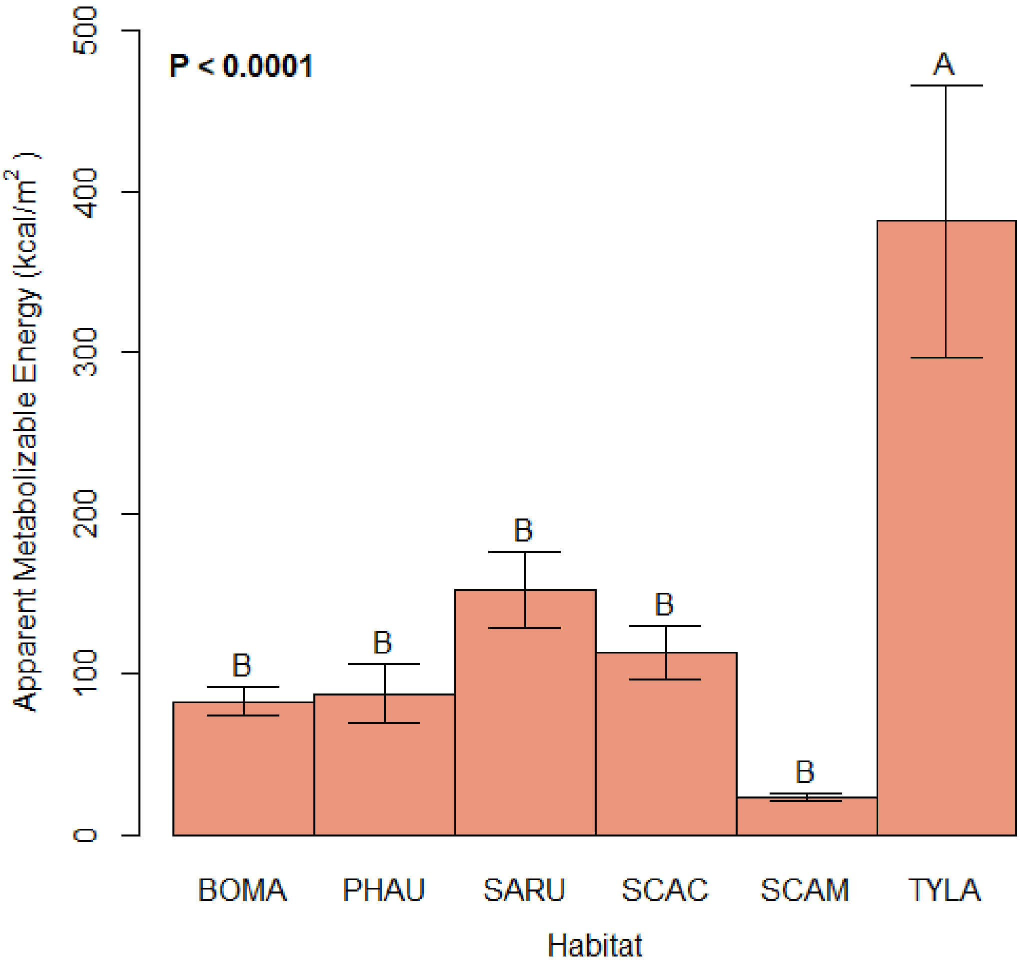

Fig. 6. Average (± s.e.) apparent metabolizable energy (kCal/m^2) in different Great Salt Lake wetland habitats. Letters above bars show significant differences between habitat types. (BOMA= *Bolboshoenus maritimus*, PHAU= *Phragmites australis*, SARU= *Salicornia rubra*, SCAC= *Schoenoplectus acutus*, SCAM= *S. americanus*, and TYLA= *Typha latifolia*,).

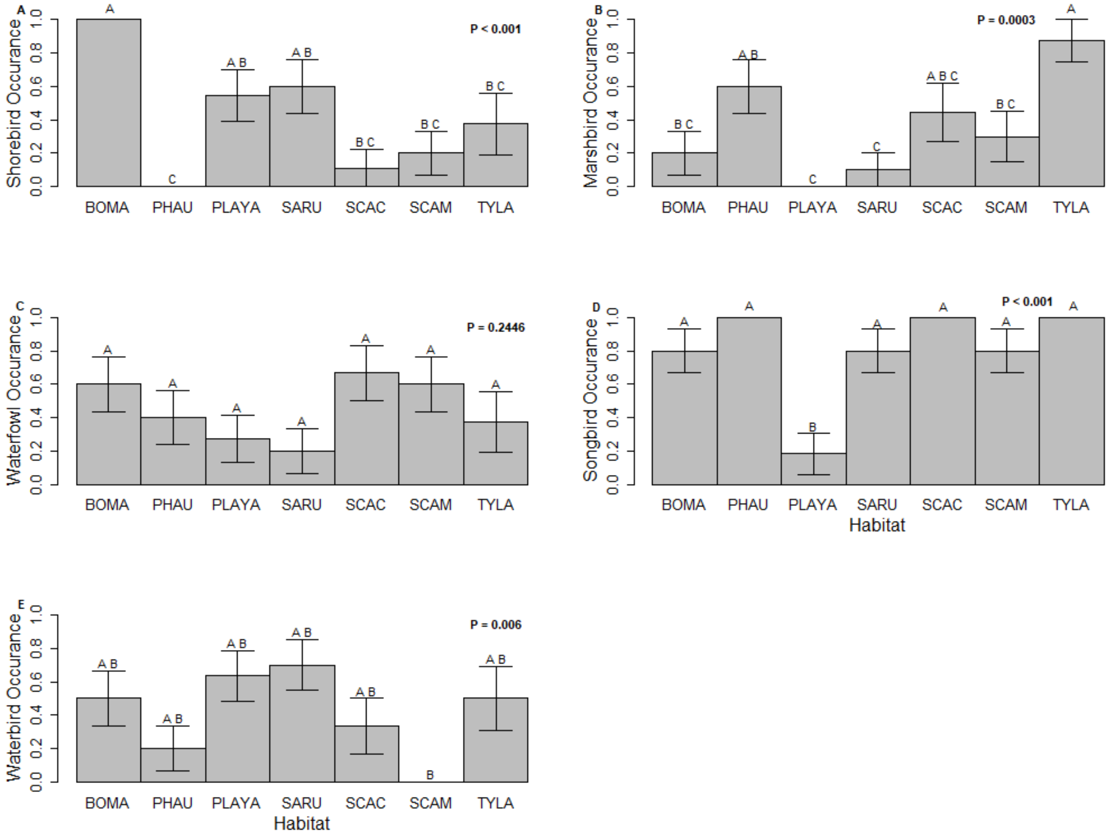

Fig. 7. Average (± s.e.) occurrences (based on presence/absence surveys) of five different avian guilds in different Great Salt Lake wetland habitats: Shorebirds (A), Marshbirds (B), Waterfowl (C), Songbirds (D), and Waterbirds (E). Letters above bars show significant differences between habitat types. (BOMA= *Bolboshoenus maritimus*, PHAU= *Phragmites australis*, PLAYA= playa, SARU= *Salicornia rubra*, SCAC= *Schoenoplectus acutus*, SCAM= *S. americanus*, and TYLA= *Typha latifolia*,).

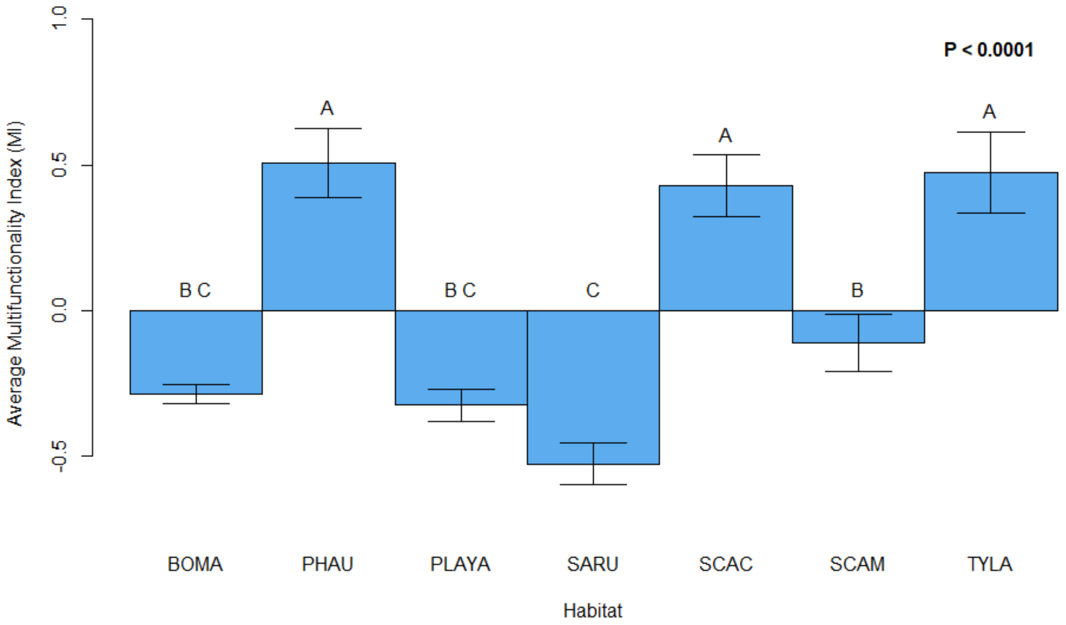

Fig. 8. Average (± s.e.) multifunctionality index (MI) score among Great Salt Lake wetland habitat types. Letters above bars show significant differences between the habitat types. (BOMA= *Bolboshoenus maritimus*, PHAU= *Phragmites australis*, PLAYA= playa, SARU= *Salicornia rubra*, SCAC= *Schoenoplectus acutus*, SCAM= *S. americanus*, and TYLA= *Typha latifolia*,).

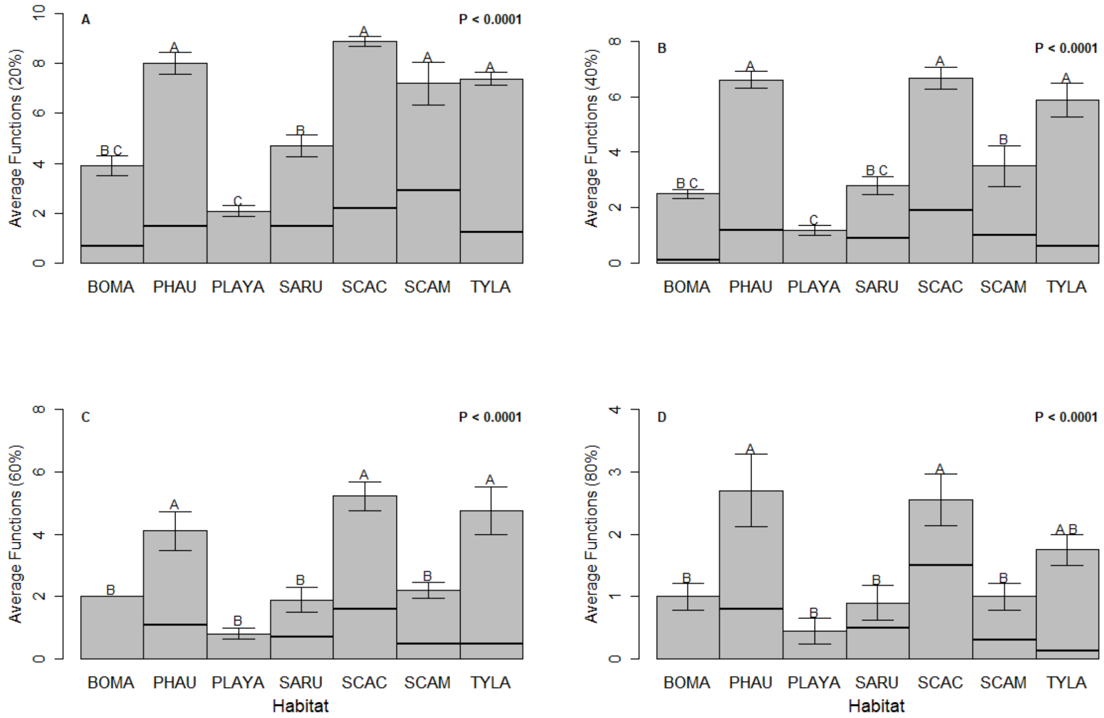

Fig. 9. Average (± s.e.) number of functions being performed by different Great Salt Lake wetland habitats at four different thresholds of maximum functional value: 20% (A), 40% (B), 60% (C), and 80% (D). Letters above bars show significant differences between the habitat types. Black solid lines within bars indicate the average number of metals contributing to the threshold index. (BOMA= *Bolboshoenus maritimus*, PHAU= *Phragmites australis*, PLAYA= playa, SARU= *Salicornia rubra*, SCAC= *Schoenoplectus acutus*, SCAM= *S. americanus*, and TYLA= *Typha latifolia*).

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APPENDICES

Table A1. The individual carbon and nitrogen factors for each Great Salt Lake wetland habitat type. These conversion factors were used to determine above-ground carbon and nitrogen stocks in each habitat type. (BOMA= *Bolboshoenus maritimus,* PHAU= *Phragmites australis,* SARU= *Salicornia rubra,* SCAC= *Schoenoplectus acutus,* SCAM= *S. americanus,* and TYLA= *Typha latifolia,*).

Habitat Type	Nitrogen Conversion Factor	Carbon Conversion Factor
BOMA	0.00521	0.393209
PHAU	0.017959	0.393966
SARU	0.015651	0.253707
SCAC	0.017674	0.398884
SCAM	0.014109	0.402797
TYLA	0.005181	0.40311

Table A2. Predictive equations used to determine the total number of seeds in a head for different Great Salt Lake wetland habitats. Equations were made by making an allometric equation based on weight and total seeds in ~15-20 seed heads of each species. (BOMA= *Bolboshoenus maritimus*, PHAU= *Phragmites australis*, SCAC= *Schoenoplectus acutus*, SCAM= *S. americanus*, and TYLA= *Typha latifolia*,).

Species	BOMA	PHAU	SCAC	SCAM	TYLA
Predictive Equation	$y = 328.09x - 8.7864$	$y = 3325x + 10.168$	$y = 776.55x - 85.666$	$y = 532.47x - 3.5517$	$y = 13690x + 12.56$
R^2 value	0.9666	0.9321	0.9546	0.9636	0.9532

Table A3. Averaged nutritional composition of different Great Salt Lake wetland species. MC= moisture content, CP= crude protein, CF= crude fat, ADF= acid detergent fiber, NDF= neutral detergent fiber, GE= gross energy, and AME= apparent metabolic energy. (BOMA= *Bolboshoenus maritimus*, PHAU= *Phragmites australis*, SARU= *Salicornia rubra*, SCAC= *Schoenoplectus acutus*, SCAM= *S. americanus*, and TYLA= *Typha latifolia*,).

Species	**BOMA**	**PHAU**	**SARU**	**SCAC**	**SCAM**	**TYLA**
% MC	6.9	7.2	6.2	7.3	6.7	5.8
% CP	7.9	30.1	8.2	7.2	7.2	22.2
% CF	3.3	3.6	7.1	3.7	3.5	19.5
% Ash	2.7	3.8	25.4	3.4	4.5	4.1
% ADF	28.0	22.1	21.7	52.6	52.4	43.8
% NDF	44.0	52.7	41.5	64.1	64.3	56.0
GE (kcal/g)	4.329	4.656	3.594	4.310	4.252	5.414
AME (kcal/g)	2.848	2.793	2.281	2.307	2.491	3.172
AME (kcal/m^2)	82.510	87.224	152.14	113.57	23.027	381.60

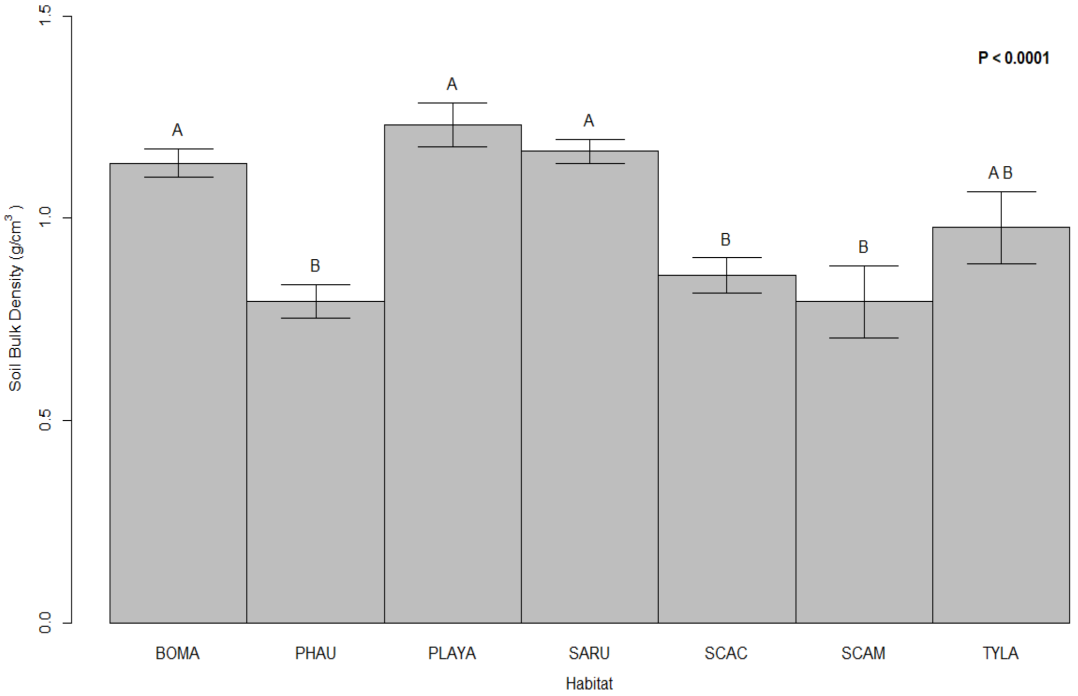

Fig. A1. Average (± s.e.) soil bulk density (g/m^3) among Great Salt Lake wetland habitat types. Letters above bars show significant differences between habitat types. (BOMA= *Bolboshoenus maritimus*, PHAU= *Phragmites australis*, PLAYA= playa, SARU= *Salicornia rubra*, SCAC= *Schoenoplectus acutus*, SCAM= *S. americanus*, and TYLA= *Typha latifolia*,).