Great Salt Lake Wetland Vegetation and What it Tells Us About Environmental Gradients and Disturbance

Becka Downard
Utah Geological Survey, Salt Lake City, Utah, beckad@utah.gov

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ABSTRACT

Great Salt Lake (GSL) wetlands support more than 300 species of migratory birds and provide many ecosystem functions, including flood and drought attenuation, dust mitigation, and water quality improvement. Wetland vegetation is a key factor in providing those functions and can also tell us about how healthy a wetland is. From 2013 to 2022, 135 GSL wetlands were surveyed to develop a multi-metric index of GSL wetland condition. That wetland condition data, along with environmental variables like soil and water chemistry and physical disturbance, are summarized here as 1) an ecological characterization of the three main types of GSL wetlands, 2) a description of how the plant community differs across environmental and anthropogenic disturbance gradients, and 3) assessment of the major risks to GSL wetland health. GSL wetland plant species are generally resistant to environmental disturbance because of the anatomical and physical adaptations that allow them to survive in dynamic wetland environments. However, land use conversion and the rapid expansion of invasive species, the major threats to GSL wetland health, have seriously degraded wetland condition around GSL. In addition to being useful in wetland monitoring and assessment, the results presented here can also identify wetlands in need of enhanced protection or those with restoration potential as well as setting realistic wetland restoration goals for the region.

INTRODUCTION: THE GREAT SALT LAKE ECOSYSTEM

Great Salt Lake (GSL) and its surrounding wetlands are often described in superlative terms: great, immense, critical, and essential. GSL is the largest saline lake in North America and eighth-largest in the world. More than 1,500 square kilometers of wetlands thrive on the margins of GSL where freshwater flows toward the lake (Figure 1). Millions of birds representing 338 species rely on GSL wetlands to power their migrations across the Western Hemisphere (Sorenson and others, 2020). Studying the plant community that thrives in GSL wetlands highlights significant features of natural history, the impacts of wetland management and human disturbances the GSL ecosystem experiences, and how to best protect and restore the wetlands in the future.

GSL Natural History

GSL is all that remains of historical Lake Bonneville which occupied much of northern and western Utah 15,000 years ago but shrank as the regional climate became much drier (Inkenbrandt, 2021). GSL is a terminal lake with no surface water outlets, water only leaves through evaporation. The solutes rivers bring to GSL have concentrated over time and currently the lake is more than three times saltier than ocean water, ranging in salinity between 125 and 185 g/L (U.S. Geological Survey, 2023). The Bear, Weber, and Jordan rivers provide approximately 90% of the water to GSL. The GSL watershed occupies a total of 91,908 square kilometers, an immense area within which changes in climate, water availability, and water quality can impact the GSL ecosystem (Zedler and Kercher, 2004; Ramsey and others, 2009). The rivers supplying GSL terminate in massive deltas composed of diverse wetland types, from sparsely vegetated saline playas to freshwater marshes and ponds.

Wetlands are defined by three characteristics: the presence of water for part of the year, soils with low oxygen (hydric soils), and plants adapted to flooding and low oxygen (Mitsch and Gosselink, 2015). Within that definition, a variety of environmental conditions create diverse wetland types with their own suite of ecosystem functions, from water quality improvement to hydrologic and climate regulation (Wetzel, 2006). The diversity of wetland types in GSL river deltas as well as their expansive size allows the ecosystem to support many species of birds, from tiny Snowy plovers to massive American white pelicans (Aldrich and Paul, 2002).

Though GSL wetlands are a reliable place for migratory birds to feed and nest, they are hardly static. Wetlands are dynamic habitats, shifting between

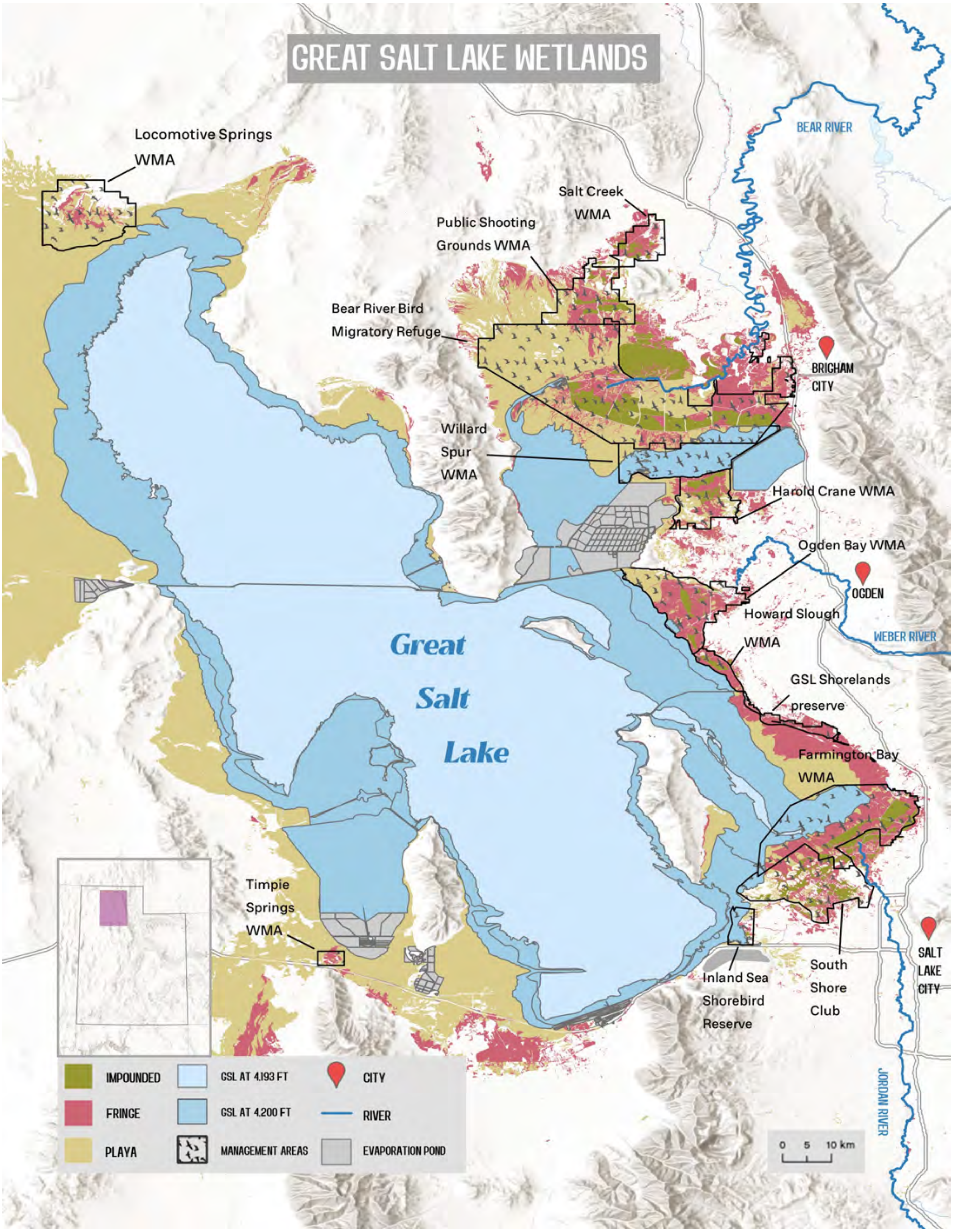

Figure 1. *Great Salt Lake ecosystem includes the lake and 1,500 sq. km of wetlands. Map by Grant Mauk. Wetlands layer (U.S. Fish and Wildlife Service, 2018), rivers and lakes layer (U.S. Geological Survey, 2020), Digital Elevation Model (Quantum Spatial, Inc, 2017)*

flooded and dry over the growing season and bridging the transition between aquatic and terrestrial environments; GSL wetlands are especially dynamic. Terminal lakes fluctuate in area much more than other lakes and this has big implications for GSL wetlands (U.S. Geological Survey, 2023). In high water conditions, the hypersaline waters of GSL can rise to inundate the wetlands, but as the lake retreats during drought, wetlands occupy the lakebed. These changes in area are significant; by one estimate, 180 square kilometers of lakebed are exposed for every foot in elevation that GSL falls (Aldrich and Paul, 2002). Within the wetland complexes, changes in water availability shift the boundaries between terrestrial, wetland, and fully aquatic environments.

GSL Human History

Peoples of the Ute, Paiute, Goshute, and Shoshone nations utilized GSL wetlands for centuries, but European settlers have left the most distinct marks on the system (Madsen, 2015). When John C. Fremont saw the Bear River delta in 1843, he described the sound of birds taking off as having "wings of thunder" because the birds were so numerous. European settlers arrived in the Salt Lake Valley in 1847 and immediately began diverting tributaries of the Jordan River to support agriculture. The Transcontinental Railroad was completed at the northern end of GSL in 1869 bringing industry and transportation of agricultural goods (Baxter and Butler, 2020). By the 1920s the Bear River delta had been dewatered so severely that avian botulism was leading to massive bird die-offs in the few locations migratory birds found habitat (Wilson and Carson, 1950). Local communities pressed Congress for the establishment of a federal wildlife refuge in the Bear River Delta and the first act of refuge building was the construction of a series of dikes to hold water in the river delta when it was available in the spring and manage drawdown more slowly during the irrigation season (Downard and Endter-Wada, 2013). This intense impounded wetland water management practice was successful in preserving migratory bird habitat and has been adopted by state waterfowl management areas, private hunting clubs, and conservation areas (Figure 1) (Downard and others, 2014).

According to both researchers and stakeholders, upstream consumptive water use and subsequent drought downstream is the primary threat to GSL wetlands and the lake itself (Wurtsbaugh and others, 2017; Utah Division of Water Quality, 2019). In the last century, the elevation of GSL has fallen approximately 11 feet due to diversion of surface water for human needs (Wurtsbaugh and others, 2016). In October 2022, GSL fell to a record low elevation of 4,188.7 feet which exposed thousands of square kilometers of lakebed (U.S. Geological Survey, 2023). Water quality threats, most notably legacy phosphorus bound to soils, also impact the GSL ecosystem and become more problematic as water availability decreases (Utah Division of Water Quality, 2014). Invasive species, especially *Phragmites australis*, complicate the water situation even further by changing how water flows across the very flat landscape and altering nutrient cycles in wetlands (Kettenring and others, 2020).

GSL Wetlands Ecology and Ecosystem Services

The path surface water follows through GSL wetlands from river to lake is a complex mix of deliberate management actions and unintended consequences of upstream water diversions and nearby water discharges. GSL wetlands are divided into three classes—impounded, fringe, and playa wetlands— that shift in area according to where water is available and how long and deep flooding is. Impounded wetlands are the most deeply flooded wetland class and are flooded for the longest part of the year. Fringe wetlands may be flooded nearly as deeply as impounded wetlands, but water depth often fluctuates between flooded and dry stages over the growing season. Playa wetlands are often not flooded, but saturated. The relatively permanent flow of water into impounded and fringe wetlands keeps them fresh to brackish, especially compared to the saline waters of playa wetlands and GSL.

Wetland vegetation is both a defining feature of wetlands and an indicator of the ecosystem functions wetlands perform and integrates the environmental stresses and anthropogenic disturbances a wetland faces over time (Moor and others, 2017). Differences in the growth form, life cycle, wetland indicator status, and habitat specificity of plant species present in wetlands vary over gradients of water regime, management history, and disturbance (Lytle and Poff, 2004). Wetlands present a suite of challenges to plant life and wetland species have a number of common adaptations that allow them to grow and reproduce. A wetland plant in this region must deal with unpredictable water regimes, soil anoxia when water is present and drought stress when water is absent, a range of salinities, and periodic catastrophic flooding. Wetland environmental gradients, especially water depth and salinity, act like a sieve, filtering the species that can occupy that space (Van Der Valk, 1981).

Water regime—the pattern of flooding and drying in a wetland— is largely considered the most important factor in determining the wetland plant community (Mitsch and Gosselink, 2015). In wetlands with relatively permanent flooding, perennial species with specialized adaptations to flooding like aerenchyma and floating seeds are dominant (Cronk and Fennessy, 2001). Wetlands that fluctuate between flooded and dry states more frequently (i.e., those with more seasonal hydroperiods) have a unique suite of species as well, often rapidly growing species with dense networks of rhizomes that allow clonal species to share gases when wetlands are flooded and water when wetlands are dry (Cronk and Fennessy, 2001). Temporarily or ephemerally flooded wetlands in turn tend to have communities dominated by annual species, those that can complete their lifecycle in a single growing season if conditions are right (Keddy, 2010).

In addition to the broad life history traits outlined above, botanists can also characterize how specific a species' ecological requirements are (i.e., how conservative their habitat is) and the complementary measure of how tolerant it is to ecological or anthropogenic disturbance. Highly conservative species with a Coefficient of Conservatism (CC score) of 10 are only found in a specific type of habitat and are sensitive to disturbance (Lopez and Fennessy, 2002). Species that occupy a wider range of habitat types and tolerate more disturbance have lower CC scores. The most successful and widespread invasive species tend to be disturbance specialists—species that can exploit a disturbance that leaves exposed soils and elevated water nutrients—and have a default CC score of zero (Hazelton and others, 2014).

Wetland condition is analogous to ecosystem health or biological integrity and is most often measured by the plant community because the species occupying a wetland integrate multiple impacts over time. Ecologically, wetland condition is the ability of a plant community to maintain its structure and function, compared to wetlands in undisturbed locations. A wetland in good condition looks and functions similarly to pristine wetlands, whereas wetlands in poor condition have experienced enough disturbance that they no longer support the same plant community or ecosystem functions (Davies and Jackson, 2006). Unlike birds or macroinvertebrates, plants cannot migrate when conditions get tough. Some plant species can abide in places with high levels of disturbance where other species will be eliminated, and a multimetric index (MMI) captures the ways disturbance tolerators or more sensitive species shape the wetland community (Magee and others, 2019). An MMI is a combination of multiple variables describing some aspect of the plant community that changes with increasing anthropogenic disturbance (i.e., it measures the overall health of a wetland).

A discussion of stress and disturbance terminology is merited before jumping into the methods and results. Stress, natural disturbance, and anthropogenic disturbance have similar effects on the wetland plant community but differ in origin and the time scale they operate at. In this paper, stress is a factor that limits a plant's ability to grow and reproduce, like living in an environment with limited oxygen, extreme temperatures, or low nutrient availability (Grime, 1989). Stress is a relatively constant feature of the environment, while disturbance is more episodic (Borics and others, 2013). Flooding and drought, fire, herbivore grazing, and plant species invasions are common natural disturbances in wetlands that can alter the plant community (Cronk and Fennessy, 2001). Anthropogenic disturbances include converting land uses from natural types to developed sites, diverting water from streams or adding points of discharge with water quality contaminants (Miller and Wardrop, 2006). Though it is possible to define those three terms separately on paper, it is difficult to distinguish between the three in the wetlands because anthropogenic disturbances like water diversion and climate change can increase the frequency of natural disturbances and lead to long-term stress. Further, plant communities respond similarly to stress and both types of disturbance, often becoming less diverse and dominated by fast-growing species (Cronk and Fennessy, 2001). This paper focuses on plant community adaptations to environmental stresses of the dominant species in each wetland class as well as the overall wetland response to anthropogenic disturbances.

Impounded wetlands form the heart of managed wetland complexes where dikes impound the terminus of a river or stream. Impounded wetlands are the only GSL wetland class that has firm boundaries because they are defined by the presence of dikes or berms that are designed to increase the depth and length of time this wetland class is flooded. Water depth is managed throughout the year with headgates. The primary goal of impounded wetland management is to grow submerged aquatic vegetation (SAV) that supports migrating waterfowl (ducks, geese, and swans) (Figure 2a), though emergent vegetation is also a component of the impounded wetland community (Aldrich and Paul, 2002).

Fringe wetlands are defined by emergent vegetation that forms deltas where water sources like streams, springs, and impounded wetland water control structures discharge onto the bed of GSL (Figure 2b) (Utah Division of Water Quality, 2016). The mix of short and tall emergent species provides critical nesting habitat for waterfowl and ample food for waterbirds like white-faced ibis and egrets. The extent of fringe wetlands changes based on freshwater availa-

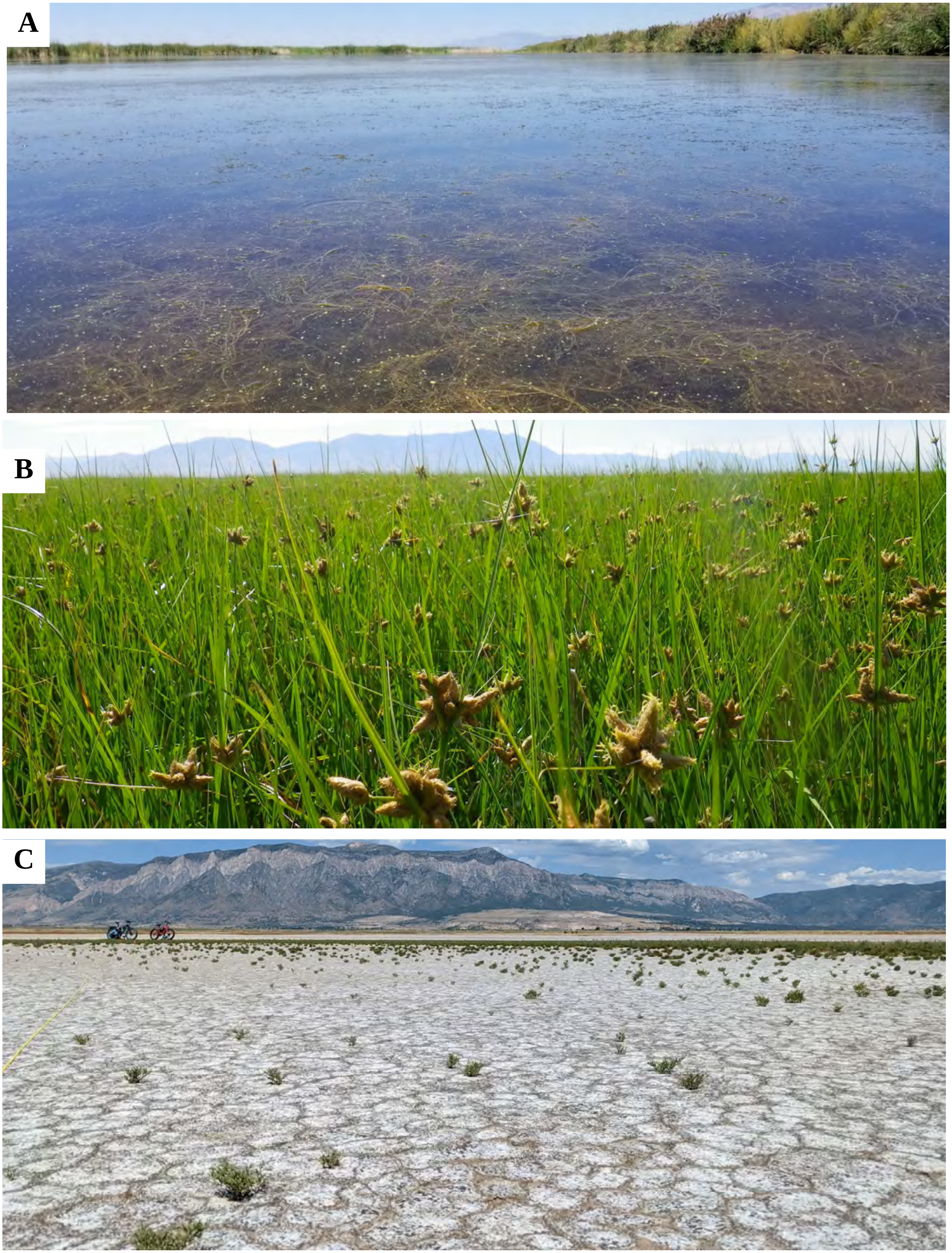

Figure 2. *Characteristic examples of A) impounded, B) fringe, and C) playa wetlands near GSL.*

bility, expanding where water is perennial and contracting when water is diverted elsewhere. Fringe wetlands are located outside the boundaries of impoundments and are commonly referred to as marshes and meadows.

Playa wetlands are ephemerally flooded or saturated, sparsely vegetated, often saline wetlands that support astounding populations of shorebirds, who probe the soils for macroinvertebrates (Figure 2c). This class contains two types of features, playas and mudflats. Playas are a geological feature that form in depressions often supported by shallow groundwater or precipitation (Oviatt, 2014). Mudflats are the exposed surfaces of drying lakes and wetlands. Though the processes that form playas and mudflats are different, they support the same vegetation communities and will be considered together here. As GSL has retreated over the last decade, playa wetlands have expanded to occupy the exposed lakebed. Depending on GSL elevation, playa wetlands account for as little as 40% or as much as 85% of the wetland acreage around GSL (U.S. Fish and Wildlife Service, 2018).

GSL WETLAND SURVEY METHODS AND ANALYSIS

The wetlands around GSL are a critical resource for Utahans and of great interest to many stakeholders, including the state agencies that pursued the projects described below. The data presented here are the result of more than ten years of vegetation monitoring in GSL wetlands with the overall objective of developing an MMI to measure wetland condition specific to this region. Altogether we have detailed vegetation data from five separate surveys that sampled 135 wetlands from all three GSL wetland classes. A summary of the site selection, field methods, and data analysis are presented below with citations to the supporting field protocols and detailed analysis documentation.

Site Selection

Survey sites were primarily selected via Generalized Random Tessellation Stratified (GRTS) samples. GRTS sample design creates spatially balanced samples that can be stratified by factors of interest and include factors that create unequal probabilities (Stevens and Olsen, 2004; Kincaid and others, 2019). Site selection for surveys conducted in 2019–2022 built on prior work with one key update: wetlands remained in the sample regardless of whether they had surface water during the time of sampling, in contrast to earlier surveys that required the presence of surface water to sample.

Forty impounded wetlands were surveyed in 2019, adapting protocols established in 2012. The GRTS samples were stratified so that an equal proportion of sites were drawn from the major watersheds of GSL (Bear, Weber, and Jordan) and an equal proportion of each size class (small, medium, and large) was represented (Utah Division of Water Quality, 2020) (Figure 3). The first fringe wetland surveys were conducted in 2013 and 2015 and gathered vegetation data from a targeted selection of sites. Rather than a random sample, project leaders selected sites they believed would represent the best and worst condition wetlands to capture the full range of condition possible (Utah Division of Water Quality, 2016). In 2020, 15 sites from a GRTS sample with no stratification were assessed to bring the collective number of fringe sites surveyed to 50. Finally, a 50-site GRTS sample of playa wetlands was surveyed in 2022. The playa sample was stratified by wetland system (palustrine or lacustrine) and an unequal probability factor was added to select more sites from HUC12 watersheds with higher percentage of riverine wetlands (Utah Division of Water Quality, 2022).

Field Methods

For all surveys, data were collected from 100 meter transects, though the placement and segmentation of those transects was adapted for each wetland class to capture the most representative vegetation (Utah Division of Water Quality 2020, 2022). Vegetation data was central to the analysis of each project, so each site visit was conducted during the index period that began on July 1 and ended on September 30, which captures the most representative and reliably identifiable vegetation. Impounded wetlands were visited twice during the survey, once during the early summer and later in the season. For all surveys, the identity and absolute cover of each species present along the 100-m transect was recorded as well as cover of bare ground, open water, and filamentous algae.

Water (surface water or pore water) and composite soil chemistry as well as on-site disturbance data were gathered in addition to vegetation data. Observations of physical disturbance within a 100-meter buffer surrounding the center point of each transect were recorded as well. Further details of laboratory analyses, data quality control, and individual project objectives are elaborated on in each survey's Sampling and Analysis Plan (Utah Division of Water Quality 2020, 2022).

Landscape disturbance data were gathered after field work from statewide geospatial layers. Small (100-meter) and large (1-kilometer) buffers were added to the center point of each wetland sampled and the prevalence of the following features were calcu-

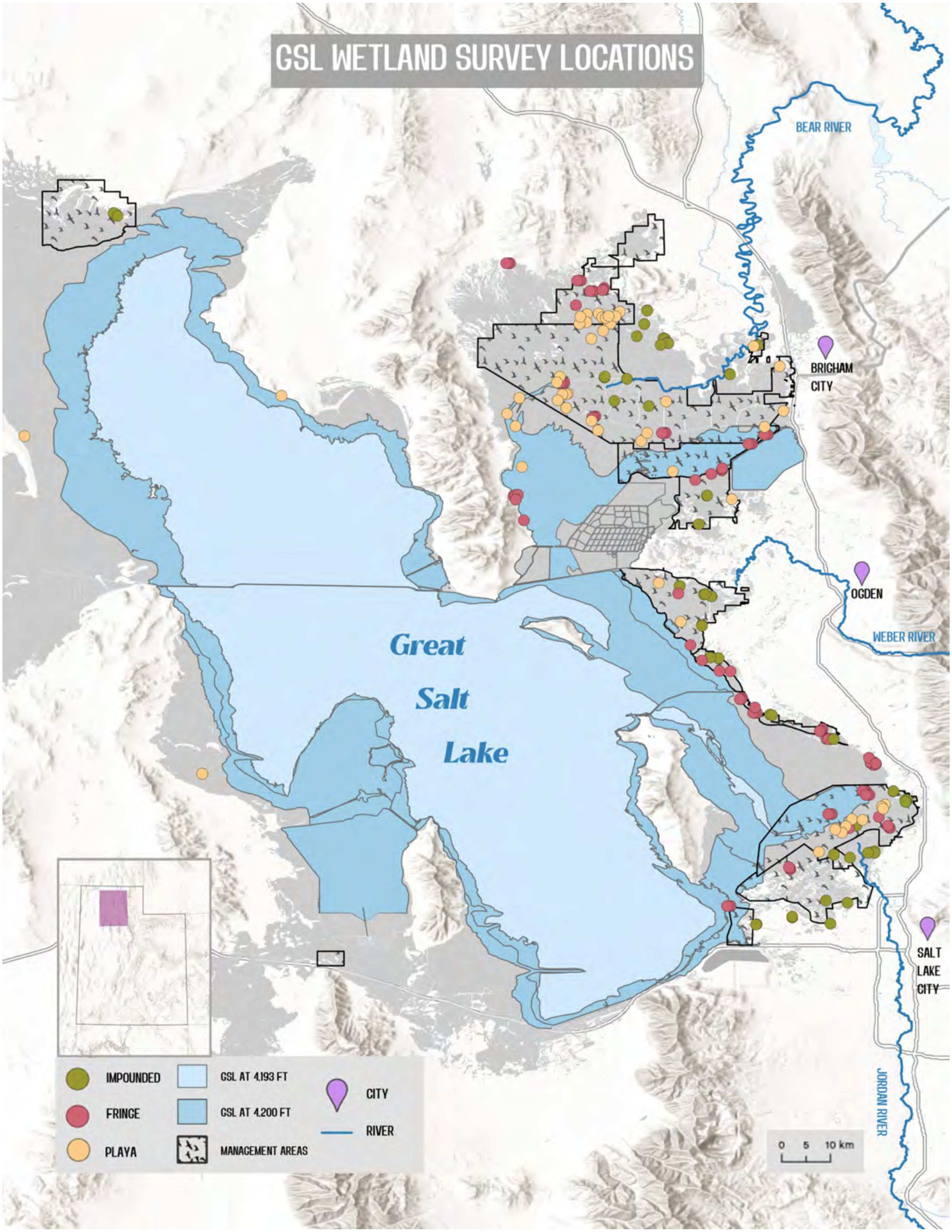

Figure 3. *Location of wetlands surveyed for this ecological characterization. Map by Grant Mauk. Wetlands layer (U.S. Fish and Wildlife Service, 2018), rivers and lakes layer (U.S. Geological Survey, 2020), Digital Elevation Model (Quantum Spatial, Inc, 2017).*

lated within those buffers: 1) agricultural and developed land uses; 2) impervious surface; 3) length of roadways; 4) water right points of diversion; 5) permitted point source and stormwater discharges; and 6) mineral mines and oil and gas wells (U.S. Geological Survey, 2019a and 2019b; Utah Geospatial Resource Center, 2020a, 2020b, 2020c, and 2020d).

Analysis

Data analysis occurred in three stages. First, a cumulative Disturbance Score was calculated for all GSL wetlands, which was in turn used to define reference condition for each wetland class. Second, a large group of vegetation metrics were calculated and then screened for their utility in measuring condition and built into MMI's. The third stage used the disturbance and condition indices to estimate the influence of individual anthropogenic disturbances on wetland condition. See Downard (2021) for further details of the analyses.

The Disturbance Score, modeled on the Anthropogenic Stress Indices developed for the National Wetland Condition Assessment (NWCA) is a cumulative measure of disturbance a wetland experiences based on nine measures (Lomnicky and others, 2019). The first four measures quantify land use impacts within the large one-kilometer site buffers: agricultural and developed land uses, extractive industry claims, and hydrologic modifications (impervious surface, roadways, diversions, and discharges). The fifth human disturbance metric is a standardized summary of the four large buffer metrics. Two disturbance measures are captured within the small 100-meter buffer: hydrologic modifications and vegetation removal by cattle grazing and herbicide use. The final two disturbance metrics that form the overall Disturbance Score were recorded from site visits—the number of heavy metals in soils that exceeded background concentrations and the relative cover of introduced species. Soil metal background concentrations were established specifically for GSL wetlands. Metals and metalloids selected for inclusion followed the recommendations of Nahlik and others (2019) and used a regression approach developed by Alfaro and others (2015).

Defining reference condition, the baseline against which wetland condition is compared to, is a critical step in any condition assessment. The simplest definition of reference condition is pristine, the state of a wetland that is not impacted by human activities (Stoddard and others, 2006). Wetland condition then measures how different a wetland is from reference (Davies and Jackson, 2006). However, un-impacted wetlands are nearly impossible to find, given the widespread nature of anthropogenic disturbance. Instead GSL wetland reference condition was defined as Least Disturbed Condition (LDC): the best available condition of wetlands is assumed to be those wetlands with the least amount of disturbance, accepting that human disturbance has impacted all wetlands to some degree. Defining LDC for each wetland class was an iterative process of determining the threshold of each type of disturbance included in the Disturbance Score that separated LDC from the more disturbed wetlands, following the lead of Herlihy and others (2019a). Choosing reference condition based on distributional approaches, as done here, is common and controversial. Assumptions about the impacts of disturbance, outliers and skewed data, and lack of minimally disturbed conditions can distort the results, thus the discussion of condition and risk should be interpreted with that knowledge in mind (Reynoldson and others, 1997).

To build an MMI of condition we calculated 211 potential vegetation metrics that captured some aspect of the plant community which were in turn sieved through a series of screens to test for applicability as a measure of wetland condition. Each vegetation metric fell into one of six categories: taxa composition, life history traits, hydrophytic status, sensitivity or tolerance to disturbance, vegetation structure, and floristic quality (Table 1). The PLANTS database lists the status of all plant species as native or introduced, life history and growth form traits, and their wetland indicator status (U.S. Department of Agriculture Natural Resource Conservation Service, 2020). Sensitivity and floristic quality measures of each species were retrieved from the NWCA database (U.S. Environmental Protection Agency, 2016). Differences in metrics between wetland classes were assessed using two univariate statistical methods. First, an Analysis of Variance (ANOVA) was conducted to determine if a metric varied by wetland class. If the ANOVA was significant ($p \leq 0.05$) then we conducted a pairwise t-test between combinations of wetland classes to determine which had significant differences.

Magee and others' (2019) NWCA data analysis provided guidance on sifting through potential MMI metrics by identifying those that span an appropriate range, are repeatable and responsive to disturbance. Skewed metrics or those observed over a very narrow range were removed as well as metrics that varied significantly over a single growing season (repeatability screen) or failed to distinguish between high and low disturbance sites (responsiveness screen). The 35 metrics that passed all three screens were equally scaled and standardized then assembled into unique MMI's of three, four, and five metrics. These candidate MMI's were screened through tests

Table 1. *Plant community attributes calculated based on wetland survey data.* Bold attributes are those selected in the final MMI.

Category	Metrics
Taxa Composition	Species Richness, Native Species [a], Introduced Species [a], Simpson's Diversity [b], Shannon-Wiener Diversity [b], Species Evenness
Life History [b]	Annual species, Perennial species, Forb species, Graminoid species, Monocot species, ***Dicot species***
Hydrophytic Status [b]	Obligate species, Obligate + Facultative Wetland species, ***Facultative Wetland Species***, Facultative Species, Facultative Upland + Upland Species
Sensitivity/Tolerance to Disturbance [b]	Sensitive Species, Intermediate + Insensitive Species, Tolerant Species, ***Highly Tolerant Species***
Vegetation Structure [b]	Emergent Species, Submerged Species, Floating Species, Algae, Bare Ground
Floristic Quality [c]	Mean Coefficient of Conservatism (CC), Total CC, Cover-weighted Mean CC, Floristic Quality Index, Cover-weighted Floristic Quality Index

a – metrics include total richness, relative richness, total cover, relative cover, mean cover, frequency, and importance
b – metrics calculated for all species present, native species only, and introduced species only
c – calculated for all species and native species only

of redundancy, sensitivity, and repeatability. The MMI described below has component metrics that are not highly correlated with one another (redundancy screen), distinguish between high and low condition wetlands (sensitivity screen), and remained consistent over the index period (repeatability) (Magee and others, 2019).

The final Great Salt Lake Vegetation-based Multi-Metric Index (GSL-VMMI) is a combination of three metrics: dicot species richness, cover of highly tolerant species, and cover of facultative wetland species. Each of those metrics increases with disturbance, thus wetlands in good condition have more monocot species than dicot species and higher cover of species that are less than highly tolerant of disturbance and obligate wetland species. Thresholds for good, fair, and poor condition were established individually for each wetland class based on the condition scores for sites that were in least disturbed reference condition (Magee and others, 2019). Setting condition thresholds based on a distribution is suboptimal because it creates a moving target with each new survey. However, it is the most realistic option for this dataset.

The final part of the analysis was to conduct a risk assessment calculating the influence of individual anthropogenic disturbances on wetland condition, measured as relative and attributable risk (Herlihy and others, 2019b). Relative risk is a ratio that expresses the likelihood that a wetland will be in poor condition when a particular disturbance is high. Attributable risk represents the proportion of wetlands in poor condition that could improve if a particular disturbance is removed. Thresholds for distinguishing between high and moderate levels of a particular disturbance were set by analyzing the distribution of a particular disturbance and setting "high" at a point that marked the 33rd percentile for disturbances with normal data distributions or the inflection point for disturbances with skewed distributions.

Risk estimates are calculated based on contingency tables that tabulate the number of wetlands in two condition categories— Not Poor Condition and Poor Condition— and two disturbance categories—High Disturbance and Not High Disturbance (Kincaid and others, 2019; R Core Team, 2020). The risk analysis assessed both the metrics that were part of the overall Disturbance Scores and individual parts of composite metrics (e.g., diversions were assessed separately from discharges) as well as potential sources of disturbance that are of particular interest to GSL stakeholders, like soil phosphorus and individual soil metals. Three significant assumptions go into the risk analysis: 1) there is causality between a disturbance and condition; 2) a disturbance is reversible; and 3) disturbances are independent (Herlihy and others, 2019b). Both risk calculations are bounded by 95% confidence intervals and require large datasets to detect statistically significant risks. Even with this relatively large dataset, the error bars on the risk estimates are quite large. Further, if any cell in the contingency table is empty (e.g., there are no sites in poor condition with high disturbance from mines) the estimate for both risk factors will be zero. The risk results should be taken with these grains of salt— big assumptions, big error bars, and missing estimates— in mind.

RESULTS: GSL WETLAND ECOLOGICAL CHARACTERIZATION

We used the data gathered in GSL wetlands to answer three questions. First, what plants characterize GSL wetlands and how are they similar or different between classes? Second, within a given wetland class, what factors drive variation in the plant community? Finally, over all GSL wetland classes, what disturbances represent the most significant risk to wetland condition?

What Plants Characterize GSL Wetlands?

Over the nine years of plant surveys, we found 123 unique species across three GSL wetland classes. Average species richness in GSL wetlands is five species per site, so even though we have a large species list, only 13 species were common, defined by being found in at least 10% of all GSL wetlands surveyed here, and most species were rare (Downard and others, 2018). The most common species varied according to the wetland class being surveyed (impounded, fringe, or playa wetlands), though species are not exclusive to wetland class and can be found in multiple wetland classes.

The first step in characterizing the community is to calculate and plot an ordination of the data, which summarizes complex patterns by visually highlighting species and sites that group together (McCune and Grace, 2002). Figure 4 is a non-metric multidimensional scaling (NMDS) output of GSL wetland plant communities calculated based on the relative cover of the most common GSL wetland species. Each color-coded point represents a wetland we sampled and the location along the vertical and horizontal axes show how similar or different the sampled plant communities are: points closer to each other have more similar communities and points farther from each other are more different. The text and grey points represent the center of a plant species' area and indicate the most important species in that part of the ordination.

Along the horizontal axis (NMDS 1), sites are

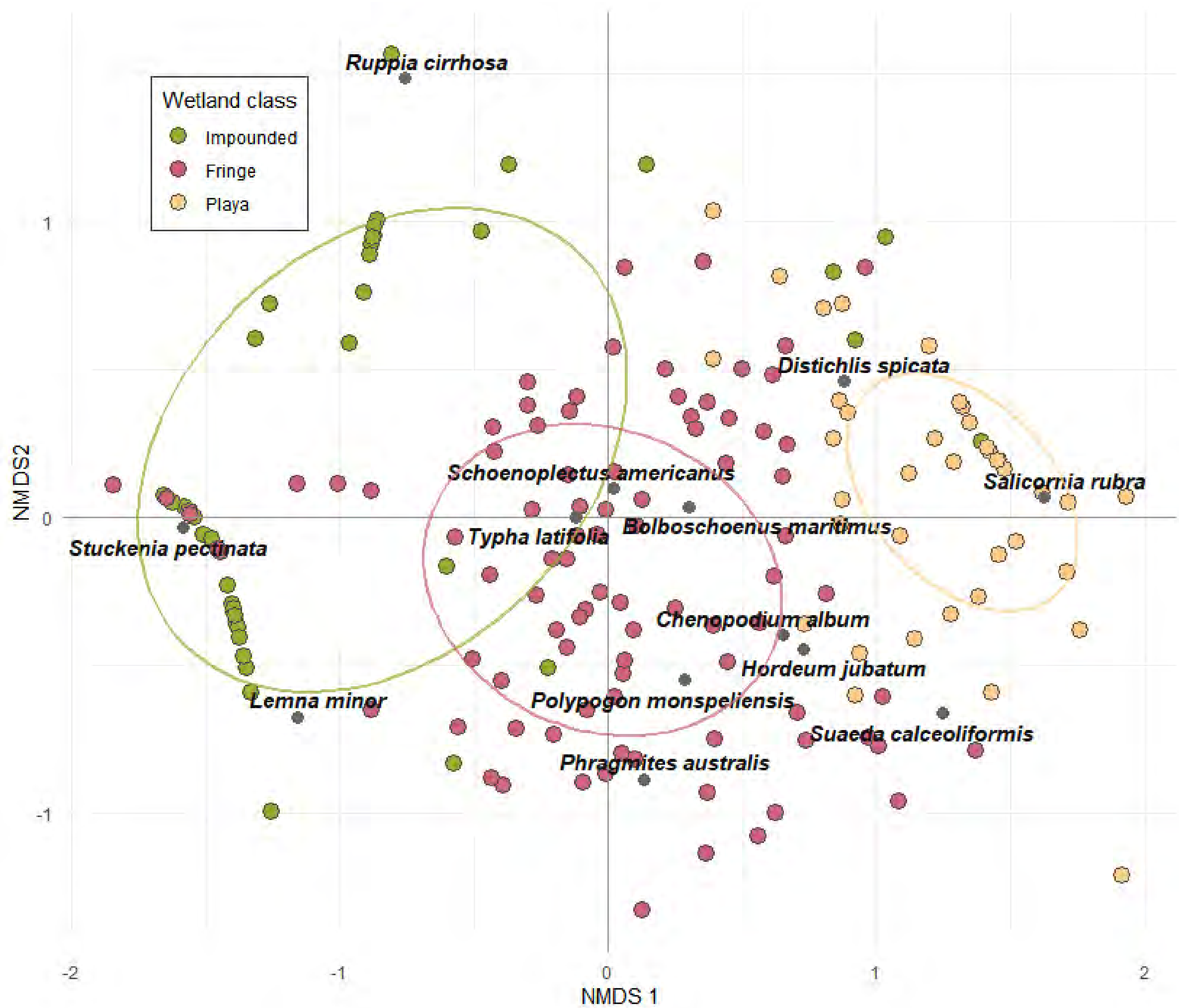

Figure 4. *Non-metric multidimensional scaling of GSL wetland plant community data. The ellipses represent a multivariate 95% confidence interval around the centroid of each wetland class.*

generally grouped according to wetland class. Impounded wetlands occupy the negative side of NMDS 1, fringe wetlands occupy the center, and playa wetlands are on the right side. This pattern also matches the differences in hydroperiod and salinity, with deepest flooding and freshest water on the left/impounded side and saturation with saline water on the right/playa side. Figure 5a shows the distribution of observed water depth measurements in each wetland class and Figure 5b shows the conductivity of surface water (impounded, fringe, and a minority of playa wetlands) or pore water (playa wetlands) recorded during field work. Impounded wetlands were flooded most deeply of the three wetland classes while playa wetlands rarely had recordable surface water. Salinity was similar between impounded and fringe wetlands, but significantly higher in playa wetlands.

Impounded wetlands are dominated by submerged aquatic vegetation (SAV) species (Table 2). For SAV to grow, these wetlands must be flooded for most or all of the growing season, which creates highly anoxic soil conditions that limits nutrient availability and drives the buildup of reduced forms of elements like selenium and mercury which can potentially be toxic (Cronk and Fennessy, 2001). Deep flooding also reduces light availability and gas exchange, which makes photosynthesis difficult (Mitsch and Gosselink, 2015). Adaptations to this challenging environment include being rootless (*Ceratophyllum demersem*, *Chara* spp), utilizing bicarbonate in photosynthesis cycles (*Stuckenia pectinata*, *C. demersem*), and having long, thin leaves that maximize surface area for light and gas exchange (all species in Table 2). Dense SAV growth drives many ecosystem functions; it provides structure for aquatic macroinvertebrates, sequesters metals and nutrients from soils temporarily, and oxygenates water through respiration (Cronk and Fennessy, 2001). All the plant and macroinvertebrate growth in impounded wetlands create critical feeding habitat for migratory birds, especially larger birds like waterfowl.

Emergent species of cattails (*Typha* spp), bulrushes (*Bolboschoenus* and *Schoenoplectus* spp), and grasses dominate in fringe wetlands (Table 3). Some emergent species can grow in water up to one meter deep (*Typha latifolia*), but really thrive in water that fluctuates between flooded and saturated or dry conditions that submerged species cannot tolerate (Larson, 1993). The species listed in Table 3 have life history strategies adapted to a variable water regime. The seeds of all four common fringe species require bare ground to germinate, though these species readily expand via clonal growth under flooded conditions. Clonal growth via adventitious rhizomes in combination with aerenchyma in their tissues allow patches of emergent species to share resources like oxygen and water across large distances, which supports the expanding margin of fringe wetlands (Cronk and Fennessy, 2001). Emergent marshes are some of the most productive habitats on Earth, enabling them to sequester soil metals and nutrients (Reddy and DeLaune, 2008). Dense vegetation also provides critical nesting habitat for migratory birds while vegetation that produces large seeds (e.g., bulrushes) also provides nutrient dense food (Sweetman and others, 2013, Marty and Kettenring, 2017).

Playa wetlands are largely defined by being mostly expanses of bare ground, but a couple species of halophytes—species that grow specifically in salty and alkaline locations—also thrive (Table 4). Most plant species cannot grow in saline environments because high salt concentration makes it difficult for plants to obtain water and acquire beneficial elements (Cronk and Fennessy, 2001). *Distichlis spicata* survives in saline wetlands through the ability to exude salt from specialized pores while *Salicornia rubra* has adopted succulence and the ability to concentrate salts in specialized cells (Welsh and others, 2004; Hauser, 2006). *S. rubra* is the only common annual species in GSL wetlands and reproduces strictly by seeds, allowing vegetation to appear seasonally based on water availability. *D. spicata*, on the other hand, most commonly reproduces through rhizomes, allowing it to share resources amongst clonal stems. While the plant species of playas do provide some food for migratory birds, the macroinvertebrates in the soils are the most crucial resource for shorebirds that can probe the soils (Sorensen and others, 2020). The isolated nature of playas also makes them critical nesting habitat for shorebirds because they are farther from infrastructure and predators than fringe or impounded wetlands.

How Do GSL Wetland Plant Communities Differ?

The simplest measure of a plant community is species richness, which is a count of how many species are present. Overall, species richness tends to be low in GSL wetlands but there are significant differences in richness between classes (Figure 6). Impounded wetlands have the lowest mean species richness (2.32), playa wetlands have intermediate richness (4.32), and fringe wetlands have the highest richness (7.92 species). Both high environmental stress and high disturbance environments tend to have low species richness (Cornk and Fennessy, 2001) and later analyses will try to parse the impacts of disturbance versus stress.

Whether plants present are native to the region or introduced from elsewhere is a clearer indicator of

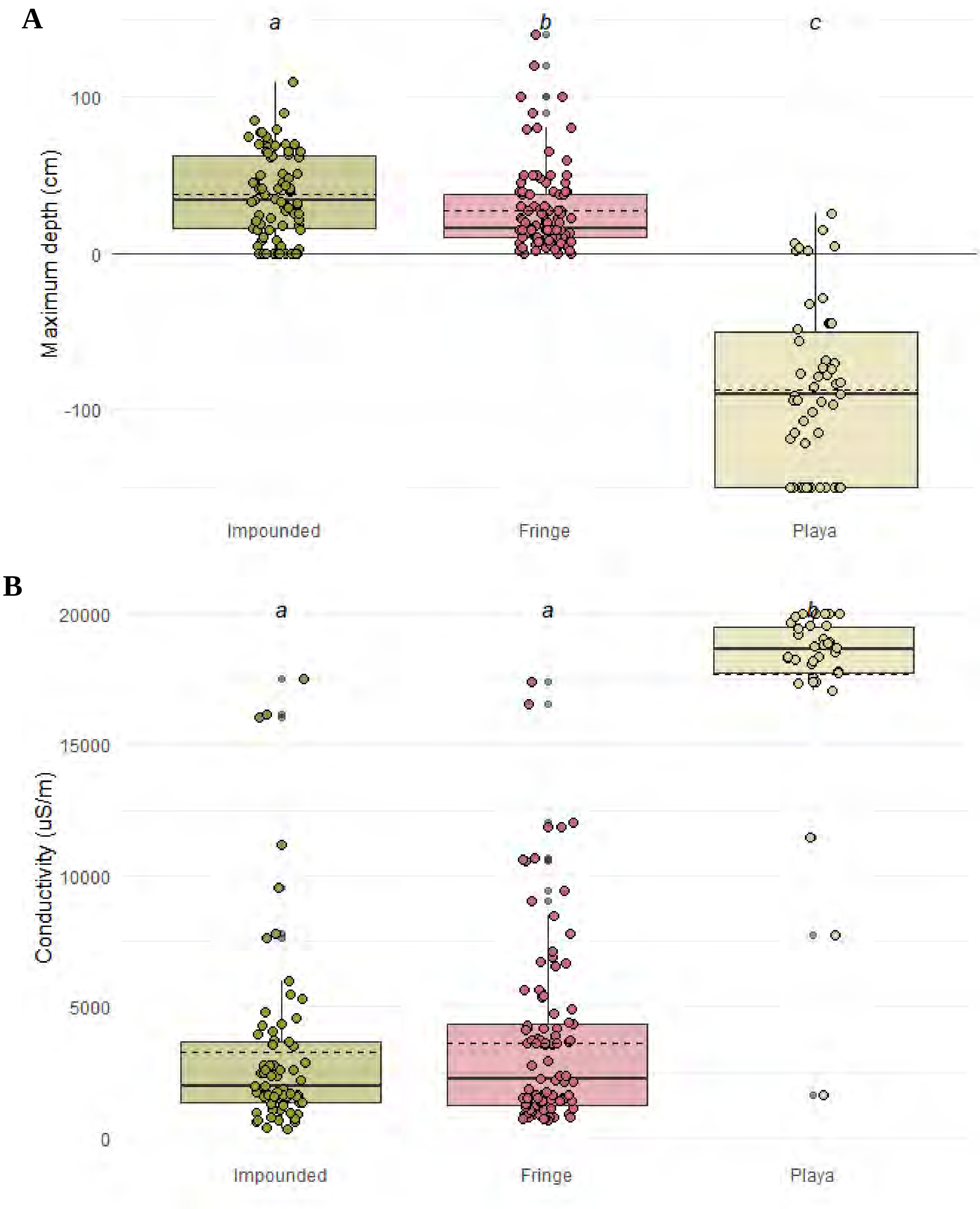

Figure 5. *A) Median (solid line) and mean (dashed line) maximum water depth; and B) median (solid line) and mean (dashed line) water conductivity in three classes of GSL wetlands.*

Table 2. *Dominant plant species in impounded GSL wetlands.*

Species	Taxonomy	Growth form	Native	CC Score / Tolerance
Chara – Stinkweed	Algae – *Characeae*	Annual or perennial, macro-algae	Native, Obligate wetland	Undetermined
Ceratophyllum demersum – Coontail	Dicot – *Ceratophyllaceae*	Perennial, submerged aquatic forb	Native, Obligate wetland	3 - tolerant
Stuckenia pectinata – Sago pondweed	Monocot – *Potamogetonaceae*	Perennial, submerged aquatic forb	Native, Obligate wetland	3 – tolerant
Ruppia cirrhosa – Widgeongrass	Monocot – *Ruppiaceae*	Perennial, submerged aquatic forb	Native, Obligate wetland	6 – intermediate

Table 3. *Dominant plant species in fringe GSL wetlands.*

Species	Taxonomy	Growth form	Native	CC Score / Tolerance
Bolboschoenus maritimus – Alkali bulrush	Monocot – *Cyperaceae*	Perennial, emergent graminoid	Native, Obligate wetland	5 – intermediate
Schoenoplectus americanus – Threesquare bulrush	Monocot – *Cyperaceae*	Perennial, emergent graminoid	Native, Obligate wetland	5 – intermediate
Phragmites australis – Phragmites	Monocot – *Poaceae*	Perennial, emergent graminoid	Introduced, Facultative wetland	0 – highly tolerant
Typha latifolia – Broadleaf cattail	Monocot – *Typhaceae*	Perennial, emergent forb	Native, obligate wetland	2 – highly tolerant

Table 4. *Dominant plant species in playa GSL wetlands*

Species	Taxonomy	Growth form	Native	CC Score / Tolerance
Salicornia rubra – Pickleweed	Dicot – *Chenopodiaceae*	Annual forb	Native, Obligate wetland	4 – tolerant
Distichlis spicata – Saltgrass	Monocot – *Poaceae*	Perennial graminoid	Native, Facultative	4 – tolerant

how disturbed an environment is. Introduced species that can establish and expand in new wetland environment often have adaptations that take advantage of gaps in vegetation because they have wide ecological tolerances, grow rapidly, and reproduce prolifically (Zedler and Kercher, 2004). This is especially true for *Phragmites australis* (hereafter, phragmites), which occupies tens of thousands of acres of GSL wetlands (Kettenring and others, 2020). Introduced species relative cover (the proportion of all plant cover that is from introduced species) differs significantly in GSL wetland classes, matching patterns in species richness—highest in fringe wetlands and lowest in impounded wetlands (Figure 7). As we explore the sources and consequences of anthropogenic disturbance in wetland plant communities, fringe wetlands and introduced species will come up again.

Growth form of the dominant plant in a type of wetland (forb, grass, or shrub) is how wetlands are mapped in the National Wetland Inventory, a comprehensive dataset of nationwide wetland extent, and those nationwide patterns also distinguish between GSL wetland classes. Impounded wetlands tend to be aquatic bed features, fringe wetlands are predominantly emergent, and playa wetlands are those with less than 30% vegetation cover (U.S. Fish and Wildlife Service, 2019). GSL wetlands are almost entirely herbaceous which means that woody species are uncommon and a small part of the overall cover when present. Herbaceous plants can be further divided into graminoids—grasses, sedges, and other plants with grass-like growth patterns—and forbs—all the other species that tend to have broader leaves. Wetland plants can also be grouped based on the length of their life cycle. Annual species only live for one year whereas perennial species persist over multiple years,

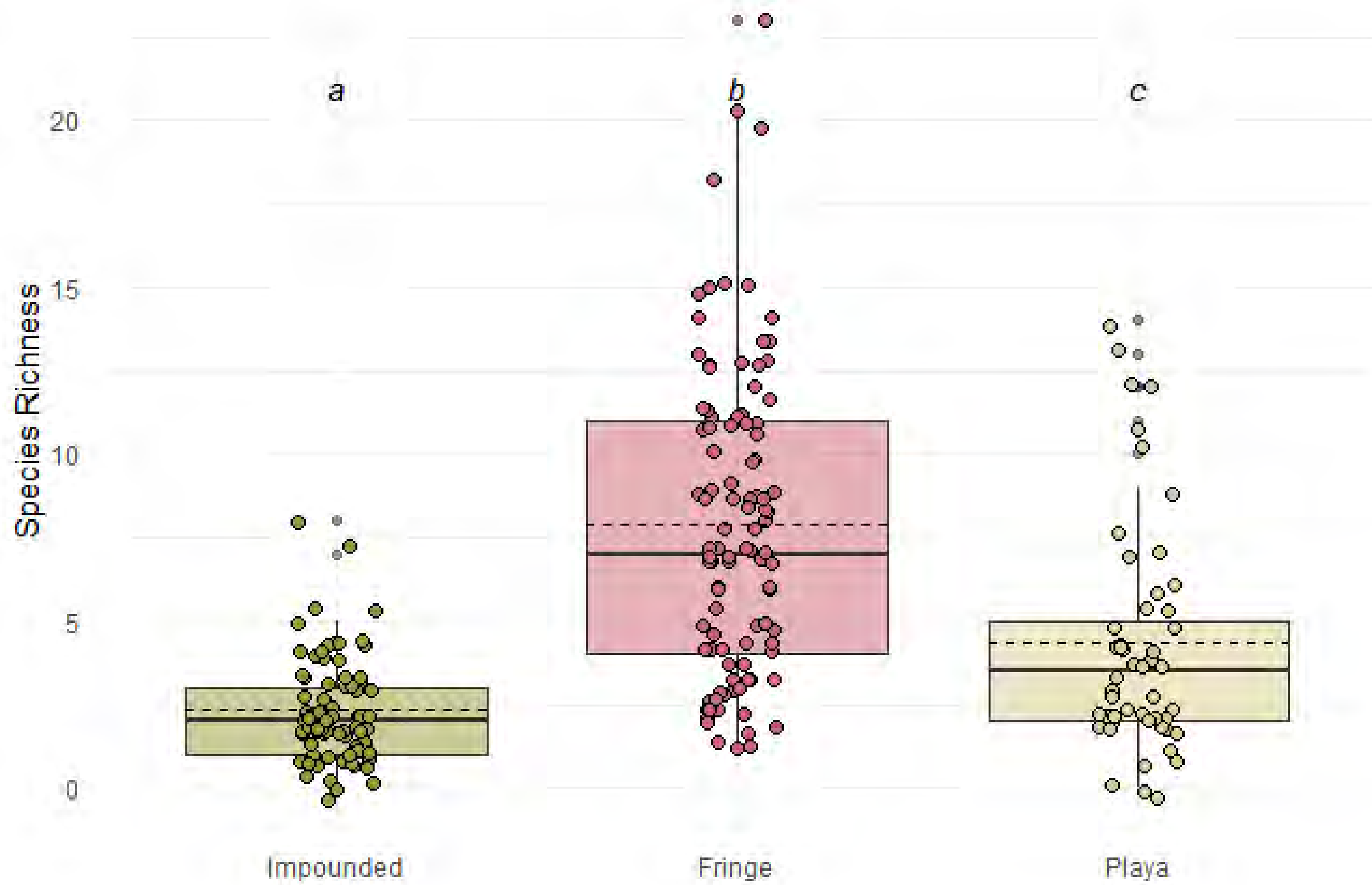

Figure 6. *Median (solid line) and mean (dashed line) species richness in three GSL wetland classes. Unique letters above boxplots indicate statistically different measures according to pairwise T-tests (α = 0.05).*

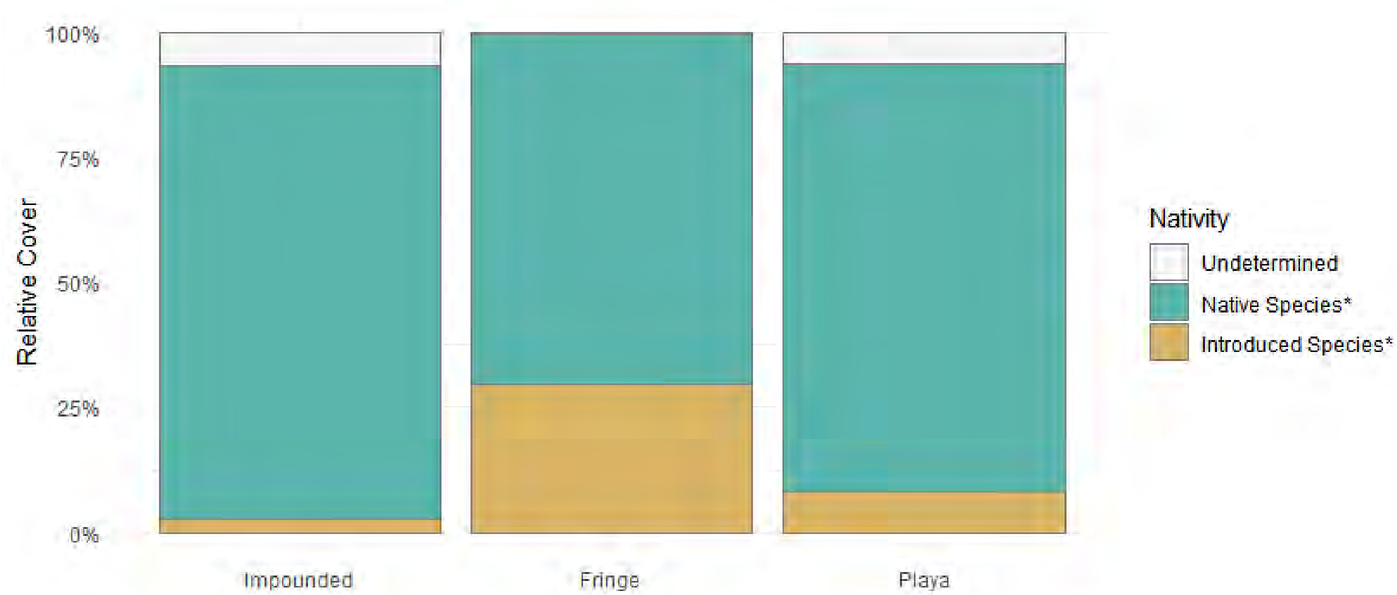

Figure 7. *Relative cover of native and introduced species in three wetland classes. Asterisks in legend indicate statistically different measures according to ANOVA (α = 0.05).*

growing back in subsequent seasons from perennating structures like rhizomes and tubers. The SAV that characterizes impounded wetlands are primarily perennial forbs, the emergent species that dominate fringe wetlands are perennial graminoids, and the most common halophytes in playa wetlands are annual forbs (Figure 8).

As discussed earlier, a limited group of species is adapted to life in wetlands. However, even with their adaptations, wetland species are not uniform in their ability to tolerate natural or anthropogenic disturbance. Sensitive plant species (as determined by U.S. Environmental Protection Agency, 2016) are a small component of cover across all GSL wetlands. Disturbance tolerant species cover the most area in GSL wetlands (Figure 9). Matching patterns reflected in introduced species cover by wetland class, the relative cover of highly tolerant species in fringe wetlands is significantly higher than in other wetland classes.

Coefficient of Conservatism (CC) scores, the continuous metric that compliments the categorical sensitivity/tolerance variable, can be built into simple or complex measures of the floristic quality of the community (Colorado Natural Heritage Program, 2022). Mean CC, the simplest of such measures, is nearly identical in impounded and playa wetlands, but significantly lower in fringe wetlands (Figure 10). The Floristic Quality Index (FQI) multiplies Mean CC by a coefficient of species richness, and in GSL wetlands that flips the floristic quality results: fringe wetlands

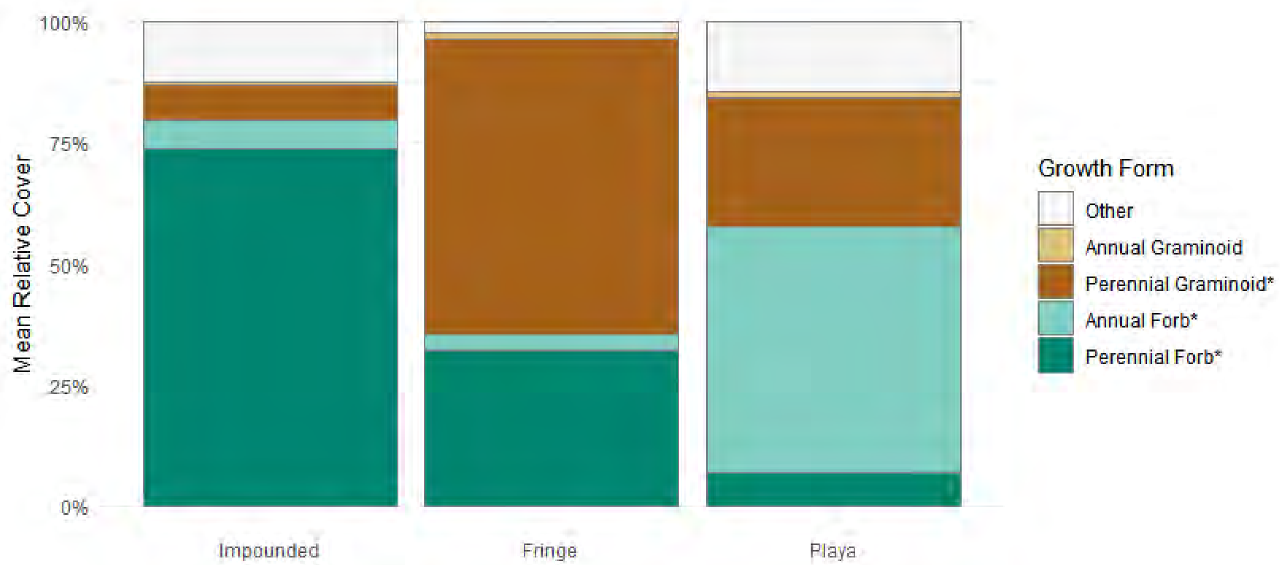

Figure 8. Relative cover of annual and perennial forb and graminoid species in three GSL wetland classes. Asterisks in legend indicate statistically different measures according to ANOVA (α = 0.05). Other growth forms include shrubs, trees, and macroalgae.

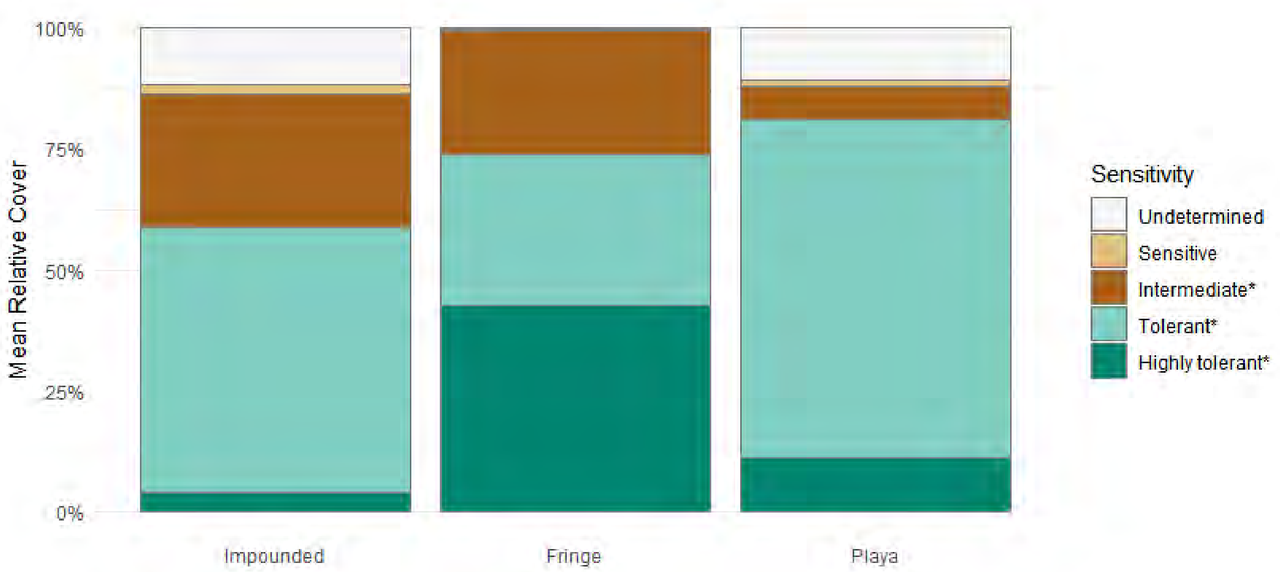

Figure 9. Relative cover of sensitive, intermediate, tolerant, and highly tolerant species in all GSL wetlands and within three wetland classes. Asterisks in legend indicate statistically different measures according to ANOVA (α = 0.05).

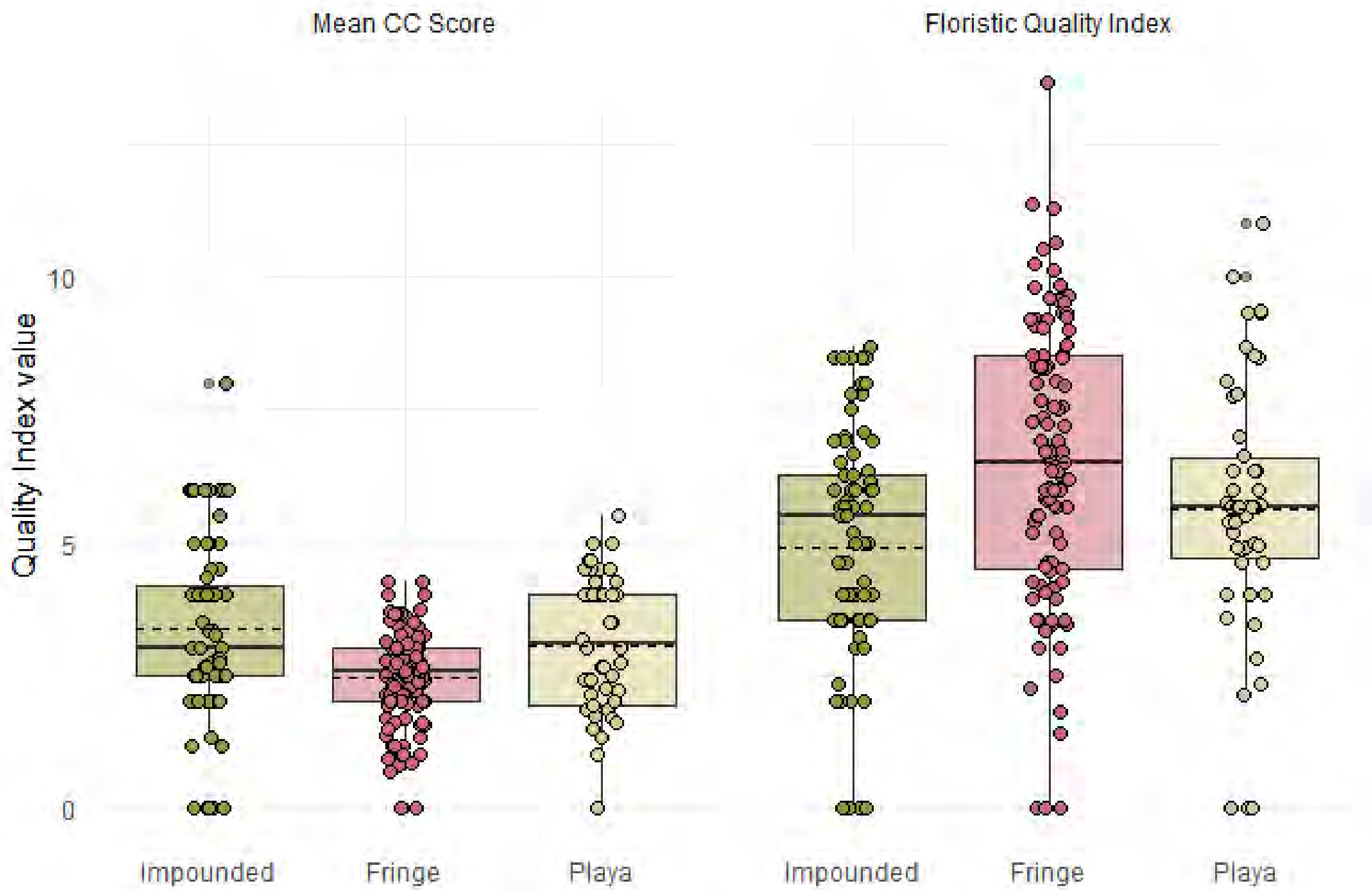

Figure 10. *Median (solid line) and mean (dashed line) Mean CC and Floristic Quality Index scores in three GSL wetland classes.*

have significantly higher FQI than the other wetland classes. The mechanisms for this switch in quality scores is clear, as fringe wetlands have higher species richness, but the implications are murky.

What Factors Are Associated with Differences in the Wetland Plant Community?

The differences in the plant community between wetland classes described above are the result of a complex mix of environmental gradients, management actions, and anthropogenic disturbance. These gradients may also drive variation with each wetland class. NMDS ordinations were generated using the most common species in each wetland class (those found in at least 10% of sites sampled for each class) and then overlaid with gradients of soil chemistry, water depth, and physical disturbances (Table 5) to visually assess important gradients to each community (Okansen and others, 2007). Only those factors with relatively high r^2 coefficients and p-values less than 0.05 were plotted because there was higher likelihood that those gradients are truly aligned with the plant community. However, measures of significance with ordinations do not hold the same rigor as in univariate data analysis and should be interpreted with that in mind (McCune and Grace, 2002).

Impounded wetland sites clustered in two distinct communities of submerged species along the horizontal NMDS1 axis and the vectors reflect common impounded wetland management practices (Figure 11a). *Stuckenia pectinata*, a highly valued habitat species for waterfowl, grows in deeper water than other SAV species (see water depth vector) which is often at the farthest downstream point of impoundments (see impervious surface vector). *Ruppia cirrhosa* favors more saline waters than other SAV species and the conductivity vector increases along the positive side of NMDS1. *Lemna minor* is an indicator of nutrient enrichment (Reddy and DeLaune, 2008) and the soil phosphorus and water quality discharge vectors both increase toward the upper left quadrant of the ordination that *L. minor* occupies. The divergent soil metal vectors are intriguing. Copper, zinc, and lead vectors increase on the negative range of NMDS 1 while selenium and barium follow the positive range of NMDS 1. Copper and zinc are both common in stormwater runoff from roads and it is possible *L. minor* and *C. demersum* could be indicators of contamination from roads (Ladislas and others, 2012).

The ordination of common species in fringe wet-

Table 5. *Environmental and anthropogenic gradients considered in NMDS and risk analysis and cutoffs that distinguish high from low stress for risk categorization.*

Gradient	High Disturbance Threshold
Environmental Factors	
Water depth	-
Conductivity – water	-
Conductivity – soil	-
Soil organic matter	-
Soil phosphorus	≥ 39.8 mg/kg
Aluminum – soil	-
Arsenic – soil	≥ 11.22 mg/kg
Barium – soil	-
Copper – soil	≥ 83.92 mg/kg
Lead – soil	-
Manganese – soil	-
Nickel – soil	-
Selenium – soil	≥ 0.17 mg/kg
Zinc – soil	-
Soil metal (exceedances of background for As, Ba, Cu, Pb, Mn, Ni, Se, and Zn)	≥ 5 exceedances
Physical Disturbances	
Water conductivity	-
Grazing severity	Severe
Herbicide severity	Severe
Impervious surface within 100m	>1
Roads within 100m	-
Discharges within 100m	-
Diversions within 100m	-
Impervious surface (%) within 1km	≥ 25%
Diversions within 1 km	≥ 3
Discharges within 1 km	≥ 1
Developed and agricultural land within 1 km	≥ 6%
Mines within 1 km	≥ 1
Introduced species cover	≥ 15% relative cover

lands does not have the clear clusters of sites that impounded wetlands displayed, but the centroids of species indicate associations of species (Figure 11b). Three factors associated with water management (diversions, water depth, and roads that are built on dikes) all increase toward the lower quadrant of the ordination occupied by two species of interest to wetland managers: *S. pectinata* and *Bolboschoneus maritimus*. It is possible the horizontal NMDS1 axis reflects the influence of or similar conditions to adjacent wetland classes—impounded wetlands on the right and playa wetlands represented by *Salicornia rubra* on the left. Two common species in fringe wetlands that are classified as highly tolerant, phragmites and *Typha latifolia*, occupy different sides of the vertical axis (NMDS 2) which suggests that multiple gradients are driving different types of highly tolerant communities, one dominated by *Typha* spp. and another by phragmites.

Based on the results of the NMDS, physical distance from infrastructure may isolate playa wetlands from anthropogenic disturbance, which is reflected in the fact that no physical disturbance factors were meaningfully aligned with the playa plant community (Figure 11c). Although playa wetland sites did not cluster in a clear pattern, the species centroids did show that the right side of the plot is dominated by the salt-loving species *S. rubra*, *Puccinellia nuttalliana*, and *D. spicata* along with a vector indicating higher soil salinity. The lack of clear vegetation patterns within playa wetlands may be due to the sparse vegetation present in this class of wetlands or the ephemeral nature of a community dominated by annual species.

What Condition Are GSL Wetlands in and Why?

While the previous sections detail the ways GSL wetlands are different between and within wetland classes, this final section will look at GSL wetlands collectively through the lens of wetland condition. Recall that GSL wetland condition is measured through the GSL-VMMI, a composite of three metrics: cover of highly tolerant species and facultative wetland species and dicot species richness. GSL wetlands that experience little anthropogenic disturbance tend to have more monocot species than dicot species and more cover of wetland obligate and less tolerant species. As condition decreases dicot species become more numerous and facultative wetland species and highly tolerant species occupy more wetland area. Through the process of selecting a VMMI explained in the analysis section, we know that condition is correlated with a cumulative measure of anthropogenic disturbance, but understanding the specific drivers of wetland condition requires a more robust analysis.

Risk analysis links the discrete measures of anthropogenic disturbance to poor wetland condition. Relative risk analysis identifies the individual factors that contribute to poor condition by estimating the likelihood of a wetland being in poor condition if it also experiences high levels of a particular disturbance. Ecological relative risk is analogous to heart disease risk: a human with high blood pressure (i.e., high stress or disturbance) is more likely to also have

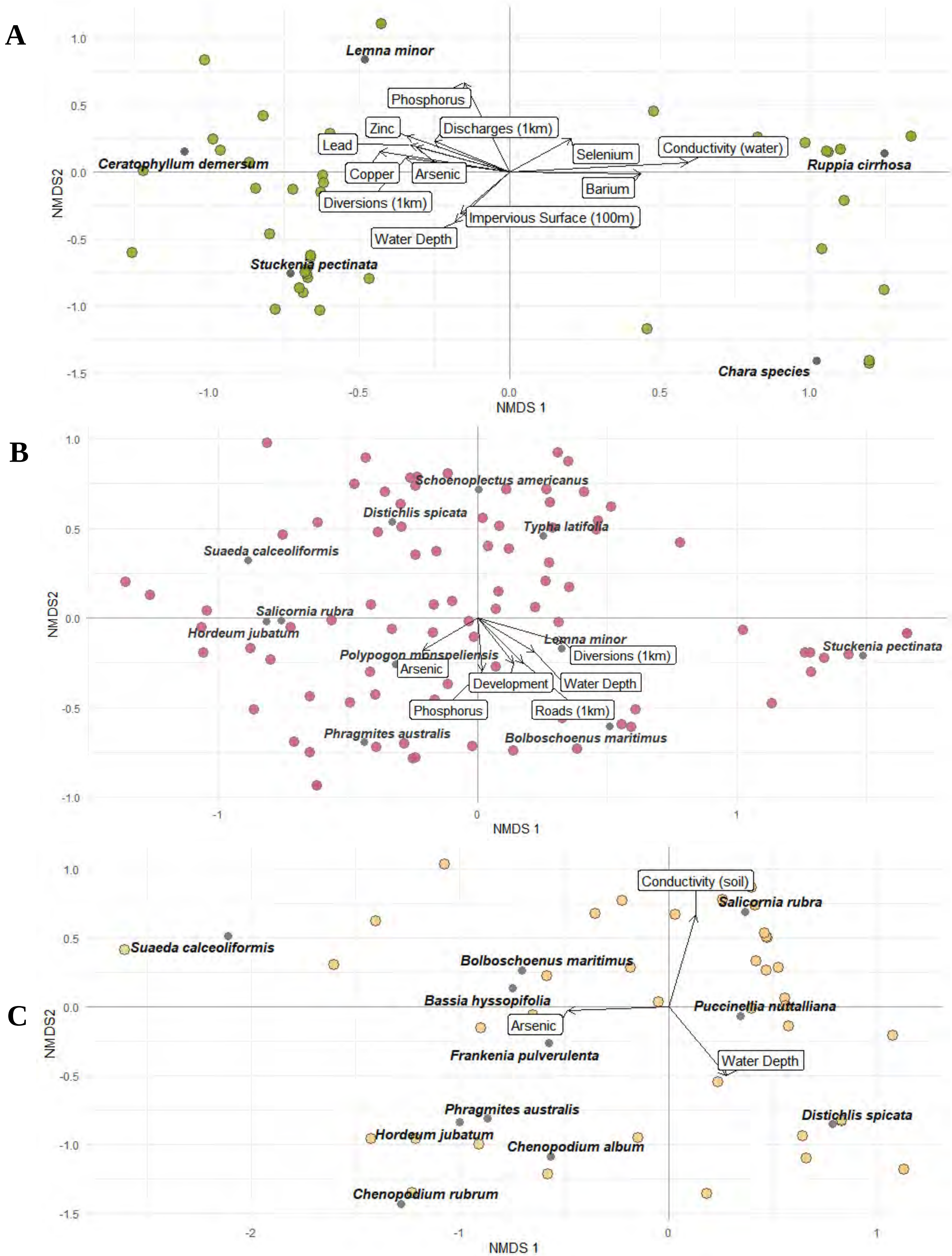

Figure 11. *Non-metric multidimensional scaling with significantly aligned environmental vectors in A) impounded, B) fringe, and C) playa wetlands.*

heart disease (i.e., poor condition) (Herlihy and others, 2019b). Attributable risk identifies the disturbances that, if removed, will result in improved condition. The estimate represents the proportion of poor condition sites that are likely to improve if a disturbance is removed. In the analogy of heart health, attributable risk is the improvement in heart health driven by decreasing blood pressure.

Risk estimates are interpreted with 95% confidence intervals; relative risk factors are considered significant if the lower confidence interval is greater than one and significant attributable risk factors have a lower confidence interval greater than zero (Van Sickle and Paulsen, 2008). Table 5 lists the disturbance factors included in the risk analysis and the threshold that separates high levels of disturbance from moderate to low disturbance.

When all wetland classes are considered together, introduced species and changes in land use near a wetland are both significant relative risks. Wetlands with more than 6% developed or agricultural land within one kilometer of the sample location are 2.6 times more likely to be in poor condition (Figure 12). When wetland class is considered, however, land use change is only a significant risk for fringe wetlands. High cover of introduced species (>15% relative cover) is a significant risk for all classes of wetlands but has especially high relative risk estimates in impounded and playa classes, 38.62 and 5.46 respectively (Table 6). The high relative risk of introduced species cover is likely driven by phragmites, which is widespread around GSL and has been a concern of wetland managers due to its propensity to crowd out native species and inability to support migratory bird use (Cranney, 2016; Long and others, 2017). Phragmites is a facultative wetland species and highly tolerant to disturbance, properties that correspond to two metrics in the GSL-VMMI, thus there is some circularity in the risk and condition estimates.

Higher soil arsenic and selenium concentrations are also a significant relative risk to all GSL wetlands (1.15), which is an interesting complement to existing concerns about selenium in the GSL open water ecosystem (Brix and others, 2004). Selenium bioaccumulates in the open water food web, from algae to brine shrimp to aquatic birds. The GSL-specific research into selenium did not look at soils or wetland macroinvertebrates but research elsewhere has found a

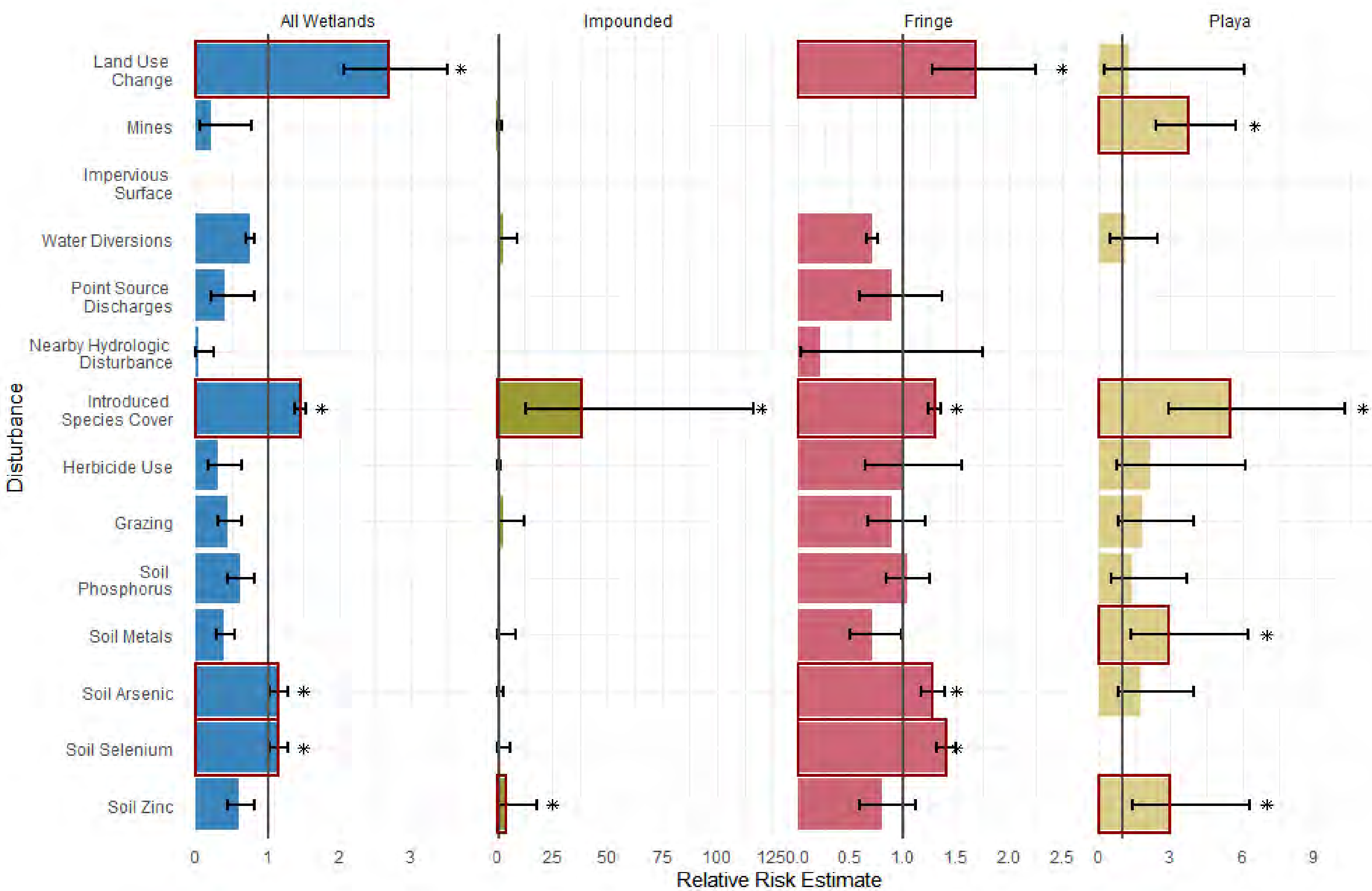

Figure 12. *Relative risk estimates for environmental and anthropogenic stressors in all GSL wetlands and in three wetland classes. Bold red boxes and asterisks indicate significant relative risk factors (estimate ± 95% confidence interval > 1).*

Table 6. *Significant relative and attributable risk estimates for disturbances in GSL wetlands.*

	Population	Disturbance	Risk Estimate	Lower CI	Upper CI
Relative Risk					
	All GSL	Land Use Change	2.70	2.07	3.51
	All GSL	Introduced Species Cover	1.45	1.38	1.53
	All GSL	Soil Arsenic	1.15	1.02	1.29
	All GSL	Soil Selenium	1.15	1.03	1.28
	Impounded	Introduced Species Cover	38.62	12.81	116.42
	Impounded	Soil Zinc	4.25	1.00	18.03
	Fringe	Land Use Change	1.69	1.27	2.25
	Fringe	Introduced Species Cover	1.30	1.24	1.36
	Fringe	Soil Arsenic	1.28	1.17	1.39
	Fringe	Soil Selenium	1.40	1.31	1.50
	Playa	Mines	3.71	2.41	5.69
	Playa	Introduced Species Cover	5.46	2.90	10.27
	Playa	Soil Metals	2.91	1.35	6.26
	Playa	Soil Zinc	2.97	1.39	6.32
Attributable Risk					
	All GSL	Land Use Change	0.59	0.48	0.09
	All GSL	Introduced Species	0.07	0.06	0.09
	All GSL	Soil Arsenic	0.02	<0.01	0.04
	All GSL	Soil Selenium	0.04	0.01	0.06
	Impounded	Introduced Species	0.63	0.13	0.84
	Fringe	Land Use Change	0.39	0.20	0.54
	Fringe	Introduced Species	0.05	0.04	0.06
	Fringe	Soil Arsenic	0.03	0.02	0.05
	Fringe	Soil Selenium	0.08	0.06	0.10
	Playa	Introduced Species	0.37	0.09	0.57

high potential for selenium accumulation in soils that are regularly flooded (Jones and others, 2017).

The most significant attributable risk factor for GSL wetlands is introduced species cover. When considered altogether, seven percent of poor condition wetlands would improve if the introduced species risk were removed (Figure 13). The attributable risk estimate is largest for impounded and playa wetlands (63% and 39% respectively). It is encouraging that introduced species removal may improve wetland condition because years of research and adaptive management directed at phragmites removal has made significant progress in alleviating pressure from that species (Rohal and others, 2017; Rohal, 2018). Though the circularity between condition metrics that reflect the presence of phragmites and risk estimates as well as the assumption of reversibility that is built into this analysis need to be remembered.

The two other significant attributable risk factors, land use changes and soil metals, are unlikely to be reversible, regardless of the impact of their removal. Land use change, a significant attributable risk for all GSL wetlands together and fringe wetlands in particular, are almost certainly permanent landscape features. Soil selenium and arsenic are also difficult to remediate, not only because soil remediation is challenging, but also because wetlands act as landscape sinks for both arsenic and selenium, continually capturing metals from across the watershed (Adams and others, 2015). However, decreasing soil metal concentrations would result in fewer poor condition fringe wetlands and have potential impacts for migratory bird populations, which can bioaccumulate both metals.

CONCLUSIONS

Characterizing the dominant plant communities and exploring the various environmental and anthropogenic gradients relevant to each class of GSL wetlands show the unique suite of factors that have filtered the plant community down to the species best adapted to each class. In impounded wetlands, deep freshwater flooding made possible by water management infrastructure supports predominantly native submerged aquatic plant species. The dynamic water regimes in fringe wetlands create an ideal environment for perennial emergent species. Playa wetlands

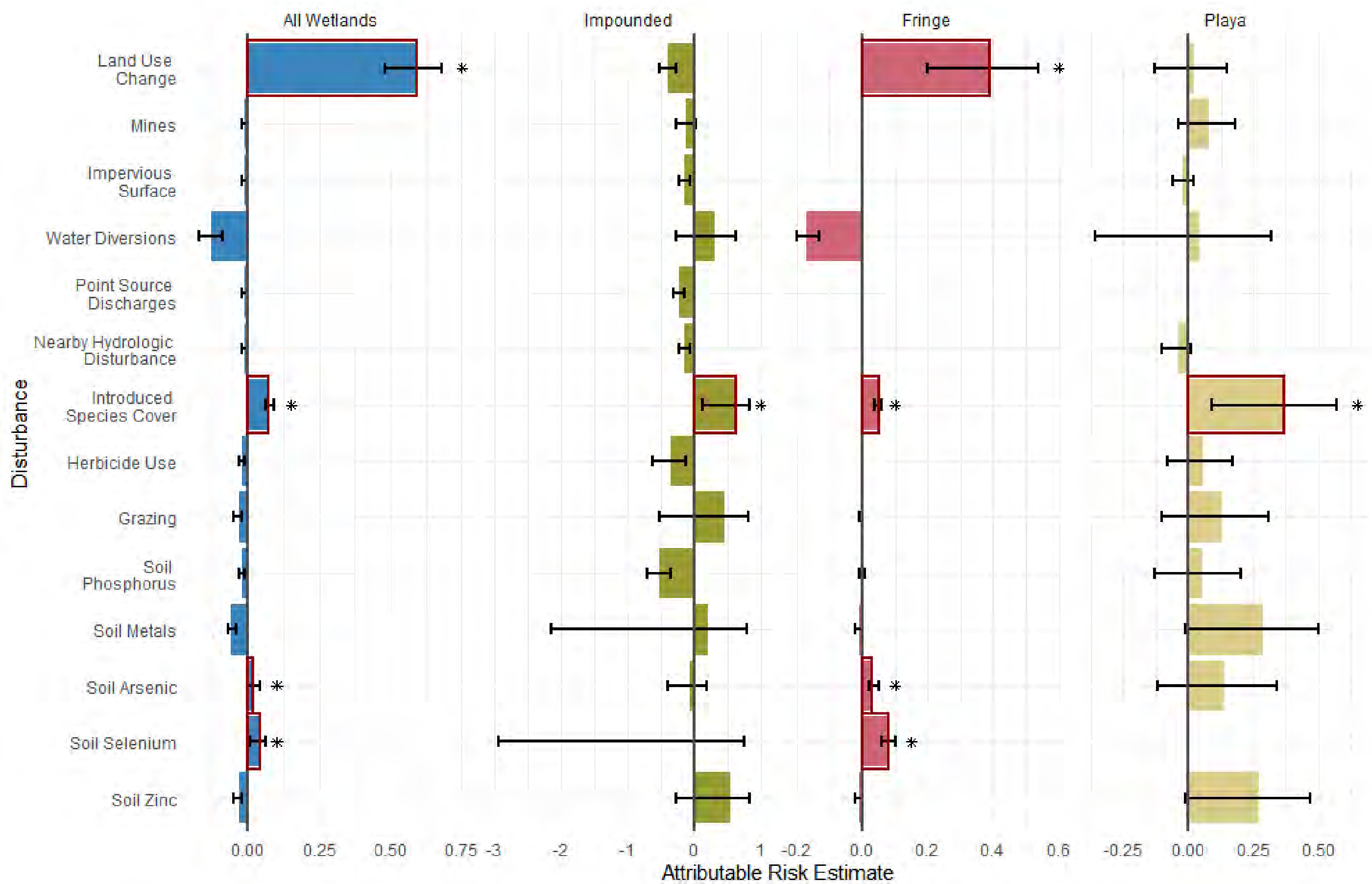

Figure 13. *Attributable risk estimates for environmental and anthropogenic stressors in all GSL wetlands and in three wetland classes. Bold red boxes and asterisks indicate significant attributable risk factors (estimate ± 95% confidence interval > 0).*

are dominated by species adapted to extremes in salinity. Water depth is associated with differences in community within each class according to ordination results. Finally, risk analysis identified land use change and introduced species as the greatest risks to condition and the greatest opportunity for restoration.

Restoration Implications

The ecological characterization presented here, the multi-metric index of wetland condition, and the risk analysis all have implications for restoration practices around GSL. Identifying the correct potential plant communities, which are specific to wetland class, is critical to any restoration project and should be carefully considered when selecting species to plant, water regimes that are possible, and ultimate restoration targets (Tarsa and others, 2022). The GSL-VMMI has a role both in identifying wetlands in need of restoration (those in poor condition) and in monitoring if a restored wetland is on a trajectory for better health over time. Finally, the results of the risk analysis should be considered when identifying appropriate sites for restoration efforts. Most especially, significant relative and attributable risk factors like introduced species should be minimized or eliminated prior to initiating restoration efforts.

Future Research Needs

GSL wetlands form vast complexes of intermingling classes, which is what drives much of the bird diversity the ecosystem supports. The entire Intermountain West region has experienced two decades of drought that pushed GSL to its lowest elevation and saltiest state. Even with the impact of climate change on precipitation patterns, humans diverting and using water to grow food and lawns has exacerbated the impacts of drought (Wurtsbaugh and others, 2016). As mentioned in the introduction, distinguishing between natural and anthropogenic disturbances is difficult and this is especially true for wetland water availability. The experience of the Bear River delta in the early 20th century provides a stark example of the impact that years of drought can have on the ability of wetland complexes to provide their ecosystems functions. However, we also know that many wetland species are adapted to periodic drying events. Future research into the natural range of hydrologic variability that GSL wetlands are adapted to and the nature of disrupted hydrology would provide crucial insight to the roles of drought and water use in shaping existing wetland plant communities and critical thresholds to avoid.

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