

DISSERTATION

TESTING HYDROLOGIC PERFORMANCE STANDARDS
TO EVALUATE WETLAND RESTORATION

Submitted by

Jeremy Paul Sueltenfuss

Graduate Degree Program in Ecology

In partial fulfillment of the requirements

For the Degree of Doctor of Philosophy

Colorado State University

Fort Collins, Colorado

Summer 2018

Doctoral Committee:

Advisor: David J. Cooper

Troy Ocheltree
Mark Paschke
Monique Rocca
John Sanderson

Copyright by Jeremy Paul Sueltenfuss 2018

All Rights Reserved

ABSTRACT

TESTING HYDROLOGIC PERFORMANCE STANDARDS TO EVALUATE WETLAND RESTORATION

Defining success in wetland restoration can be difficult and subjective, as each restoration project has distinct goals. When wetland restoration projects fail to achieve their identified goals, it is often due to inadequately restored water levels. Incorrect water levels can lead to invasion by exotic species, or can alter the type of wetland that was supposed to be restored. To provide guidance to local wetland restoration efforts I investigated the hydrologic niche of *Carex pellita*, a wet meadow species commonly planted in wetland restoration, along with *Typha latifolia*, a species of cattail which commonly invades restored sites. Restored wetlands often have higher water levels than naturally occurring wetlands, and the prevailing assumption has been that hydrologic conditions in restored wetlands are not suitable for this species of *Carex*. Using experimental transplants across a hydrologic gradient, I found that *Carex* has a much wider hydrologic niche than previously thought. It produced either the same or more biomass in the high water level transplant treatment than in the low water level control plot. *Typha* responded negatively to being transplanted into areas with lower water levels. My results indicate *Typha* have filled their entire hydrologic niche in these wetlands and have competitively excluded *Carex pellita* to a smaller portion of its potential distribution.

I also evaluated existing hydrologic and vegetation datasets from regulatory wetland restoration projects across the United States to help inform the development of wetland mitigation policy. The objective of regulatory wetland mitigation is to restore or create wetlands to offset the losses of wetland acreage and function incurred from impacts to existing wetlands.

Unfortunately, wetland acreage and function are not always successfully replaced, and performance standards are now used in hopes to improve wetland mitigation outcomes. Because of the agreement in the scientific literature about the role of hydrology in creating and maintaining wetland structure and function, hydrologic performance standards may be an ecologically meaningful way to evaluate restoration outcomes. However, a framework for hydrologic performance standards has not been created or tested to date. I analyzed existing datasets from past and ongoing wetland mitigation projects to identify the number of years it took water levels in restored wetlands to match reference sites, and to test whether similar water levels between restored and reference sites leads to higher cover of native species. Wetland types differed in the number of years it took for water levels to match reference sites. Vernal pools in California took nine years to match reference sites, fens and wet meadows in Colorado took four years, and forested wetlands in the southeastern US were hydrologically similar to reference sites the first year following restoration. Plant species cover in all three restored wetland types was related to the water level similarity to reference sites. Native cover was higher when water levels were more similar to reference sites in some vernal pools, fens, and wet meadows, and was lower in areas where water levels were different. Exotic species cover showed the opposite relationship in fens and wet meadows, where hydrologic similarity led to low cover of exotic species. Forested wetlands showed no consistent relationship between tree seedlings or species richness and hydrologic similarity with reference sites. Based on the general agreement of the importance of hydrology for wetland form and function, hydrologic performance standards should be used in wetland mitigation. My research shows that hydrologic performance standards may also lead to increased vegetation success in some wetland types.

ACKNOWLEDGEMENTS

I am deeply grateful to my advisor, mentor, and friend David Cooper. He encouraged me to pursue a PhD for many years, and remained supportive for the many years of actually doing so. David's sense of adventure and curiosity has continually provided a source of inspiration to me, and a great reminder that what we are doing is supposed to be fun. Thank you, David.

For their constructive feedback and efforts to improve this dissertation, I thank Derek Schook and Ed Gage along with my graduate committee: Mark Paschke, Troy Ocheltree, Monique Rocca, and John Sanderson. A special thanks to Troy Ocheltree for helping me through the ecophysiological portion of my research! Tom Hobbs was also instrumental in assisting with my Bayesian education.

My dissertation was part of a collaborative effort lead by the National Technical Committee for Wetland Vegetation. This project was funded under United States Army Corps of Engineers (USACE) contract IPA 16-9 and supported through the USACE Institute for Water Resources, and the Engineer Research and Development Center Wetland Regulatory Assistance Program and Cold Regions Research and Engineering Laboratory Remote Sensing and Geographic Information Systems Center of Expertise. Steve Martin was a particularly valuable asset in providing background knowledge, finding data, and organizing field excursions across the country. I am also grateful to the many organizations that provided wetland mitigation data.

My thanks go to the entire Cooper lab for their time and ideas, either in the field or at the office. Andrea Borkenhagen, Jeremy Shaw, and Ed Gage in particular provided a sounding board throughout the entire research process and a source of inspiration for new ideas. Lydia Baldwin braved the heat and mosquitos to help excavate and transplant wet meadow and cattail sod. My sanity was kept intact by these wonderful friendships.

No acknowledgement section of mine would be complete without expressing my deepest gratitude and appreciation for my best friend and wife, Amy, along with our two awesome sons Max and Ari. These three provide a daily dose of love and support, and a continual reminder of what is most important in life.

TABLE OF CONTENTS

ABSTRACT.....	ii
ACKNOWLEDGEMENTS.....	iv
TABLE OF CONTENTS.....	vi
LIST OF TABLES.....	viii
LIST OF FIGURES.....	ix
1 Introduction.....	1
2 Identifying the hydrologic niche for target wetland restoration species.....	5
2.1 Introduction.....	5
2.2 Methods.....	8
2.2.1 Study Sites.....	8
2.2.2 Transplant Experiment.....	8
2.2.3 Hydrologic Monitoring.....	9
2.2.4 Plant Measurements.....	9
2.2.5 Statistical Analyses.....	11
2.3 Results.....	11
2.4 Discussion.....	14
2.4.1 Identifying niche preferences for species.....	14
2.4.2 Ψ_{TLP} as an adjustable trait.....	15
2.4.3 Water use strategies.....	17
2.5 Conclusion.....	17
3 Hydrologic similarity drives community assembly towards reference composition in restored wetlands.....	26
3.1 Introduction.....	26
3.2 Methods.....	28
3.2.1 Study Sites.....	28
3.2.2 Hydrologic and Vegetation Monitoring.....	29
3.2.3 Data Analysis.....	29
3.3 Results.....	31
3.3.1 Hydrologic Restoration.....	31
3.3.2 Community Assembly.....	32
3.3.3 Hydrologic Similarity and Species Composition.....	33
3.4 Discussion.....	34
3.5 Conclusions.....	36
4 Testing an approach for hydrologic performance standards in wetland restoration.....	44
4.1 Introduction.....	44
4.2 Methods.....	44
4.2.1 Study Sites.....	46
4.2.2 Hydrologic Monitoring Data.....	47
4.2.3 Vegetation Monitoring Data.....	48
4.2.4 Statistical Analysis.....	49
4.3 Results.....	51
4.3.1 Years to hydrologic similarity.....	52

4.3.2	Hydrologic Similarity and Successful Vegetation Establishment.....	52
4.4	Discussion.....	53
4.4.1	Creating hydrologic performance standards	56
4.5	Conclusions	57
5	Synthesis	67
5.1	Sensitivity	68
5.2	Creating Hydrologic Performance Standards for wetland mitigation	70
6	References	73

LIST OF TABLES

Table 2.1. Hydrologic metrics for <i>Typha</i> and <i>Carex</i> communities in each study site	19
Table 2.2. Experimental transplant treatment responses	20
Table 3.1. Principal Components and their associated hydrologic metrics	38
Table 3.2. Mean species richness, mean Simpson’s Diversity Index, mean cover of <i>Salix</i> spp. and mean cover of <i>Carex</i> spp. for restored and reference wetlands	39
Table 4.1. Mitigation project information.....	59
Table 4.2. Average water level for each wetland type and project site	60
Table 4.3. Bayesian estimates for the relationship between vegetation and hydrologic similarity between restored and reference wetlands	61

LIST OF FIGURES

Figure 2.1. Alternate hypothesis for species response to experimental transplants across a hydrologic gradient	21
Figure 2.2. Experimental transplant study area in Fort Collins, CO.....	22
Figure 2.3. Hydrographs of experimental transplant locations.....	23
Figure 2.4. <i>Carex</i> and <i>Typha</i> plant responses to experimental transplants.....	24
Figure 2.5. Ψ_{mid} as a function of water level recorded in the nearest well	25
Figure 3.1. Water levels in fens and precipitation totals.....	40
Figure 3.2. Reference and restored water levels	41
Figure 3.3. NMS ordination of restored plots and reference wetlands	42
Figure 3.4. The relationship between wetland species composition and hydrologic conditions ..	43
Figure 4.1. Performance standards study sites across the United States	62
Figure 4.2. Hydrographs for restored and reference wetlands.....	63
Figure 4.3. The estimated hydrologic difference between restored and reference wetlands for each year following restoration.....	64
Figure 4.4. Average weekly absolute water table difference between restored and reference wetlands and associated vegetation metrics.....	65
Figure 5.1. Sensitivity of communities to hydrologic variation and the range of hydrologic conditions the community can withstand.....	71
Figure 5.2. The creation of hydrologic performance standards for a vernal pools restoration project using multiple reference pools.....	72

1 Introduction

Since the onset of European settlement, North America has lost well over 50% of its original wetlands to development, and many of the remaining wetlands have been severely degraded (Mitsch and Wilson 1996). Land use conversion and changing precipitation regimes are the two largest threats to existing wetland systems (Sala and Karl 2013). Hydrologic alteration from these impacts can change wetland floristic composition and diversity (Chapin et al. 1997, 2000, Tilman 1999, Hooper et al. 2005), as well as the varied ecosystem services provided by wetlands, including flood attenuation, carbon sequestration, and water quality improvements. Wetland restoration is one approach to combat this degradation.

Wetland vegetation has been linked to hydrologic regimes across many wetland types (Silvertown et al. 1999, Magee and Kentula 2005, Dwire et al. 2006, Johnson et al. 2014), and the vegetation that develops in restored wetlands is often directly tied to these restored water levels (Caldwell et al. 2011). A wetland's hydrologic regime incorporates the ground and surface water levels throughout the year. Unfortunately, restored wetlands often have different hydrologic regimes than reference wetlands (Zedler and Callaway 1999, Ambrose 2000, Ambrose and Lee 2007). When the hydrologic regime of a restored wetland is not representative of a natural analog of the community to be created, hydrologic conditions limit restoration success (Fennessy et al. 2004, Acreman et al. 2007).

Understanding the hydrologic niche for species of interest remains a research priority in restoration ecology to ensure adequate water levels are restored to support those species. A species' niche, the "n dimensional hypervolume" of a species' existence (Hutchinson 1957), includes its interactions with other species and the abiotic environment. Because water levels in wetlands are a primary abiotic driver of species distributions, some restoration projects monitor

water levels in reference wetlands to inform their restoration designs. The occurrence and distribution of plant species in reference wetlands are thus assumed to be related to the hydrologic conditions where they are found. However, a species' niche can be separated into a "fundamental niche", which describes the entire set of conditions where a species could *potentially* be found, and its "realized niche", where a species *actually* occurs. The realized niche is often more restricted than the fundamental niche due to biotic interactions such as competitive exclusion, where weaker competitors are relegated to a smaller portion of their fundamental niche. Assuming the hydrologic conditions where a species is currently found may lead to restoration designs that are overly restrictive or inaccurate. Identifying the difference between the fundamental and realized niche for target species is helpful for both voluntary wetland restoration as well as regulatory wetland mitigation.

Wetland mitigation involves the creation or restoration of wetlands to offset impacts to existing wetlands as a requirement under §404 of the US Clean Water Act. The intent of this regulation is "no net loss" of wetland acreage or function, although it often fails to meet this objective (Ambrose 2000). An incorrect hydrologic regime, with water levels different than originally planned or different from reference sites, is often identified as a primary reason for poor restoration results (Fennessy et al. 2007). Adequate wetland hydrology in a regulatory context is defined as a water table within 30 cm of the ground surface for 12.5% of the frost free growing season for any wetland type. Although this may be thought of as the regulatory "minimum" for wetland hydrology, it certainly isn't the "optimum" for most wetland types across the country (Eggers 2015).

The recognition of widespread failure in wetland mitigation led to new regulation in 2008 requiring the use of ecological performance standards to increase the effectiveness of future wetland mitigation. Because wetland types vary widely across the United States, a wide array of

indices and performance standards have been developed to judge the success of wetland restoration projects. Many of these are based on rapid assessment techniques to evaluate specific flora or fauna of a site (Environmental Law Institute 2004). While readily observed features of a site facilitate rapid monitoring, the indicators of focus may not be well suited to identify whether the targeted wetland type has been restored. Because of the agreement in the scientific literature about the role of hydrology in creating and maintaining wetland structure and function (Cook and Hauer 2007, Sieben et al. 2010), hydrologic performance standards may be an ecologically meaningful way to evaluate restoration outcomes.

Monitoring data from reference sites have rarely been used to create hydrologic performance standards to ensure the proposed wetland type has been restored. Whether hydrologic performance standards created from reference sites is meaningful in the long term development of a restored wetland remains unknown. Less than 50% of published papers compare the vegetation of a restored site to a reference site, and only a subset of those monitor water levels (Moreno-Mateos et al. 2015). Lack of long-term monitoring data has limited our understanding of the utility in using reference sites to evaluate restored water levels and vegetation.

In this new age of the Anthropocene, it is increasingly important to integrate the science of restoration ecology into the practice of ecological restoration (Cooke et al. 2018). A ubiquitous challenge in applying science to address ecological problems is related to issues of scale (Levin 1992). Research is often conducted at the plot scale, yet ecological challenges exist at local, regional and global scales. The research presented in the following chapters aims to address questions and apply solutions at these various scales. Hydraulic and physiological mechanisms within individual wetland plants are used to explain plant species distributions within a restored wetland in Chapter 2. These findings are then scaled up to the level of a

restoration project in Chapter 3 where plant species composition is evaluated across a hydrologic gradient for thirteen different wetlands in the Colorado Rocky Mountains. This chapter aims to test whether restored wetlands with similar water levels as reference sites also have a similar plant species composition. I then evaluate whether these findings are applicable at the national level across multiple wetland types in Chapter 4. This national scale analysis is meant to provide a data-driven framework with which to evaluate future wetland mitigation projects. From the micro-level of the xylem in an individual plant to the macro-level of various wetland types across the nation, my research is aimed at improving the practice of wetland restoration and providing guidance to inform the development of federal wetland mitigation policy.

2 Identifying the hydrologic niche for target wetland restoration species

2.1 Introduction

Hydrologic alteration due to land management or altered precipitation regimes has important consequences for regional and global biodiversity (Sala et al. 2000, Konar et al. 2013). Plant species in wetlands are particularly sensitive to hydrologic alteration (Findlay and Houlihan 1997, Brinson and Malvárez 2002) because most tolerate only a narrow range of water depth and duration (Jung et al. 2009, Hudson et al. 2014). However, our understanding of a species' hydrologic niche has largely come from observational research (García-Baquero et al. 2016). Experimental manipulations are needed to gain a mechanistic understanding of the hydrologic niche for species commonly used in wetland restoration (Fennessy et al. 1994).

Freshwater mineral soil wetlands have been impacted more than any other wetland type in North America (Bridgham et al. 2006). Of these, wet meadows are a commonly impacted wetland community, although efforts to establish wet meadows in restored wetlands are often unsuccessful. Naturally occurring wet meadows are highly diverse, though restored wet meadows often have lower plant species diversity and higher exotic species cover (Gutrich et al. 2009).

Establishment of wet meadow species following restoration requires suitable water levels. Observational studies have quantified the restricted range of water levels that support wet meadow communities in the western U.S. (Dwire et al. 2006). However, restored wetlands often have higher water levels than reference wetlands (Fennessy et al. 2004), and cattail (*Typha*) invasion is common (Kercher and Zedler 2004). *Typha* can live in higher water levels than most wetland plant species (Grace and Wetzel 1981) yet are also more drought tolerant than some species (Asamoah and Bork 2010). Because wet meadows commonly surround areas of higher

water levels dominated by *Typha*, a common assumption is that hydrologic differences separate the two communities.

Wetland water levels often create distinct vegetation zonation (Snow and Vince 1984, García-Baquero et al. 2016), and restoration of the altered hydrologic regime can be sufficient to restore the biotic structure in some wetland types (Sanderson et al. 2008). Plant species distributions across hydrologic gradients are influenced by their morphological and physiological adaptations (Baastrup-Spohr et al. 2015). High water levels limit oxygen diffusion into soils and create anoxic conditions (Sanderson et al. 2008), while water levels further below ground allow oxygen movement into shallow soil layers, though they may also limit root access to water. Plant roots can thus be limited by oxygen availability at high water levels or by water availability at low water levels (Lovell and Menges 2013). Morphological adaptations, such as aerenchyma that deliver oxygen to roots, allow wetland plant species to withstand high water levels and low soil oxygen concentrations (Blom and Voeselek 1996). Alternatively, some wetland plants use physiological mechanisms to withstand periods of low water availability similar to the drought tolerance mechanisms of dryland species (Touchette et al. 2007). A species ability to colonize and reproduce in a restored wetland is directly tied to its ability to withstand these variations in restored water levels.

Most experimental transplant studies have relied on plant density or biomass to infer vegetation response to different hydrologic conditions, and there have been few evaluations of physiological mechanisms to explain these responses (Grace and Wetzel 1981, Wetzel et al. 2004, Kotowski et al. 2006, Toogood et al. 2008). The ability of a species to physiologically adjust to different hydrologic conditions may determine where it can exist across the landscape and its response to restoration (Silvertown et al. 2015). Soil anoxia from high water levels commonly leads to root dysfunction, resulting in water deficits in plants (Pezeshki 2001). As

such, both flooding and drought cause similar physiological constraints to plants. Tolerance to water deficits in plants is often estimated using pressure-volume curves to identify the leaf water potential at which a plant loses turgor pressure and can no longer transport water for photosynthesis (Tyree and Hammel 1972). Leaf water potential close to or below the turgor loss point indicates hydraulic stress, whereas hydraulic function is maintained above this point. Species adapted for drought tolerance have a lower turgor loss point. Additionally, drought tolerance can be achieved through changes to osmotic potential or leaf dry matter content. Plants can adjust their osmotic potential by changes to the amount of solutes within their cells, maintaining turgor at low water availabilities. Leaf dry matter content is related to the density of leaves, and plants with higher leaf dry matter content have less water lost from leaves.

I used a reciprocal transplant study to evaluate the potential and realized hydrologic niche of *Carex pellita*, a common wet meadow sedge, and *Typha latifolia* to test whether physiological limitations explain their current distribution in a restored wetland. Previous experimental transplant studies have concluded that wetland species have reduced performance when transplanted away from where they were originally found (Figure 2.1A) (Snow and Vince 1984, Sanderson et al. 2008). When competition plays a strong role in structuring wetland vegetation zonation, however, species are limited by competition along their upper border and abiotic stress along their lower border (Figure 2.1B) (Grace and Wetzel 1981, Bertness and Ellison 1987, Wetzel et al. 2004). However, wet meadow species can be limited by light availability in the presence of taller plants (Kotowski et al. 2006). The presence of *Typha* may potentially displace shorter species to less optimal areas (Figure 2.1C). If species are functionally equivalent and stochastic dispersal explains their distribution (Hubbell 2005), the response of both species to transplanting would be neutral (Figure 2.1D). I asked; (i) do species transplanted across a hydrologic gradient have altered above ground biomass and/or shoot density; (ii) do individual

plants within the transplants have altered drought tolerance characteristics (leaf dry matter content and osmotic potential); and (iii) do mid-day leaf water potentials in *Typha* and *Carex* remain above the turgor loss point for each species across treatments? I hypothesized that individuals transplanted across the hydrologic gradient away from their original location would have lower mid-day potentials leading to lower above ground biomass (Figure 2.1A).

2.2 Methods

2.2.1 Study Sites

I studied two wetlands (“north” and “south”) in the Riverbend Ponds Natural Area (RPNA) on the historic floodplain of the Cache la Poudre River in Fort Collins, CO (Figure 2.2). RPNA is a historic gravel pit reclaimed to wetland in the 1980s by the City of Fort Collins. Wetlands include fresh water marshes dominated by *Typha latifolia* that are surrounded by wet meadows dominated by *Carex pellita*. Wetlands are recharged by alluvial groundwater from the river and water levels typically follow the pattern of river discharge, being highest in early summer during the period of mountain snow melt, and low in the fall and winter. The Poudre River has an average peak discharge in late May or early June of 76.5 m³/s and an average minimum flow in December of 0.85 m³/s (www.waterdata.usgs.gov), although discharge can be highly variable due to irrigation diversions and storm water runoff.

2.2.2 Transplant Experiment

I established two 20 m transects in each wetland parallel to and within five meters of a clearly defined *Typha-Carex* boundary in April 2016, with one transect each in the *Carex* and *Typha* communities. Each transect was divided into 10 blocks, with each block containing three square 0.25 m² plots alternating on either side of the transect (Figure 2.2). Each of the three plots in a block were assigned as a control or as one of two treatments, including 1) a “cross-boundary transplant” where turf in that plot was transplanted to the corresponding plot along the opposing

transect, or 2) an “in-situ transplant” which was excavated and replaced into the same location to test the effects of transplanting. The cross-boundary and in-situ transplants were excavated with a shovel to the underlying cobble, typically 30 cm deep, and placed on plywood for relocation and planting. Existing plants within 0.5 m of each plot were trimmed to ground level every two weeks to reduce competition for light.

2.2.3 *Hydrologic Monitoring*

Four groundwater monitoring wells were installed along each transect to quantify the water table during the year. Monitoring wells were hand augered, cased with slotted Schedule 40 PVC, and backfilled with native soil. Depth to water was manually measured within each monitoring well approximately every other week by inserting a tape measure to the point of contact with water.

2.2.4 *Plant Measurements*

Plant response to treatments was evaluated during the summer of 2017, the second growing season following transplanting. Plant growth responses included above-ground biomass of all species and shoot density of *Typha latifolia* and *Carex pellita*. Shoot density and above ground biomass were quantified in a 0.25 x 0.25 m quadrat in the center of each plot. The number of *Typha* and *Carex* shoots were tallied within the sampling frame, and all above ground biomass was clipped at ground level in August. Above ground biomass samples were cleaned of dead plant material, oven dried for at least 3 days at 55° C, and weighed to the nearest 0.0001 g using a semi-micro analytical balance. *Carex* and *Typha* plants were removed and weighed separately.

Physiological responses of *Typha* and *Carex* shoots to the treatments in the north experimental wetland included mid-day xylem water potential (Ψ_{mid}) measured monthly, and leaf

dry matter content (LDMC), osmotic potential at full turgor (Ψ_{osm}), and turgor loss points (Ψ_{TLP}) measured in June of the second growing season. I selected a single *Carex* or *Typha* shoot in the center of each control and transplant treatment plots for Ψ_{mid} measurements and an adjacent plant for LDMC, Ψ_{osm} , and Ψ_{TLP} measurements. Ψ_{mid} was measured in June, August and early September on one individual from each transplant and control plot. For Ψ_{mid} , the top third of the tallest living leaf from the plant closest to the center of the plot was cut and quickly placed into a Scholander-type pressure chamber (PMS Instrument Co., Albany, OR, U.S.A.) to measure xylem water potential. *Typha* and *Carex* LDMC, Ψ_{osm} , and Ψ_{TLP} was measured in June 2017, with samples collected from the same plots selected for Ψ_{mid} measurements. A different individual from that used for Ψ_{mid} measurement was chosen from the center of the plot, with the top third of the tallest living leaf cut in the evening, placed into a ziplock bag with a moist towel for transport, and transferred into a jar of water overnight to fully hydrate. The following day, a pressure-volume curve was generated for each leaf to estimate Ψ_{TLP} by repeated measurements of leaf mass and leaf water potential on the leaf as it dehydrated on a lab bench, resulting in a non-linear curve when the data were plotted (Tyree and Hammel 1972). Ψ_{TLP} was identified as the water potential where the curve switched from the non-linear to linear phase and osmotic potential is estimated by extrapolating the straight-line section to 100% relative water content. Each leaf was subsequently scanned at 600 dpi resolution and its surface area measured using ImageJ (Eliceiri et al. 2012). Each leaf was then dried in an oven at 55°C for three days and weighed. LDMC was calculated as dry mass/fresh mass of each leaf, where ‘fresh mass’ of each leaf was taken as the first weight from the pressure-volume curve.

2.2.5 Statistical Analyses

I evaluated treatment effects on above ground biomass and shoot density for each species in R version 3.4.3 (R Core Team 2016) using a linear mixed effects model with site and treatment as fixed effects to account for the hydrologic differences between the two sites using the package ‘lme4’. I evaluated treatment effects on Ψ_{TLP} , Ψ_{osm} , and LDMC for each species, and for water table depths and Ψ_{mid} across treatments and months using the ‘anova’ function and the ‘lsmeans’ package for all tukey adjusted pairwise comparisons.

2.3 Results

The maximum water levels for each community occurred in June, and were higher in the *Typha* communities than the *Carex* communities. The maximum water level in 2017 was 6.9 cm above ground in the north *Typha* community and 8.7 cm above ground in the south *Typha* community. In contrast, the maximum water levels in the *Carex* communities were 3.3 cm above ground in the north wetland and 3.8 cm above ground in the south wetland (Table 2.1).

Seasonal water table variation differed between wetlands (Figure 2.3). The water table remained relatively stable during the summer in the south wetland, while in the north wetland the water table declined during July and August. Water table depths on the dates of Ψ_{mid} measurements in the north wetland were representative of the seasonal water table (Figure 2.3). The first Ψ_{mid} reading in June occurred during the highest recorded water levels, the second when water tables were at their lowest below ground, and the third when the water table had risen slightly due to late summer rain and decreased evaporative demand.

There was no significant difference in above ground biomass or shoot density between the control and in-situ transplant for either species in either wetland, indicating the disturbance of transplanting had minimal impact on growth during my experiment. Although there was no

significant difference in total above ground biomass between the control and cross-boundary transplant for wet meadow plots in the north wetland ($p = 0.36$) or the south wetland ($p > 0.99$), transplanting significantly increased the above ground biomass of *Carex* plants within the meadow plots by 150.6% in the south wetland (93.5 g/m^2) (Table 2.2; $p = 0.001$, Fig 2.4A: blue-open symbols). Above ground biomass of *Carex* was not significantly different between the control and cross-boundary transplant in the north wetland ($p = 0.99$, Fig 2.4A: blue-closed symbols). *Carex* biomass accounted for 25.8% (± 1.1) of the total biomass in meadow plots in the south wetland and 30.9% (± 2.8) in the north wetland. Other species occurring in the wet meadow plots included *Juncus arcticus*, *Eleocharis macrostachya*, and *Schoenoplectus pungens*. Transplanting across the hydrologic gradient significantly reduced *Typha* biomass by 54.5% (330.2 g/m^2) in the north wetland ($p = 0.001$, Fig 2.4A: orange-closed symbols) and 28.8% (209.9 g/m^2) in the south wetland ($p = 0.04$, Fig 2.4A: orange-open symbols). *Typha* biomass accounted for 94.9% (± 9.1) of the biomass in *Typha* plots in the South wetland and 93.6% (± 13.5) in the North wetland.

Carex shoot density in the south wetland increased significantly from 353.6 shoots/ m^2 in the meadow control to 564.8 shoots/ m^2 in the cross-boundary transplant ($p = 0.04$, Fig 2.4B: blue-open symbols), though no statistical difference in shoot density occurred between the control and cross-boundary transplant for *Carex* in the north wetland ($p = 0.87$, Fig 2.4B: blue-closed symbols) or for *Typha* in either the north ($p = 0.10$, Figure 2.4B: orange-closed symbols) or south wetland ($p = 0.58$, Figure 2.4B: orange-open symbols).

Typha LDMC decreased from 0.34 g g^{-1} in the control to 0.32 g g^{-1} in the cross-boundary-transplant ($p = 0.04$, Figure 2.4C: orange symbols), although this change may not be biologically meaningful (Duru et al. 2009, Lhotsky et al. 2016). No statistical difference occurred in *Carex*

LDMC between the control and transplant ($p = 0.82$, Figure 2.4C: blue symbols). Ψ_{TLP} significantly increased in transplanted plants compared to controls for both species. *Carex* Ψ_{TLP} increased from -2.17 MPa in the control to -1.72 MPa in the transplant ($p = 0.0025$, Figure 2.4D: blue symbols). *Typha* Ψ_{TLP} increased from -0.49 MPa in the control to -0.42 MPa in the transplant ($p = 0.001$, Figure 2.4D: orange symbols). Significant increases in Ψ_{TLP} in each species corresponded to a significant increase in Ψ_{osm} for each species. *Carex* Ψ_{osm} increased from -1.51 MPa in the control to -1.26 MPa in the transplant ($p = 0.045$) and *Typha* Ψ_{osm} increased from -0.29 MPa in the control to -0.27 MPa in the transplant ($p = 0.04$).

Typha Ψ_{mid} was significantly lower in the cross-boundary transplants than controls in June ($p = 0.003$), but did not differ in July or August when the water table was at its deepest below ground (Table 2.2). *Typha* Ψ_{mid} differed across months in the transplant plots ($p = 0.002$), with the lowest Ψ_{mid} occurring in June (-0.83 MPa) when water levels were highest, but did not significantly differ across months in the control plots. *Carex* Ψ_{mid} were more negative in the controls than transplants in July ($p = 0.02$), though did not differ in June or August. *Carex* Ψ_{mid} was most negative in the control plots in July when the water table was at its deepest (-2.93 MPa). Ψ_{mid} for both species was significantly related to water table depth (Figure 2.5), though the response differed by species. *Typha* Ψ_{mid} was negatively related to water table depth, with higher Ψ_{mid} occurring at lower water table depths ($r^2 = 0.09$, $p = 0.04$). Based on the slope of the regression, however, the change in *Typha* Ψ_{mid} across the range of water table depths is only 0.19 MPa. Conversely, *Carex* Ψ_{mid} was positively related to water table depth, with more negative Ψ_{mid} when water tables were deeper ($r^2 = 0.08$, $p = 0.05$). The change in *Carex* Ψ_{mid} across the range of water table depths based on the regression would be 0.65 MPa.

2.4 Discussion

Ponded conditions imposed no measured physiological constraints to *Carex pellita* and appears to provide better growing conditions than their “control” plots. *Carex* transplanted into the flooded *Typha* habitat grew as well or better than in control plots in both study wetlands. In contrast, *Typha* biomass was reduced when transplanted into the wet meadow community, compared to controls. Increased biomass of *Carex* transplants and reduced biomass in *Typha* transplants indicates that *Typha* occupy their entire hydrologic niche while *Carex pellita* occupy only a portion of potential habitat. *Typha* often dominate wetlands with long duration standing water and little water depth variation (Fennessy et al. 1994), yet can also withstand lower water availability than other deeper marsh species (Asamoah and Bork 2010). It has been unknown whether wet meadow species like *Carex pellita* were excluded from *Typha* marshes due to physiological constraints or competitive exclusion. Jung et al. (2009) suggested that, in general, plant communities in wetlands may be limited by physical stress in deeper water and competition along their upper borders. In my study wetlands physical stress limited *Typha* along their upper border but was not limiting for *C. pellita*. Consequently, the hydrologic niche of *C. pellita* is much wider than its current distribution indicates.

2.4.1 Identifying niche preferences for species

The environmental requirements of species are thought to limit their distribution (Hutchinson 1957). While the presence of a species tells us a great deal about its habitat requirements, many reasons beyond environmental conditions can explain a species’ absence (Hirzel et al. 2002). The role of competitive exclusion remains underappreciated in current wetland management and restoration. Restoration practitioners often design new wetlands based on what they presume to be the hydrologic requirements of their target species based on data from existing sites. My results highlight the danger of this approach for planning and

implementing wetland restoration plant introductions. Although water levels in the *Typha* communities in each wetland were higher than in *Carex* communities, *Carex* responded neutrally or favorably to the studies water levels. Restoring a wetland to only the limited range in water levels of the realized niche of *Carex* would be difficult. The environmental requirements we presume to represent each species based on their current distribution are likely to be overly restrictive and/or inaccurate.

Typha may have a competitive advantage due to its tall leaves and thatch accumulation that reduces light availability at the ground level. Farrer and Goldberg (2009) found that *Typha* litter accumulation over time, rather than simply its live standing biomass, reduced light penetration and altered the community composition in Great Lakes coastal marshes. That *Typha* can similarly exclude wet meadow species has not been previously identified, as shifts from *Carex* to *Typha* are often ascribed to water levels. *Carex pellita*'s ability to survive in higher water levels is informative for designing wet meadow restoration, though more research is needed to identify mechanisms to limit the invasion and establishment of *Typha* to maintain site biodiversity.

2.4.2 Ψ_{TLP} as an adjustable trait

Ψ_{TLP} is often treated as a static trait of a species, determining species distributions within and across biomes in response to water availability (Bartlett et al. 2012). My results contradict this paradigm by showing adjustments in Ψ_{TLP} across individuals within a species, and within an individual in response to changing water levels. Because the species evaluated in this study are clonal and long lived, leaves sampled from the transplanted plot were from the same individual that existed prior to the transplant. The time scale over which species can adjust their Ψ_{TLP} remains unknown, although I found altered Ψ_{TLP} 13 months after transplanting. *Juniperus*

monosperma have been shown to adjust their Ψ_{TLP} within hours (Meinzer et al. 2014), and a meta-analysis on the plasticity of Ψ_{TLP} in response to water shortages found a wide range of Ψ_{TLP} plasticity across species and biomes (Bartlett et al. 2014). Interestingly, *Casuarina obesa*, a wetland plant from Australia, can adjust its Ψ_{TLP} up to 2 MPa, compared to the 0.65 MPa recorded for *Carex* here. Greater plasticity in Ψ_{TLP} may correlate with a broader hydrologic niche.

The large change in Ψ_{TLP} for *Carex pellita* highlights this species' ability to withstand low Ψ_{mid} (Meinzer et al. 2014), but also to adjust its Ψ_{TLP} in response to changing conditions. *Carex* Ψ_{mid} and Ψ_{TLP} were lower in the drier control plots than the inundated transplant plots, and Ψ_{mid} was lower in the late summer when water levels were low compared to June when water levels were high. *Carex* Ψ_{mid} was near the Ψ_{TLP} in control plots in June, indicating *Carex* operated near its safety margin when water levels were at their highest. Interestingly, both *Carex* and *Typha* Ψ_{mid} were below Ψ_{TLP} in the control and transplant plots, indicating they had lost hydraulic functioning at mid-day. Each species operated with a safety deficit, the difference between the Ψ_{mid} and Ψ_{TLP} when Ψ_{mid} is lower, through much of the growing season. More research is warranted to identify the amount of time each day the plants lose hydraulic functioning, which greatly limits its ability to grow and reproduce.

Changes in Ψ_{TLP} over the course of a season could be the result of osmotic adjustments or structural changes in leaves (Touchette et al. 2007). Increased allocation to cell wall material, leading to higher LDMC, limits water loss from leaves (Jung et al. 2009). I would have thus expected higher LDMC in the *Carex* mesic-control or the *Typha* mesic-transplant. However, LDMC only differed across treatments for *Typha*, and *Typha* transplanted into the drier meadow had reduced LDMC compared to the flooded control. In contrast, Ψ_{osm} differed across treatments

for both species in accordance with changes in Ψ_{TLP} . My results indicate that osmotic adjustments, rather than structural changes, are likely responsible for changes in Ψ_{TLP} .

2.4.3 Water use strategies

Plants regulate stomatal openings to conserve water and their internal Ψ_{mid} . The degree to which plants allow their Ψ_{mid} to vary determines their growth response to hydrologic restoration. In this experiment, I found *Carex pellita* had a wider range of Ψ_{mid} across treatments and months, while *Typha* Ψ_{mid} remained relatively stable. *Carex* Ψ_{mid} was lower in the controls than cross-boundary transplants and was lower in the late summer when water levels were lower than in early summer. These findings suggest *Carex pellita* keep their stomata open under reduced water potential (anisohydric), while *Typha* close their stomata to preserve their internal xylem water potential (isohydric), although additional measurements (i.e. stomatal conductance) would be required to validate this result. The ability of *Carex* to make physiological adjustments in response to altered hydrologic conditions likely means it can respond favorably to a wider range of restored water levels than previously thought (Dwire et al. 2006).

2.5 Conclusion

Wetland restoration design often relies on the current distribution of plant species in reference wetlands to identify the hydrologic niches of target species. My hypothesis that species would grow optimally where they were currently found was not validated by the results. I found *Carex pellita*, a common target species in wetland restoration, had a wider hydrologic niche than its distribution in this wetland indicated and grew as well or better when transplanted into the flooded areas dominated by *Typha*. Conversely, *Typha* growth was reduced when transplanted into the meadow, indicating *Typha* occupied nearly the entire area where their hydrologic niche overlapped with *Carex pellita*. Physiologically, individual plants can adjust Ψ_{TLP} in response to

changing environmental conditions, and the two species studied here may differ in their Ψ_{TLP} plasticity. The mechanism for Ψ_{TLP} adjustment and the time scale on which it occurs deserves more study, although our results indicate adjustments in Ψ_{TLP} were primarily due to osmotic adjustments. Additionally, identifying a mechanism to mitigate the competitive advantage of aggressive dominants before and after they invade, and to identify the true hydrologic requirements of target species planted in restoration projects remains a research priority for restoration ecology. Our understanding of the environmental requirements of species may be limited when we assume environmental requirements match current distributions.

Table 2.1. Hydrologic metrics for *Typha* and *Carex* communities in each study site. The maximum water level, average water level over all monitoring dates, and the water level depth corresponding to the day Ψ_{mid} were measured are provided. All comparisons between species at each site were significant at $p < 0.05$.

Site	Community	Maximum Water Level	Average Water Level	Water Level on June Ψ_{mid}	Water Level on July Ψ_{mid}	Water Level on August Ψ_{mid}
North	<i>Typha</i>	6.9	-5.3	5.65	-17.80	-15.15
	<i>Carex</i>	3.3	-11.5	-0.35	-24.70	-19.78
South	<i>Typha</i>	8.7	5.5	6.90	3.98	5.85
	<i>Carex</i>	3.8	0.4	2.58	-1.73	-1.08

Table 2.2. Treatment response from each species in each study location. Leaf Dry Matter Content, Ψ_{osm} , Ψ_{TLP} , and monthly Ψ_{mid} were only measured in transplant and control treatments in the north wetland. Asterisk (*) denotes statistical significance at $p < 0.05$ from the linear mixed effects model.

Species (treatment)	Biomass (g/m ²)	Density (shoots/m ²)	LDMC (mg/g)	Ψ_{osm} (-Mpa)	Ψ_{TLP} (- Mpa)	June Ψ_{mid} (-MPa)	July Ψ_{mid} (-MPa)	August Ψ_{mid} (-MPa)
<u>North Wetland</u>								
<i>Carex pellita</i>								
Control	120.0 ± 36.3	521.3 ± 151.3	0.39 ± .01	1.51 ± .11	2.17 ± .11	2.21 ± .17	2.93 ± .22	2.72 ± .27
In-Situ	71.7 ± 26.9	441.6 ± 131.8	---	---	---	---	---	---
Transplant	117.6 ± 29.6	476.8 ± 118.8	0.39 ± .02	1.26 ± .05*	1.72 ± .05*	2.25 ± .13	2.16 ± .32*	2.46 ± .19
<i>Typha latifolia</i>								
Control	606.1 ± 80.5	128.0 ± 12.8	0.34 ± .01	0.29 ± .01	0.49 ± .01	0.58 ± .04	0.59 ± .03	0.51 ± .03
In-Situ	432.5 ± 32.9	110.4 ± 10.0	---	---	---	---	---	---
Transplant	275.9 ± 64.0*	91.2 ± 12.6	0.32 ± .004*	0.27 ± .01*	0.42 ± .01*	0.83 ± .11*	0.56 ± .04	0.53 ± .04
<u>South Wetland</u>								
<i>Carex pellita</i>								
Control	62.1 ± 14.4	353.6 ± 60.6	---	---	---	---	---	---
In-Situ	99.4 ± 54.5	516.8 ± 84.1	---	---	---	---	---	---
Transplant	155.6 ± 27.6*	564.8 ± 108.9*	---	---	---	---	---	---
<i>Typha latifolia</i>								
Control	728.3 ± 89.1	129.6 ± 13.8	---	---	---	---	---	---
In-Situ	626.2 ± 53.9	105.6 ± 10.2	---	---	---	---	---	---
Transplant	518.4 ± 53.0*	112.0 ± 14.7	---	---	---	---	---	---

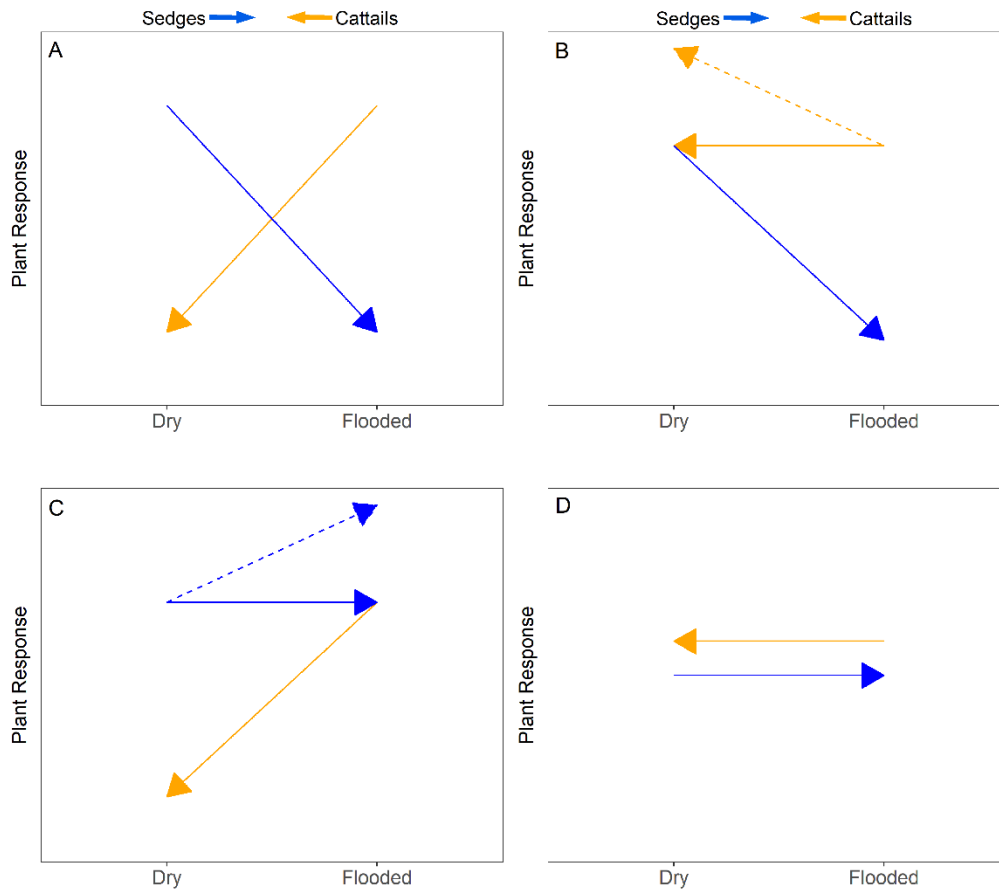


Figure 2.1. Alternate hypotheses for species response to experimental transplants across a hydrologic gradient. Arrows above the figure panels indicate the transplant direction for each species, and the arrows within each panel indicate the species response to that transplant. When species occur in their physiological optima, plant responses to transplant treatments would be negative (A). *Carex* dominance and exclusion of *Typha* (B) versus *Typha* dominance and exclusion of *Carex* (C) shows when one species has a competitive advantage, the weaker competitor will respond positively or neutrally to the transplant while the stronger competitor will have a negative response. If the species distribution is independent of the environmental gradient no response may be detected (D).

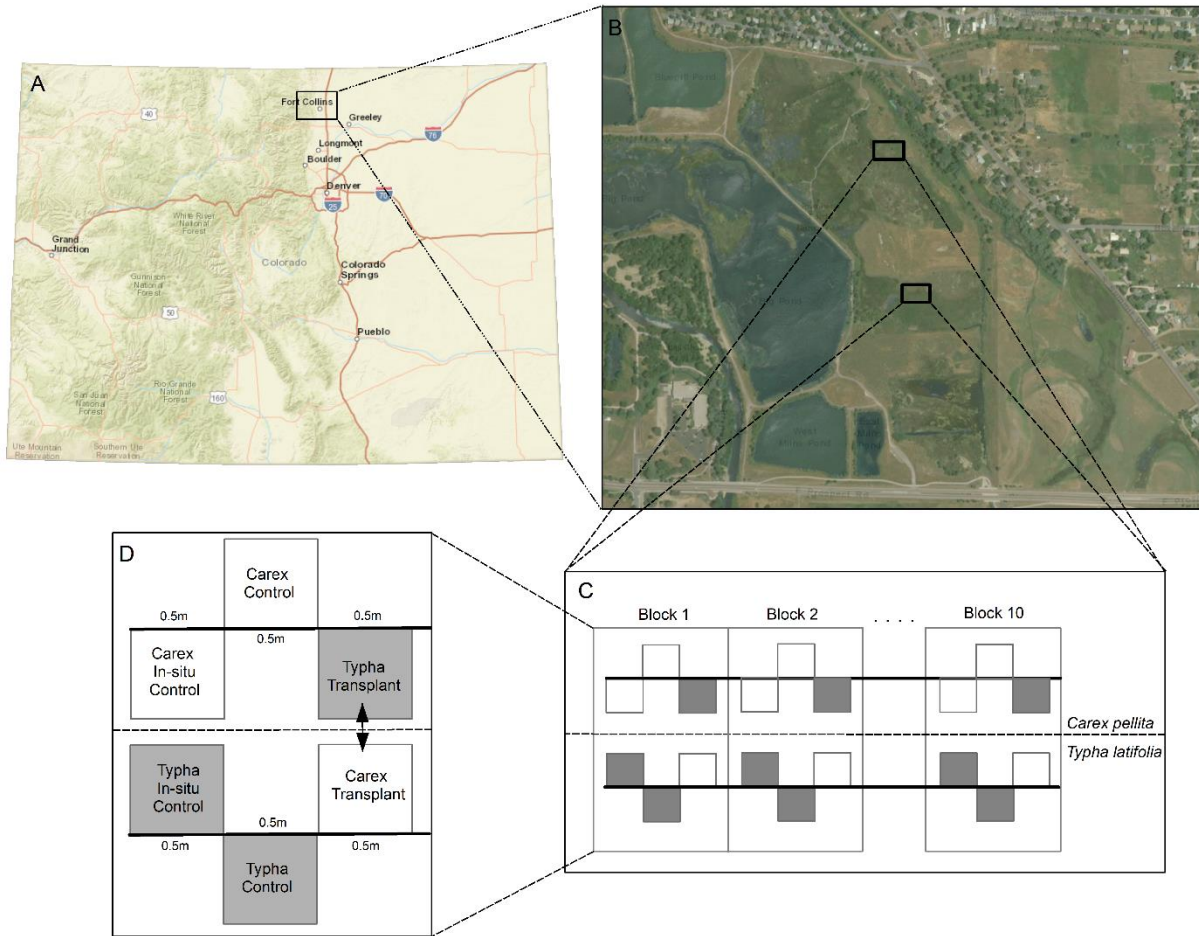


Figure 2.2. Study area in Fort Collins, CO (A) in two different wetlands (B). Experimental transects were established on either side of each *Typha-Carex* boundary (dotted line C). Blocks include two treatments and one control replicated every 0.5 m in each community (D), and each block replicated 10 times across a 20 m long transect (bold line in C and D). Treatments included a control, an in-situ transplant, and a cross community transplant for both *Carex* and *Typha*.

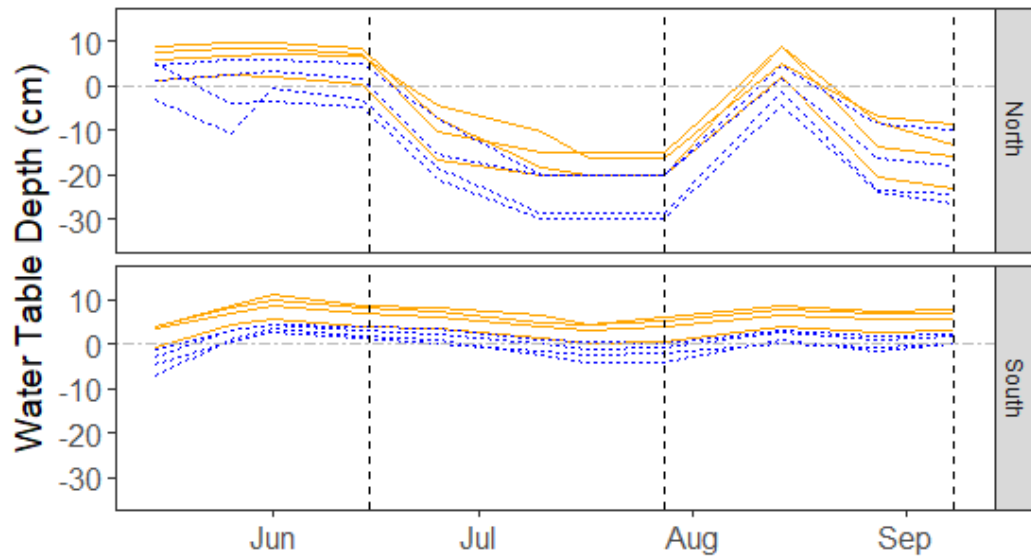


Figure 2.3. Hydrographs of four wells occurring in each community in the north wetland, top panel, and south wetland, lower panel. The *Typha* community (solid orange) had consistently higher water tables than the *Carex* community (dashed blue) in each site. The timing of Ψ_{mid} occurring in June, late July, and early September are shown by the vertical dashed lines. Water table fluctuations differed across study sites, with the north wetland experiencing a drawdown of water tables during the summer and the south wetland experiencing stable water table depths throughout the growing season. Ground level is at 0 along the y-axis and is denoted by a dashed grey line. Water levels above this indicate above ground flooding, whereas water levels below this indicate water below the ground surface.

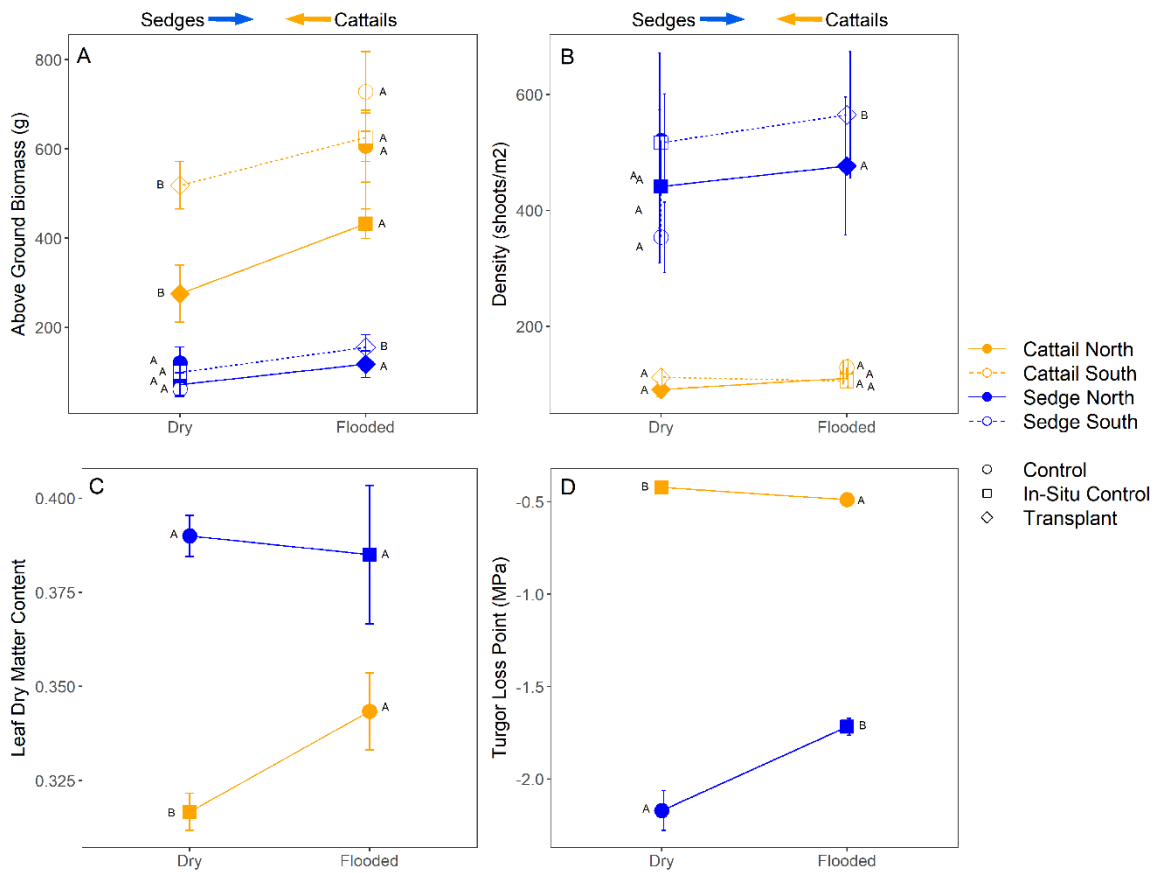


Figure 2.4. Above ground biomass (A), Shoot density (B), Leaf dry matter content (g g^{-1}) (C), and Turgor Loss Point (D) in controls (circles), in-situ treatments (square), and transplant treatments (diamond) for the north wetland site (filled symbols and solid line) and the south wetland site (open circles and dashed line) for both *Typha* (blue) and *Carex* (orange). Statistical significant groups within each species and site are denoted by letters. Arrows above the figure panels indicate the transplant direction for each species; from mesic-control to flooded-transplant for *Carex* and from flooded-control to mesic-transplant for *Typha*.

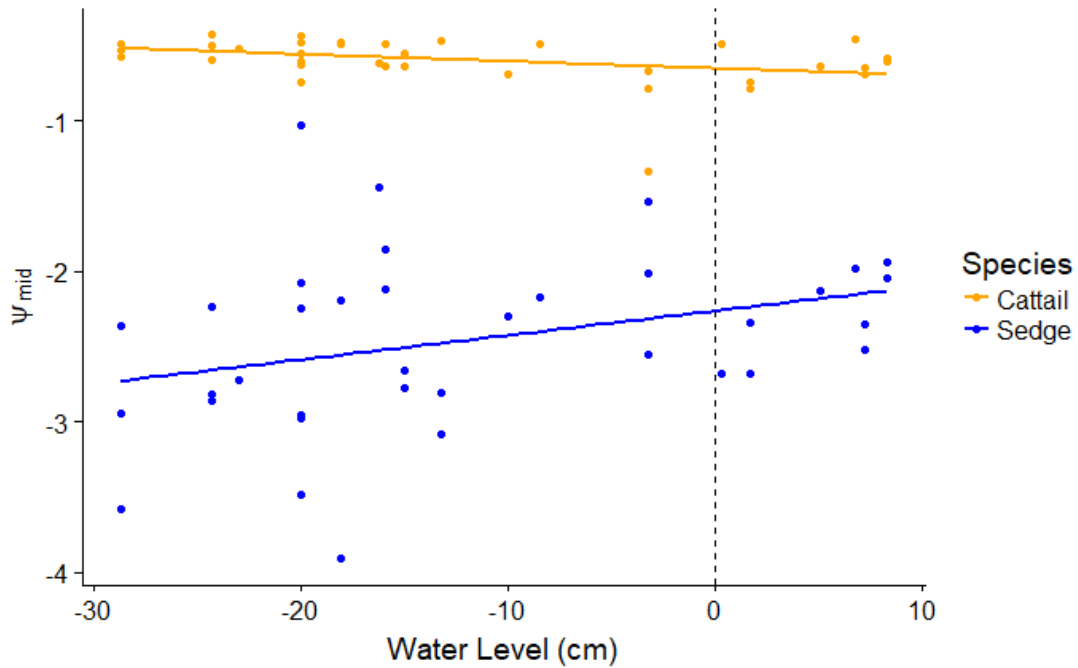


Figure 2.5. Ψ_{mid} (MPa) as a function of water level recorded in the nearest well at the time of leaf water potential measurements for *Carex* (blue) and *Typha* (orange). Along the gradient of water level, when water levels were high *Carex* leaf water potential was significantly higher ($r^2 = 0.08$, $p = 0.05$) and *Typha* leaf water potential was significantly lower ($r^2 = 0.09$, $p = 0.04$). The vertical dashed line indicates the ground surface.

3 Hydrologic similarity drives community assembly towards reference composition in restored wetlands

3.1 Introduction

Our ability to predict long-term restoration outcomes using ecological monitoring data remains limited (Brudvig et al. 2017). While ecologists would ideally have the same predictive capability when designing an ecosystem as an engineer does a bridge (Keddy 1999), the comparison between ecology and engineering neglects the stochasticity and variability inherent in nature (Zedler 1996). Although vegetation can be notoriously variable following a restoration effort (Laughlin et al. 2017), many restoration projects are judged solely by their plant species composition after restoration is complete. Just as the form and function of a bridge relies on its physical structure for support, so too do the biotic components of ecosystems reflect underlying physical processes.

The study of species' niches over the past 100 years (Grinnell 1917, Hutchinson 1957) has led to increased confidence in predicting community assembly and species distributions once the potential niche of a species is known (Mouquet et al. 2015). Although competition can be important in shaping communities, abiotic conditions determine the outcome of community assembly more in stressful environments (Chase 2007). Because water depth and soil oxygen availability physiologically constrain many plant species, hydrologic conditions are one of the primary filters in wetland community assembly following restoration (Caldwell et al. 2011).

Vegetation does not always develop as expected in restoration programs (Martin et al. 2005, Moreno-Mateos et al. 2012). Plant dispersal and colonization are inherently stochastic, but wetland vegetation is often distributed across a hydrologic gradient (Silvertown et al. 1999). When restored water levels are different than planned, the vegetation that develops is likely to

differ as well. The sensitivity of species composition to restored hydrologic gradients may also vary between wetland types (Cleland et al. 2013). Few wetland restoration projects include long-term data collection (Bernhardt et al. 2007), and very few projects monitor surface and ground water levels at all (Fennessy et al. 2007). The lack of long term hydrologic data following wetland restoration has limited our knowledge of the hydrologic characteristics of successful and unsuccessful wetland restorations and of the sensitivity of these restored wetlands to different water levels. Although a true predictive capability following restoration is unlikely (Zedler 1996), identifying hydrologic mechanisms that control community assembly can help guide future restoration activities (Johnson et al. 2012).

The use of reference sites to evaluate restoration success has become increasingly common (Moorhead 2013). For example, reference sites have been used to guide restoration designs and evaluate outcomes in forested wetlands in the eastern US (Caldwell et al. 2011, Johnson et al. 2014), vernal pools in California (Schlatter et al. 2016), tropical riparian forests in Brazil (Suganuma and Durigan 2015), and coastal wetlands in Louisiana (Steyer et al. 2003). However, it remains unclear whether the use of reference wetlands as a design guide for hydrologic restoration leads to similar plant communities in the restored wetland.

I evaluated long-term hydrologic and vegetation composition datasets from reference and restored wetlands in the Colorado Rocky Mountains to identify relationships between vegetation composition and water levels in restored fens, wet meadows, and riparian wetlands. I tested whether similar water levels in reference and restored sites leads to vegetation composition similarity after 15 years. I specifically asked: 1) how do vegetation species assemble across a restored hydrologic gradient; 2) does hydrologic similarity between restored and reference wetlands lead to similar vegetation composition; and 3) does the sensitivity of plant species composition to restored water levels differ among wetland types?

3.2 Methods

3.2.1 Study Sites

Study sites were in Mountain Village, Colorado, located in the San Juan Mountains near the town of Telluride, CO. Regional topography is the result of large post-Pleistocene landslides following the melting of valley glaciers common to the San Juan region. Mountain peaks above 4000 m slope down to glacially carved valleys with a series of steep slopes and level bench areas of unconsolidated landslide material (Purinton 1897).

The study area receives a significant snowpack from November through April, with an annual average of 445 cm (www.usclimatedata.com). Snowmelt in the spring and summer infiltrates into the landslide substrate and discharges in locations where the slope flattens, forming headwater wetlands and streams which eventually discharge into the San Miguel River in the Colorado River watershed.

As part of a mitigation settlement with the Environmental Protection Agency and Department of Justice, 13 wetlands that had been filled without a US Army Corps of Engineers permit during golf course construction were restored from 1998-2001 (Cooper et al. 2017). Restored wetland types included stream side riparian wetlands, wet meadows with mineral soils, and fens with peat soils. Hydrologic restoration methods for all wetland types included removing underground drainage features and excavating fill that had been placed over the wetland. Restored wetlands were planted with either a purely herbaceous community dominated by the sedges *Carex utriculata* or *C. aquatilis*, or a willow-sedge community with an overstory primarily of *Salix monticola*, *S. geyeriana*, *S. drummondiana*, and *S. bebbiana* with a *Carex* understory. Hydrologic monitoring of 10 reference wetlands provided design guidance prior to restoration, and evaluation of outcomes after restoration. Reference sites represented the range of wetland types, and were often contiguous to the restored wetlands.

3.2.2 *Hydrologic and Vegetation Monitoring*

Wetlands were instrumented with groundwater monitoring wells hand augured to around 1 m deep, cased with slotted Schedule 40 PVC, and backfilled with native soil. Water table depth measurements were collected manually from each well on a weekly basis from May through October. Reference wetlands were monitored from 1998 through 2007 and again in 2013. Restored wetlands were monitored starting in the year following restoration, which ranged from 1998 to 2001 and ceased once the restored wetland had met its regulatory requirements, which ranged from three to five years for individual wetlands. Further hydrologic monitoring occurred in 2013 and 2016. Pressure transducers were installed in a subset of wells in 2016 and recorded hourly water table levels within each wetland. A total of 403 wells were monitored over the life of the project. Precipitation data were obtained from station COOP:058204 from the Western Regional Climate Center (wrcc.dri.edu).

Plant species cover was visually estimated to the nearest percent within 3x5m vegetation plots located adjacent to each monitoring well on an annual basis from 1998 through 2007, and again in 2013.

3.2.3 *Data Analysis*

I used the Indicators of Hydrologic Alteration (IHA) to evaluate the hydrologic data from each well. Originally developed to characterize the hydrologic regime of rivers (Richter et al. 1996), the IHA includes 64 metrics designed to describe the shape of the annual hydrograph. For example, the IHA identifies the timing of the maximum and minimum water level along with the average monthly water level for each well. In addition to the IHA metrics, water level minimum, maximum, and the standard deviation in water levels were calculated for each month and year for each well. I performed a Principal Components Analysis (PCA) on the hydrologic metrics from the restored and reference wetlands to account for the correlation and redundancy of the

IHA metrics (Olden and Poff 2003). Hydrologic metrics with the highest PC score were selected from each of the first four principal components to use in further analyses (Table 3.1).

3.2.3.1 Community Assembly

I used a partial Mantel test to evaluate the relationship between the vegetation composition and the selected hydrologic metrics from restored wetlands. Species found in fewer than 5% of plots were removed to reduce the influence of infrequent species on the analysis (McCune and Grace 2002) and the resulting species rows and columns were relativized prior to calculating a Bray-Curtis distance matrix from the plant species cover data. A hydrologic similarity matrix between plots was created from the hydrologic metrics selected from the PCA using Euclidean distance. A Euclidean geographic distance matrix was created using the coordinates of each groundwater monitoring well to account for spatial autocorrelation between plots. The mantel test correlated the Euclidean distances of the hydrologic metrics to the Bray-Curtis distance matrix of the species composition, while removing the influence of geographic proximity between the plots using the geographic Euclidean distance matrix. I used the function ‘bioenv’ for model selection, which identified the hydrologic metrics most correlated with the species composition matrix. The partial Mantel test and model selection were performed using the ‘vegan’ package in R (Oksanen et al. 2017).

3.2.3.2 Hydrologic Similarity and Species Composition

Percent cover by plant species in restored and reference plots was evaluated using Non-Metric Multidimensional Scaling (NMS) in the ‘vegan’ package. A stable solution was sought using 1000 iterations each with a random start and 2 final dimensions. Hydrologic metrics for each plot were scaled and fit to the NMS ordination, and the ordination was rotated to orient the highest correlated hydrologic metric with NMS axis 1.

To identify the sensitivity of plant species composition to hydrologic conditions, a linear regression was used to relate plant species composition, as indicated by each plot's position along NMS axis 1, to the restored water levels in the associated well. A steeper regression slope, indicating a more rapid change in species composition across different water levels, indicated greater sensitivity.

To test whether hydrologic similarity between the restored and reference plots lead to floristic similarity, a linear regression was used to relate the NMS axis 1 distance between the restored plot and its reference site to the average annual water table difference between them. Regression models were created for each wetland type. Regressions were run using the 'stats' package and evaluated using the 'anova' function in R (R Core Team 2016).

3.3 Results

3.3.1 Hydrologic Conditions

Inter-annual variation in water table depths occurred in all three wetland types. In the three years immediately following restoration, the highest and most stable water levels across all wetland types occurred in 1999 (Figure 3.1). Water levels in fens remained at or above the ground surface through 1999, though dropped to -40 cm during late summer 2000 before increasing to ground level in the fall (Figure 3.1a). A similar fen water table decline, though of less magnitude, occurred in the late summer of 2001. Water levels in wet meadows and some riparian wetlands had a similar inter-annual trend to fens. Summer monsoon precipitation patterns can explain these differences in water tables across years (Figure 3.1b). Large weekly rain totals from June through August in 1999 supported high water levels throughout the summer, while lower rain totals in 2000 and 2001 led to lower water levels.

Water levels differed across wetland types, and restored wetland water levels were similar to reference sites. Water levels averaged -2.0 cm (± 1.1) in reference fens and -6.8 cm (\pm

0.9) in restored fens across all study years (Figure 3.2). The water level in wet meadows was lower than in fens, averaging -26.6 cm (± 0.4) in reference meadows and -26.4 cm (± 0.2) in restored meadows. Riparian wetlands had the lowest water levels at -42.4 cm (± 0.6) in reference and -41.9 cm (± 0.3) in restored riparian wetlands. Average water levels were similar between reference and restored wetlands, although the range in water table depths in restored wetlands was higher.

Nine hydrologic metrics provided the most explanatory power of the original 64 IHA metrics to characterize the hydrologic conditions across all sites (Table 3.1). The PCA identified the annual mean, minimum, and maximum water level as the dominant variables associated with the first principal component, the annual range and annual standard deviation in water table depths for the second principal component, the calendar date for the water table minimum and maximum for the third principal component, and the base flow index and number of water level reversals for the fourth principal component. The base flow index calculated the seven day minimum water level divided by the average annual water level, meant to approximate soil moisture stress experienced by plants (Poff and Ward 1989).

3.3.2 *Community Assembly*

Species richness was higher in reference than restored sites for all wetland types (Table 3.2). The mean number of species was highest in riparian sites and wet meadows at 11 each, and lowest in fens with five. Similarly, species diversity was higher in reference than restored wetlands for each wetland type, and higher in riparian wetlands and wet meadows than fens. The dominant species in all vegetation plots reflected the originally planted species of *Salix* and *Carex*. *Salix* cover was higher in reference riparian (60.0%) and wet meadow (40.0%) than in restored riparian (32.5%) and wet meadow (18.7%) wetlands, although *Salix* cover was higher in restored fens (44.5%) compared to reference fens (27.5%). Among all wetlands, *Carex* spp.

cover was highest in the reference fens (77.5%) and restored fens (70%). *Carex* spp. cover was similar in reference wet meadows (33.3%) and restored wet meadows (42.8%), and the same between reference riparian wetlands (40.0%) and restored riparian wetlands (40.0%).

The hydrologic and species distance matrices were significantly correlated after the impact of geographic similarity between plots was removed ($R = 0.15$, $p = 0.005$). The annual mean water table and the standard deviation of water table depth were the best correlated hydrologic metrics with the community distance matrix ($R = 0.30$). The partial Mantel using only these two hydrologic metrics increased the correlation between the two distance matrices from the full model ($R = 0.24$, $p = 0.001$).

3.3.3 Hydrologic Similarity and Species Composition

The NMS ordination converged after 20 iterations with a final stress of 0.229 and an r^2 non-metric stress fit of 0.948. The most significant hydrologic metric was the annual mean water table depth ($r^2 = 0.40$, $p < 0.001$), which was used to rotate the ordination such that the mean annual water table depth was perfectly correlated to axis 1 (Figure 3.3). Of the included hydrologic variables, the standard deviation of water table depth was best correlated with axis 2 ($R = 0.48$, $p = 0.004$). Plots with lower water levels are towards the left of the plot, and plots with higher water levels are towards the right. Wetland types follow this gradient, with fens in the right portion of the ordination space, and meadows and riparian wetlands scattered to the left.

Plot location along NMS axis 1 was significantly related to the annual water table depth (Figure 3.4a, $r^2 = 0.43$, $p < 0.001$), although the sensitivity of the plant species composition to the restored water levels differed among the three wetland types. Species composition was the most sensitive in riparian wetlands (regression slope = 0.03), followed by wet meadows (regression slope = 0.02), and was the least sensitive in fens (regression slope = 0.0).

Hydrologic similarity between restored and reference sites led to similarity in plant species composition between restored and reference sites (Figure 3.4b, $r^2 = 0.35$, $p < 0.001$). When the water table in the restored wells was more similar to its reference site, the distance in ordination space between the restored and reference plot was low, indicating a similar species composition. Conversely, as the hydrologic difference between restored and reference wells increased, the distance in ordination space between the restored and reference plot vegetation increased. Regression slopes indicated wetland types were similarly sensitive to these hydrologic differences, within similar slopes for fens (0.011) and wet meadows (0.013), and slightly higher for riparian wetlands (0.034).

3.4 Discussion

Plant species composition of restored wetlands more closely resembled the species composition of reference sites when their hydrologic conditions were similar. The correlation between the mean annual water table difference between reference and restored plots and the distance between them along NMDS axis 1 indicated a convergence in species composition when restored water levels were similar to reference water levels. This convergence in species composition was seen in all three wetland types.

While hydrologic similarity can lead to similar plant species composition, the low correlation between plant species composition and water levels in restored wetland plots indicated a limited role for the hydrologic gradient in determining the final species composition. Relating species composition to hydrologic conditions in restored wetlands has utility in predicting restoration outcomes (Fennessy et al. 1994), but community assembly following restoration is highly variable (Laughlin et al. 2017). Community assembly is often described as a series of filters, which allow species from the broader set of the regional species pool to filter through various attributes, including each species' ability to colonize the site, its environmental

requirements, and competitive interactions that may facilitate or preclude it (Keddy 1992). The resulting community composition is one of many possible combinations. Restoration often focuses on manipulation of the physical environment, making the abiotic filter for community assembly of primary interest (Matthews et al. 2009). Many restoration projects, including the one evaluated here, treat this abiotic filter as the dominant control over community assembly, with the restored abiotic gradients determining the resulting plant species composition. Because restored abiotic conditions may play a more limited role in community assembly in some wetland types, caution is warranted in creating restoration goals around specific vegetation composition.

Plant species composition of some wetland types may be more sensitive to hydrologic restoration than others. I found the species composition in fens, where water levels were high, to be less sensitive to the studied hydrologic gradient than wet meadows or riparian wetlands, where water levels were lower. These results are consistent with results from North American grasslands showing greater sensitivity to different rainfall amounts in drier areas (Cleland et al. 2013). However, few plant species can tolerate the level of flooding and duration of saturation in fens, compared to the lower water levels of wet meadows and riparian wetlands. It has been previously suggested that less variation in species composition can be expected when environmental factors constrain most species (Brudvig et al. 2017). Due to lower sensitivity to water levels, species composition may be the least meaningful indicator of restoration success in fens than the other two wetland types. However, fens are an important wetland type for other ecosystem services, particularly carbon sequestration (Belyea and Malmer 2004). While species composition in fens is insensitive to different water levels, water level declines of as little as 6 cm can significantly reduce the carbon accumulating function of Rocky Mountain fens (Chimner and Cooper 2003).

The long term implications of the order of arrival of a species can play a lasting role in community assembly (Egler 1954, Fukami et al. 2005). The clonal sedges dominating most of the restored wetlands in this study were the original species planted and may be resilient to a wide range of hydrologic conditions as they are the dominant wetland plants in mountain valleys throughout the Rocky Mountains. The success of these species across wetland types may provide an opportunity to include them in generic planting lists for local restoration efforts, but also underscores the danger of evaluating restoration using only the plant species composition. One may restore a completely inappropriate hydrologic regime for the given wetland type, and still get some of the species of interest because of their broad hydrologic niche.

Restoring the physical processes that drive ecosystem structure and function is a primary task in restoration (Beechie et al. 2010). Growing season water levels in this study differed between wetland types within years and differed for each wetland type across years. Most notably, water levels in fens remained near the ground surface for most of each year, though summers with little precipitation led to fen water tables dropping far below the ground surface. Although water levels during May and June rely on melting winter snow packs, wetland water levels in July through September may be more a function of monsoon rains. Late summer monsoons can bring high levels of rain to the San Juan Mountains in Colorado, which has also been shown to impact regional forest fire return intervals (Grissino-Mayer et al. 2004). Not only will significant changes to summer monsoons alter the forests of Colorado, but my results suggest changes in summer monsoon will also alter the biotic structure of wetlands in the San Juan Mountains.

3.5 Conclusions

I provide a rationale for evaluating restoration outcomes using hydrologic comparisons to reference sites. Although restored vegetation was similar to reference sites when growing season

water levels were similar, the overall correlation between water levels and vegetation composition was low. Vegetation is notoriously variable following restoration, and the vegetation in some wetlands was found to be more sensitive to restored water levels than other wetland types. Wetland water levels in these study sites relied on late summer monsoon rains, and restored wetlands responded to differences in precipitation totals similarly to reference sites. Water levels may be a more reliable metric of restoration outcomes than vegetation. Although species composition in some wetland types may be insensitive to water level variation, future changes in climate are likely to have significant impacts on the form and function of these wetlands.

Table 3.1. Principal Components (% variance explained) and the variable loadings for associated hydrologic metrics. Annual mean, minimum, maximum, range, and standard deviation (SD) refer to water level descriptive statistics of water levels in each well. The Julian date minimum and maximum refer to the day the highest and lowest water level was recorded. The base flow index is the seven day minimum water level divided by the average annual water level, meant to approximate soil moisture stress experienced by plants. Reversals indicate the number of times in which water levels switched from a rising period to a falling period or from a falling period to a rising period. Original hydrologic metrics identified here were further used in the NMS analysis. All principal components were used in the partial Mantel correlation.

	PC1 (0.62)	PC2 (0.11)	PC3 (0.08)	PC4 (0.07)
Annual Mean	-0.3269			
Annual Minimum	-0.3236			
Annual Maximum	-0.3120			
Annual Range		-0.5078		
Annual SD		-0.5311	-0.5850	
Julian Date Minimum			0.3458	
Julian Date Maximum			-0.6014	
Base Flow Index				-0.8381
Reversals				-0.4955

Table 3.2. Mean species richness, mean Simpson's Diversity Index, mean cover of *Salix* spp. and mean cover of *Carex* spp for restored and reference fens, wet meadows, and riparian wetlands.

		Species Richness	Simpson's Diversity	<i>Salix</i> spp. cover (%)	<i>Carex</i> spp. cover (%)
Fen	Reference	5	0.57	27.5	77.5
	Restored	3	0.42	44.5	70.0
Wet Meadow	Reference	11	0.70	40.0	33.3
	Restored	6	0.63	18.7	42.8
Riparian	Reference	11	0.74	60.0	40.0
	Restored	8	0.72	32.5	40.0

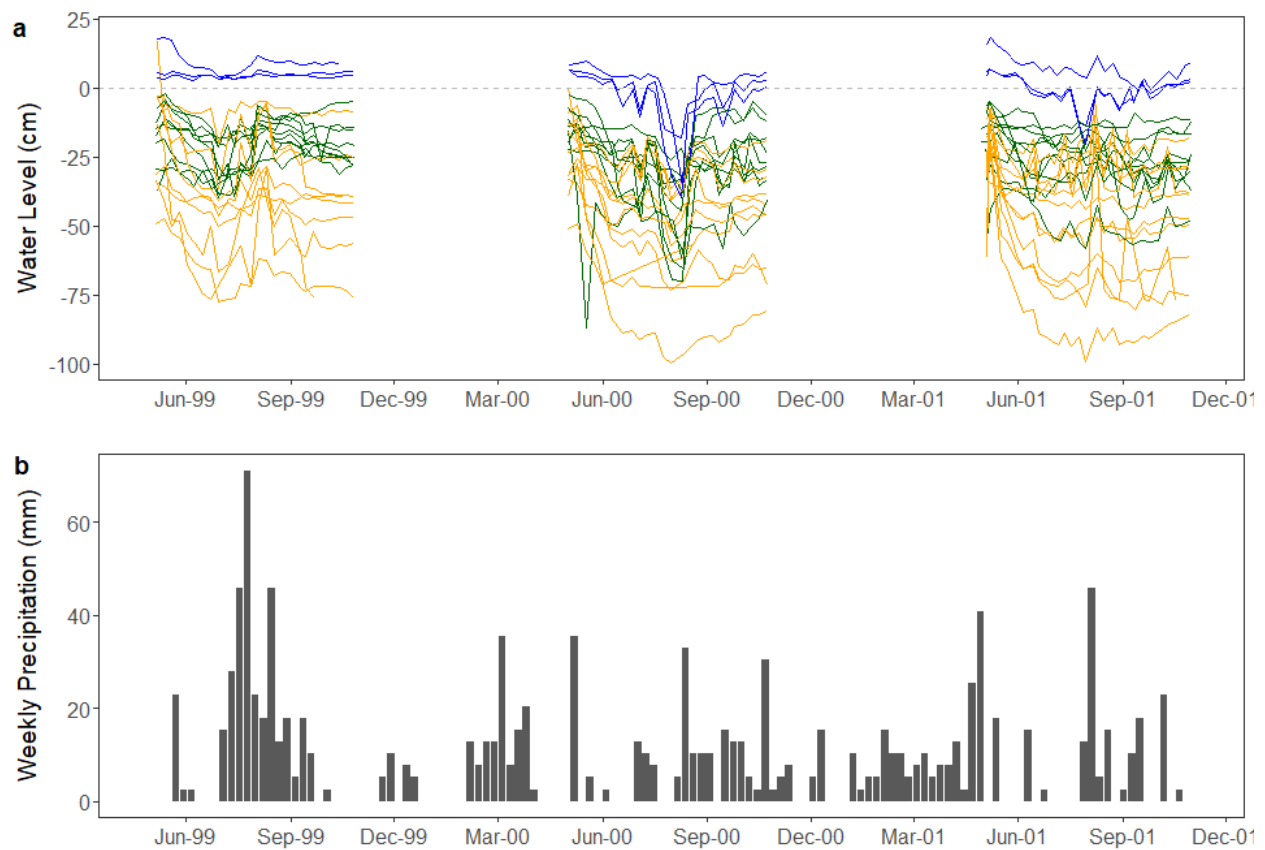


Figure 3.1. Water levels in reference fens (blue), wet meadows (green), and riparian wetlands (orange) for 1999, 2000, and 2001 (a). Each colored line represents a different well and the grey dashed line at 0 represents ground level. Weekly precipitation totals for 1999, 2000, and 2001 (b). Water levels were more consistent across months during 1999, coinciding with high weekly precipitation totals. Water levels at these same times in 2000 and 2001 dropped due to lower weekly precipitation.

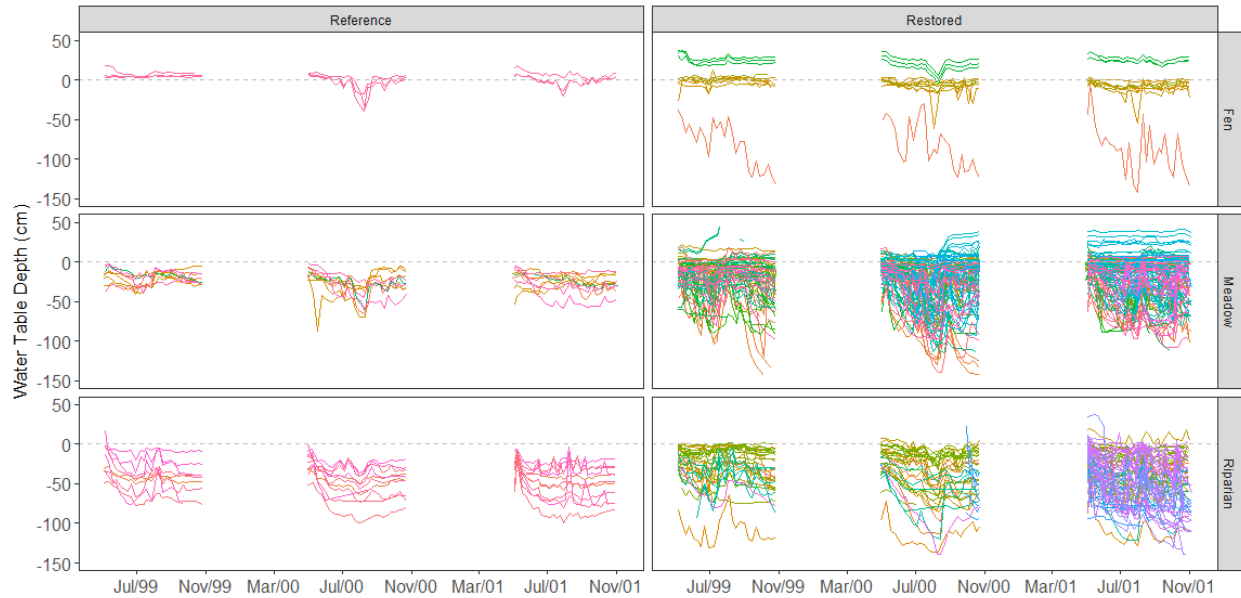


Figure 3.2. Reference and restored water levels for fens (top row), wet meadows (middle row), and riparian wetlands (bottom row) in 1999 (first pair), 2000 (middle pair) and 2001 (last pair). Reference fens had water levels near the ground surface throughout each year. Reference wet meadows and riparian wetlands had water levels deeper below ground, with riparian wetlands having the lowest water levels. Restored wetlands of all three types had a wider range in water levels than their respective reference sites. Each line and color represent a different monitoring well.

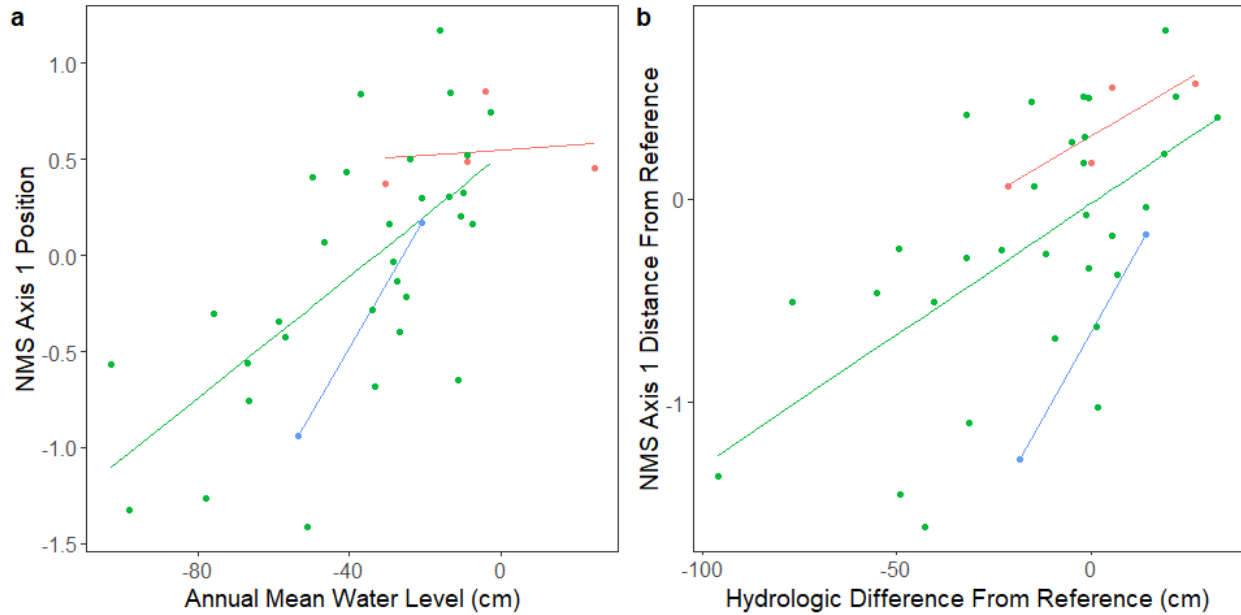


Figure 3.4. Vegetation plot location along NMS axis 1 as a function of the annual water table depth for fens (red), wet meadows (green) and riparian wetlands (blue) (a). Shorter distances in ordination space indicate similarity in species composition. Fens were the least sensitive to differences in growing season water table depth, while riparian wetlands were the most sensitive. The distance between restored plots and reference plots along NMS axis 1 compared to the hydrologic difference between them for each wetland type reveals fens and wet meadows are similarly sensitive to hydrologic similarity to reference sites, while riparian wetlands are more sensitive (b). Restored hydrologic conditions similar to reference sites have more similar species compositions for all wetland types than restored wetlands with differing hydrologic conditions.

4 Testing an approach to evaluate wetland restoration through hydrologic performance standards

4.1 Introduction

Defining success in ecological restoration has been difficult for many ecosystem types (Suding 2011). For permits authorized under Section 404 of the US Clean Water Act (CWA), the US Army Corps of Engineers (USACE) may require compensatory mitigation consisting of restored wetlands to offset unavoidable losses to existing wetlands. These mitigation projects are required to specify quantitative performance standards to indicate success, which has been shown to improve restoration outcomes (National Research Council 2001, Fennessy et al. 2007, Schlatter et al. 2016). Unfortunately, even when meeting defined standards, mitigation wetlands can have simplified vegetation (Gutrich et al. 2009), soils with higher bulk density and lower organic matter content (Fennessy et al. 2004), and lower rates of carbon and nitrogen cycling (Hossler et al. 2011). Current performance standards are primarily related to vegetation (Environmental Law Institute 2004), with little to no evaluation of wetland hydrologic regimes.

Wetland hydrologic regimes, including their depth, duration, and seasonality of surface and ground waters, vary among wetland types and are a primary control over wetland form and function (Cook and Hauer 2007, Sieben et al. 2010). In contrast to this variation among wetland types, however, the CWA defines wetlands as having saturation within 30 cm of the ground surface for 12.5% of the frost-free growing season (Environmental Laboratory 1987). Wetland restoration under the CWA needs to meet this hydrologic criterion. This simple requirement ignores important differences in water table depth and dynamics within and among wetland types (Johnson et al. 2012). Additionally, hydrologic regimes of mitigation wetlands that meet the USACE minimum requirement can differ from reference sites (Fennessy et al. 2007).

Ecological performance standards are required for many CWA permitted wetland mitigation projects (USACE and USEPA 2008). Performance standards are designed to indicate whether a project has met its stated goals. Existing standards often focus on plant species richness and cover (Environmental Law Institute 2004), but vegetation and habitat structure may not develop within the typical mitigation monitoring timeframe of five years (Dee and Ahn 2012). Wetland water levels can develop rapidly following restoration in some wetland types (Schimelpfenig et al. 2014), though can take multiple years to adjust to restored conditions in others (Black and Zedler 1998). Changes in restored water levels over time can be due to compressed soils following construction (Cole and Brooks 2000), as well as legacy effects from the original disturbance (Sun et al. 2001). Identifying the number of years required for water levels to become similar to reference wetlands can inform required monitoring timelines following restoration.

An approach to create ecologically meaningful hydrologic performance standards would provide a robust tool for the analysis of wetland mitigation programs (Gardner et al. 2009). Hydrologic performance standards are most effective when they are developed using site specific success criteria (Schlatter et al. 2016). Because hydrologic regimes create the template for wetland biotic composition, structure, and function (Silvertown et al. 1999, Gowing 2005), restored wetlands with a hydrologic regime similar to reference sites should be more likely to develop vegetation and ecosystem processes similar to reference sites.

In this paper, I present and evaluate a new approach for creating quantitative hydrologic performance standards using water level data collected concurrently from wetland reference and mitigation sites. I test this approach in three wetland types from across the continental US: California vernal pools, Colorado Rocky Mountain fens and wet meadows, and forested mineral soil wetlands in Virginia and North Carolina. I specifically ask: 1) do wetland types differ in the

time required for restored water levels to match water levels in reference sites; and 2) does similarity in water levels between restored and reference sites lead to successful vegetation development in restored wetlands? I use these analyses to evaluate whether one approach for creating hydrologic performance standards can be used to evaluate different wetland types.

4.2 Methods

4.2.1 Study Sites

I obtained existing hydrology and vegetation datasets for wetland mitigation projects conducted over the last 20 years from individual researchers and the Regulatory In-lieu Fee and Bank Information Tracking Systems (RIBITS) database managed by the USACE (<https://ribits.usace.army.mil/>) (Figure 4.1). Seventeen datasets were selected based on their inclusion of water level data and vegetation cover in both restored and reference wetlands (Table 4.1). Wetland types occur in regions with distinct climate, landforms, vegetation and hydrologic conditions. Construction and planting methods were similar among projects for each wetland type and each project had reference wetlands concurrently monitored with the restored wetlands.

4.2.1.1 Fens and Wet Meadows

Fen and wet meadow data were obtained from the Telluride Ski and Golf Company (Telski) in Mountain Village, Colorado. More than 30 hectares of wetlands had been filled during the 1980s and 1990s without a USACE permit. Following a legal settlement with the United States Environmental Protection Agency (EPA), Telski restored about half of the impacted wetland area from 1998 to 2003. The two dominant wetland types restored were ground water driven wet meadows with mineral soils and fens with organic soils. Fens and wet meadows were restored by removing fill to recreate historic grade, disabling artificial drainage features, and planting native shrubs and herbs (Cooper et al. 2017).

4.2.1.2 *Vernal Pools*

Vernal pool data were obtained from two restoration and creation projects in San Diego and six projects in Sacramento. These regions have distinct substrate, landforms and climate and represent the range of environmental conditions in the region. Restoration reestablished pools that had been filled and levelled over time, and many areas retained undisturbed pools that were used as reference sites. Suitable restoration or creation sites had a shallow, low-permeability clay-rich aquitard. Pools were created by excavating surface sediments to reach the aquitard, with the final pool geometry designed to simulate reference pools. Restoration and creation projects ranged from 4 to 30 hectares in size and from 40 to 1,379 restored pools.

4.2.1.3 *Non-Riverine Forested Wetlands*

Forested wetland data were from eight restoration projects near the Great Dismal Swamp in Virginia and North Carolina (Table 4.1). Forested wetlands in the eastern US have been drained for more than a hundred years, with drainage canals installed to lower the local water table to create suitable conditions for agriculture. Restoration of forested wetlands in this area involved converting cropland to forested wetlands by filling or blocking drainage ditches and planting native wetland trees. Forested wetland restoration projects ranged from 6 to 200 hectares.

4.2.2 *Hydrologic Monitoring Data*

Groundwater monitoring wells in the Telluride study site were installed in restored and reference fens and wet meadows using slotted schedule 40 PVC installed to a depth of approximately 1 m (Cooper et al. 2017). Water levels in wells were measured weekly from May through October from one year prior to restoration (1997 to 2000) through the final approval of each wetland by the USACE and EPA (2001 to 2007), and again in 2013 and 2016.

Vernal pool ponded water depth was manually measured using staff gauges in the center of each monitoring pool and recorded every 3-7 days for the period when pools were filled. Many projects identified a subset of restored and reference pools for monitoring, as it was not feasible nor required by their mitigation permit conditions to monitor all pools.

Groundwater monitoring wells in restored and reference forested wetlands included slotted PVC installed to a depth of at least 50 cm, measured manually or using recording pressure transducers or capacitance rods. Groundwater monitoring wells were measured daily if automated loggers were used and weekly if done manually. Water level monitoring typically occurred every other year following restoration through final approval by the USACE.

4.2.3 Vegetation Monitoring Data

Vegetation monitoring methods differed among wetland types in accordance with regional permit conditions. In fens and wet meadows, 3x5 m plots were established adjacent to monitoring wells in reference and restored sites. Plant cover by species was visually estimated to the nearest percent in 1999, 2000, 2001, and 2013 within each plot. Vernal pool plant species absolute cover was monitored annually. Although monitoring methods were consistent within each vernal pool project, vegetation plot size varied between projects. Some projects used the entire vernal pool as a single vegetation plot, while others established multiple plots within each pool. Forested wetland vegetation plots were 10 x 10 m. Living tree stems were identified to species and counted within each plot on an annual basis.

Vegetation metrics used to evaluate projects were consistent with existing vegetation performance standards in use by the USACE and included the cover of native vs. exotic species for fens, wet meadows, and vernal pools, and the number of tree seedlings and species richness of trees in forested wetland plots.

4.2.4 Statistical Analysis

4.2.4.1 Years to hydrologic similarity

The time required for restored water levels in each wetland type to match reference sites was defined as the number of years until no statistical difference existed between the restored and reference average annual water table depth. Average annual water table depth for restored wetlands was compared to project specific reference sites each year following restoration for each wetland type using a hierarchical Bayesian model. Annual mean water depths were created by averaging water depths from each well over the most common monitoring time frames for each wetland type. Fens and wet meadows were monitored from May through October, vernal pools were monitored January through April, and forested wetlands were typically monitored from March through June. The statistical model was based on a linear deterministic equation commonly used in Bayesian analyses (Eqn 1) to estimate the effect size of an experimental treatment (Hobbs and Hooten 2015).

$$g(\boldsymbol{\beta}, x_{ijt}) = \beta_{0j} + \beta_{1t}x_{ijt}$$

Eqn. 1

All parameters were evaluated for the i^{th} reading in the j^{th} wetland type in the t^{th} year. Restored plots are given an x value of 1 and reference sites are given the x value of 0. Using this design, the β_0 coefficient identifies the reference mean for wetland j , and the β_1 coefficient identifies the difference in water levels between reference and restored wetlands. The β coefficients were distributed independently for each wetland type and year using a normal distribution with vague priors. The number of years required for restored water levels to match reference sites for each wetland type was defined as the estimated time between restoration and when the 95% credible intervals of the β_1 coefficient include zero.

4.2.4.2 *Vegetation Response to Hydrologic similarity*

I estimated the vegetation response to hydrologic similarity between restored and reference wetlands for each wetland type using a different Bayesian model. Vegetation metrics included the summed absolute cover of all native and exotic species in fens, wet meadows, and vernal pools, and the number of tree seedlings and tree species richness in forested wetlands. I used a linear model (Eqn 1) where the β_0 coefficient estimated the cover of each vegetation metric for plot i when the hydrologic conditions in the restored wetland perfectly matches the reference site (intercept term), and the β_1 coefficient is the slope of the regression line relating mean weekly hydrologic similarity in monitoring well i from its reference site to changes in vegetation in the restored site.

Each well's mean weekly hydrologic similarity to the reference site was calculated by averaging the weekly water table depth in each reference site and subtracting it from the restored water levels for the same week. This value was then averaged across all weeks in each year to calculate a mean weekly hydrologic similarity between the restored and reference sites for each year. Vegetation metrics from each plot were paired with the hydrologic conditions in the adjacent well. Only two of the forested mitigation projects used paired wells and vegetation plots and were included in this analysis. Absolute percent cover in fens, wet meadows, and vernal pools was modelled using a normal distribution, while tree seedling counts and species richness in forested sites were modelled with a Poisson distribution. All parameters were estimated in JAGS using the R package *rjags*, with convergence evaluated using the Gelman statistic. Posterior predictive checks were evaluated by using the squared error from the observed data and a simulated data set. Bayesian p-values were obtained from the squared error for standard deviation, mean, and the discrepancy between the observed and simulated datasets.

4.3 Results

Each wetland type had a distinct hydrologic regime (Figure 4.2). Fens and wet meadows had consistent water table depths from May through November, vernal pools were ponded from December to May, and forested wetlands had water tables near the ground surface from October through June. Water levels in reference fens averaged -2.0 cm (± 1.1) compared to -6.8 cm (± 0.9) for restored fens (Figure 4.2a). Reference wet meadows had an annual water table average of -26.6 cm (± 0.4), compared to -26.4 cm (± 0.2) for restored wet meadows (Table 4.2). The mean summer water table across restored fens ranged from -20.1 to $+35.7$ cm and -108.2 to $+7.9$ cm for restored wet meadows.

Vernal pools filled with water during rain events in December and January and were dry by May of most years. Ponding depth was much lower in San Diego than Sacramento pools (Figure 4.2b). The two San Diego reference sites had average water depths of 1.8 cm (± 0.2) and 4.5 cm (± 0.3) during the spring, while in Sacramento the reference pools ranged from 7.3 (± 0.2) to 12.3 cm (± 0.3). Average restored water depth for San Diego pools was similar to reference sites and averaged 4.4 cm (± 0.1) and 5.2 cm (± 0.1). Restored Sacramento pools were also similar to their reference pools with average water depths from 6.7 (± 0.1) to 15.3 cm (± 0.3).

Restored and reference forested wetlands had similar seasonal water table variation, with water levels near the ground surface from October through June and much lower from July through September (Figure 4.2). Restored forested wetlands had lower water table depths in the fall, winter, and spring than reference areas. March through June water levels averaged across all monitoring years were similar in restored and reference forested wetlands, and ranged from -25.7 cm (± 0.4) to -14.1 cm (± 0.5) in reference sites and -30.0 cm (± 0.5) to -7.3 cm (± 0.2) in restored sites (Table 4.2).

4.3.1 *Years to hydrologic similarity*

The number of years required for water levels in restored wetlands to match reference wetlands differed among wetland types (Figure 4.3). Restored fens and wet meadows had higher ground water levels than reference sites following restoration ($\text{Pr}(\beta_1 > 0) = 0.96$), though no difference between restored and reference water levels existed after four years ($\text{Pr}(\beta_1 > 0) = 0.90$; Figure 4.3a). Restored vernal pools had higher water levels than reference pools for six years following restoration ($\text{Pr}(\beta_1 > 0) = 1.00$), lower water levels in years seven and eight ($\text{Pr}(\beta_1 > 0) = 0.02$), and were not statistically different nine years after restoration ($\text{Pr}(\beta_1 > 0) = 0.69$; Figure 4.3b). Restored and reference forested wetlands had similar water levels the first year following restoration ($\text{Pr}(\beta_1 > 0) = 0.50$; Figure 4.3c). The 95% credible intervals included zero during the entire monitoring period except year six when restored forested wetlands had higher water levels than reference sites ($\text{Pr}(\beta_1 > 0) = 0.99$).

4.3.2 *Hydrologic Similarity and Successful Vegetation Establishment*

Hydrologic similarity between restored and reference sites influenced the percent canopy cover of native and exotic plant species in fens and wet meadows, native plant species cover in vernal pools, and tree species richness and seedling density in forested wetlands (Figure 4.4; Table 4.3). Native species cover in fens and wet meadows was highest when restored water levels matched reference sites ($\beta_0 = 105.91$), and native cover decreased as restored water levels became less similar to reference sites ($\beta_1 = -0.87$, $\text{Pr}(\beta_1 < 0) = 0.98$). In contrast, exotic species cover was low in restored fens and wet meadows when water levels were more like reference sites ($\beta_0 = -0.07$), and increased as restored water levels were less like reference sites ($\beta_1 = 0.66$, $\text{Pr}(\beta_1 > 0) = 1.00$).

For three of the eight vernal pool projects, native species cover was highest when water levels in restored pools were similar to reference pools ($\text{Pr}(\beta_1 < 0) = 1.00$). Native species cover

in the other five vernal pool restoration projects, all from the Sacramento region, was not significantly related to hydrologic similarity to reference pools. Hydrologic similarity between restored and reference pools did not influence exotic species cover for any vernal pools project (Table 4.3). The number of forest seedlings and tree species richness were related to the restored hydrologic difference from reference sites for one of the two forested projects and unrelated in the other project. The highest tree seedling counts ($\beta_0 = 19.91$) and tree species richness ($\beta_0 = 5.05$) at the Roquist site occurred in areas where water levels matched the reference site, and declined where water levels were less similar to the reference (tree seedling counts: $\beta_1 = -0.82$, $\text{Pr}(\beta_1 < 0) = 0.99$; tree species richness: $\beta_1 = -0.14$, $\text{Pr}(\beta_1 < 0) = 0.99$). Tree seedling counts and tree species richness were not significantly related to hydrologic similarity to the reference at the Edge Farm site.

4.4 Discussion

Hydrologic comparisons between restored wetlands and project-specific reference sites provide an ecologically meaningful approach to evaluating wetland restoration outcomes. The hydrologic similarity between mitigation and reference sites was correlated with higher cover of native plant species and lower cover of exotic species in fens and wet meadows, higher native species cover in three vernal pool projects, and higher tree seedling counts and tree species richness in one of the two forested wetland projects. Native species cover in five of the six analyzed vernal pool projects in the Sacramento area was not related to hydrologic similarity to reference sites, although native species cover in both San Diego projects was higher in restored pools with similar water depths to reference pools. Similarly, previous research has shown greater sensitivity of plant communities to water availability in drier areas (Cleland et al. 2013). In the more arid San Diego region, hydrologic similarity to reference pools may be more important for native species colonization. There was no relationship between exotic species

cover and hydrologic similarity to reference sites in any vernal pool project, highlighting a significant challenge to restoration and conservation of California vernal pools (Gerhardt and Collinge 2003).

The number of tree seedlings and tree species richness in one forested wetland site in Virginia was highest when restored water levels were similar to reference sites. At the second forested site, these metrics were not related to hydrologic similarity with reference sites. Because most forested wetland restoration projects with available data did not have vegetation data from plots adjacent to groundwater monitoring wells, it's unclear whether the response of the number of tree seedlings and richness is related to hydrologic conditions. Natural tree seedling recruitment is often limited by hydrologic conditions (Johnson 2000). Planting mature seedlings is meant to overcome the hydrologic limitations of germination and recruitment (Young et al. 2005), although long-term forest community regeneration may be limited if restored hydrology does not permit native tree colonization (Battaglia et al. 2002).

The time required for water levels in restored wetlands to match their reference sites differed among the three studied wetland types, although hydrologic similarity for all three occurred within 10 years. Restored vernal pools in California had greater inundation depths than reference pools for their first six years, and became hydrologically similar to reference pools after eight years. Longer duration standing water in restored vernal pools occurred in other California mitigation sites and required up to 9 years to become hydrologically similar to reference pools (Black and Zedler 1998). Newly restored and created pools often have soils that are overly compacted during construction, leading to prolonged ponding. A five-year monitoring period was insufficient to detect the long-term development of hydrologic conditions similar to reference vernal pools.

Restored forested wetlands had similar water levels to reference sites within one year. However, long term hydrologic processes in restored forested wetlands are poorly understood. An increase in evapotranspiration rates as trees grow and have greater leaf area may alter ground water levels (Bruland and Richardson 2005), although this remains untested in restored forested wetlands. As forests mature, tree density decreases, and although the surviving trees have greater leaf area, the death of many trees may balance this water use. Water level changes in response to the removal of trees in forested wetlands for logging can be minimal (Sun et al. 2001), although the relationship between forest evapotranspiration and wetland water levels may depend more on climate than forest structure (Lu et al. 2009). Monitoring periods of five to 10 years are short compared to the life span of trees, and much longer data collection periods are suggested to understand the hydrologic changes that occur as restored forests mature.

Water levels in restored fens and wet meadows in Colorado took four years to match reference sites, a similar time for herbaceous plants in these wetlands to reach maximum shoot density (Cooper et al. 2017). In contrast to forested wetlands, abundant groundwater flow and the dominance of herbaceous and shrub species in these wetlands limits the importance of increased evapotranspiration as the vegetation matures. However, peatland degradation, from filling as was the case here or draining as is common in agricultural areas, can result in long term hydrologic changes due to peat decomposition and a reduction in hydraulic conductivity (van Seters and Price 2002). Any change in hydraulic conductivity can influence water holding capacity and limit colonization of the restored area by peat forming species. The time required for water tables to stabilize following restoration likely depends both on the wetland type as well as on the original disturbance, and the restoration of some highly disturbed sites may never match reference sites (Price et al. 2003).

4.4.1 Creating hydrologic performance standards

Focusing monitoring efforts within the required monitoring timeframe on variables that indicate whether a project will meet its success criteria can provide an opportunity for adaptive management. A recent analysis of mitigation sites for several wetland types identified higher cover of invasive species after the required five year monitoring period ended (Van den Bosch and Matthews 2017). Inherent intra- and inter-annual variability in water table dynamics exists among wetland types (Moorhead 2013). Hydrologic requirements specific to each project using water level data from local reference sites are thus needed to ensure long term ecological success in mitigation wetlands. The current hydrologic requirement used by the USACE to evaluate all wetland types in the US is identical to that used to determine whether a site is a regulatory wetland meeting the 1987 COE manual criterion, saturation within 12 inches of the ground surface for 2 weeks of the growing season. This criterion is an insufficient indicator to determine that the hydrologic regime for most wetland community types has been restored (Johnson et al. 2012). It is also unable to detect different water table depths from what was proposed (Petru et al. 2014). Hydrologic comparisons to local reference wetlands provide a more accurate reflection of the appropriate water levels for a proposed wetland type.

Identifying and using reference sites that encompass the natural range of hydrologic variability for the proposed wetland type provides an excellent goal for success (White and Walker 1997). However, the availability and accessibility of appropriate reference sites can be a challenge. Reference sites may have unknown disturbance histories (Moorhead 2013) and because of the wide temporal and spatial variability in wetlands and significant urban development in many regions, it can be hard to find reference sites that are hydrologically representative of the site to be restored (White and Walker 1997). Although project-specific reference sites provide a more accurate characterization of local wetlands and are ideal for

creating hydrologic performance standards, the monitoring of regional reference systems could also be used to characterize intact wetlands at a larger regional scale (Steyer et al. 2003).

However, the use of this approach remains untested (Fennessy et al. 2004).

Evaluating community assembly or the development of specific communities that form and persist under different water table regimes requires floristic and hydrologic data from the same location within each wetland. The placement of monitoring wells and vegetation plots in the same locations allows analyses of the relationship between hydrologic conditions and vegetation composition. Unfortunately, many mitigation sites with available data had monitoring wells and vegetation plots that were not co-located. Future wetland mitigation projects should prioritize the collection of vegetation and hydrologic data from the same locations within each wetland by nesting vegetation plots around monitoring wells.

4.5 Conclusions

Wetland types differ in their hydrologic regimes and in the time required for hydrologic conditions in restored wetlands to match reference sites. Project specific reference sites provide a meaningful approach for evaluating mitigation outcomes and some sites with similar water tables to reference areas had higher native species cover and tree seedling richness. Hydrologic similarity to reference sites was insufficient to restore vegetation composition and preclude the invasion of exotic species in all sites, highlighting the continued need for vegetation performance standards and invasive species management. Concurrent monitoring of reference and restored sites incorporates water level variations due to climate variance within and between years, hydrologic differences across wetland types, and can be used for both restoration design and evaluating outcomes. My analyses suggest a post restoration analysis timeline of at least 10 years for some wetlands types is needed to quantify long-term hydrologic conditions. Analyzing

mitigation outcomes using project specific reference sites and concurrent hydrologic monitoring provides an effective way to gauge long-term restoration success across wetland types.

Table 4.1. Mitigation project information including wetland type restored, site name, location, year restoration took place, the number of wetlands restored, the number of reference wetlands and the number of reference monitoring wells, the total hectares restored, the number of years of data available, the monitoring frequency water levels were recorded, and the type of vegetation data collected.

Wetland Type	Site	Location	Year Restored	# of wetlands restored	# of reference wetlands (wells)	Total Hectares Restored	Record Length (years)	Hydrologic Observation Frequency	Vegetation data type
Fens	Telluride Ski and Golf	Telluride, CO	1999-2001	2	2 (5)	1.2	12	Weekly/daily	Cover
Wet Meadows	Telluride Ski and Golf	Telluride, CO	1999-2003	9	6 (11)	10.9	12	Weekly	Cover
Vernal Pools	Dennery	San Diego	2008	40	12 (1)	4	7	biweekly	Cover
	SR125	San Diego	2006	103	20 (1)	4.9	5	weekly	Cover
	Aitken	Sacramento	2003	200	15 (1)	4.2	7	weekly	Cover
	Locust Road	Sacramento	2008	108	58 (1)	30.4	5	weekly	Cover
	Meridean	Sacramento	2012	553	11 (1)	14.6	3	weekly	Cover
	Toad Hill	Sacramento	2010	1,379	30 (1)	17.4	5	weekly	Cover
	Van Vleck	Sacramento	2009	248	50 (1)	7.9	6	biweekly	Cover
	Vincent	Sacramento	2005	224	11 (1)	5.1	10	weekly	Cover
Non-Riverine Forested Mineral Flats	ABC	North Carolina	2000	1	1 (4)	75	2	daily	Tree Counts
	Dover	Virginia	2009	1	1 (1)	71.2	6	weekly	Tree Counts
	Edge Farm	Virginia	2006	1	1 (1)	199.1	8	daily	Tree Counts
	Hall	Virginia	2000	1	1 (2)	12.5	6	daily	Tree Counts
	Roquist	North Carolina	2007	1	1 (5)	15.0	4	daily	Tree Counts
	Sliver Moon	North Carolina	2011	1	1 (1)	5.7	5	daily	Tree Counts
	Stephens	Virginia	2003	1	1 (1)	57.5	7	daily	Tree Counts
Su	Virginia	2000	1	1 (6)	22.3	13	daily	Tree Counts	

Table 4.2. Average water level (cm \pm one standard error) for each wetland type and project site. Data are averaged over all wells and all monitoring years. Fen and wet meadow data are from May through October. Vernal Pools data are from January through April. Forested wetland data are from March through June.

Wetland Type	Site	Reference	Restored
Fens	Telski	-2.0 (\pm 1.1)	-6.8 (\pm 0.9)
Wet Meadows	Telski	-26.6 (\pm 0.4)	-26.4 (\pm 0.2)
Vernal Pools - San Diego	Dennery	1.8 (\pm 0.2)	5.2 (\pm 0.1)
	SR125	4.5 (\pm 0.3)	4.4 (\pm 0.1)
Vernal Pools - Sacramento	Aitken	12.4 (\pm 0.3)	14.5 (\pm 0.2)
	Locust Road	11.0 (\pm 0.2)	15.3 (\pm 0.3)
	Meridean	9.0 (\pm 0.5)	9.7 (\pm 0.2)
	Toad Hill	7.3 (\pm 0.2)	6.7 (\pm 0.1)
	Van Vleck	9.0 (\pm 0.2)	15.0 (\pm 0.2)
	Vincent	11.5 (\pm 0.3)	10.6 (\pm 0.1)
Non-Riverine	ABC	-18.5 (\pm 0.4)	-7.3 (\pm 0.2)
Forested Mineral Flats	Dover	-24.4 (\pm 3.2)	-30.0 (\pm 0.5)
	Edge Farm	-21.0 (\pm 0.8)	-20.7 (\pm 0.1)
	Hall	-25.7 (\pm 0.4)	-23.0 (\pm 0.3)
	Roquist	-14.1 (\pm 0.5)	-23.2 (\pm 0.3)
	Sliver Moon	-17.0 (\pm 0.5)	-22.2 (\pm 0.2)
	Stephens	-24.9 (\pm 1.3)	-23.2 (\pm 0.2)
	Su	-25.7 (\pm 0.4)	-29.7 (\pm 0.1)

Table 4.3. Bayesian estimates for the relationship between vegetation metrics and hydrologic similarity between restored and reference wetlands. Vegetation metrics include native and exotic species cover in fens, wet meadows, and vernal pools, and tree seedlings/plot and tree species richness in forested wetlands. The Bayesian median estimate for each β coefficient and the 95% credible interval for the β_1 coefficient is provided, along with the probability that β_1 is less than zero. β_1 was expected to be negative for native species cover, tree seedling density and tree species richness, and positive for exotic species cover.

Wetland Type	Metric	Site	β_0	β_1	β_1 CI	Pr($\beta_1 < 0$)
Fens & Wet Meadows	Native Cover	Telluride	105.91	-0.87	-1.63, -0.04	0.98
	Exotic Cover	Telluride	-0.07	0.66	0.34, 0.99	0.00
Vernal Pools	Native Cover	Dennergy	10.34	-0.40	-0.57, -0.22	1.00
		SR125	12.55	-0.52	-0.78, -0.29	1.00
		Aitken	5.90	-0.11	-0.27, 0.05	0.92
		Locust Road	4.79	-0.08	-0.28, 0.14	0.76
		Meridean	4.88	-0.09	-0.34, 0.17	0.77
		Toad Hill	5.80	-0.05	-0.25, 0.17	0.68
		Van Vleck	13.29	-0.19	-0.30, -0.07	1.00
		Vincent	4.64	-0.06	-0.24, 0.14	0.72
	Exotic Cover	Dennergy	1.24	-0.04	-0.15, 0.08	0.77
		SR125	5.15	-0.04	-0.19, 0.08	0.78
		Aitken	4.78	-0.03	-0.14, 0.08	0.74
		Locust Road	3.50	-0.05	-0.20, 0.06	0.82
		Meridean	6.66	-0.03	-0.17, 0.12	0.68
		Toad Hill	3.88	0.00	-0.11, 0.16	0.52
Non-Riverine Forested Mineral Flats	Tree Seedlings	Edge Farm	17.70	-0.06	-0.38, 0.26	0.65
		Roquist	19.91	-0.82	-1.45, -0.19	0.99
	Tree Species Richness	Edge Farm	2.18	0.03	-0.03, 0.08	0.16
		Roquist	5.05	-0.14	-0.24, -0.03	0.99

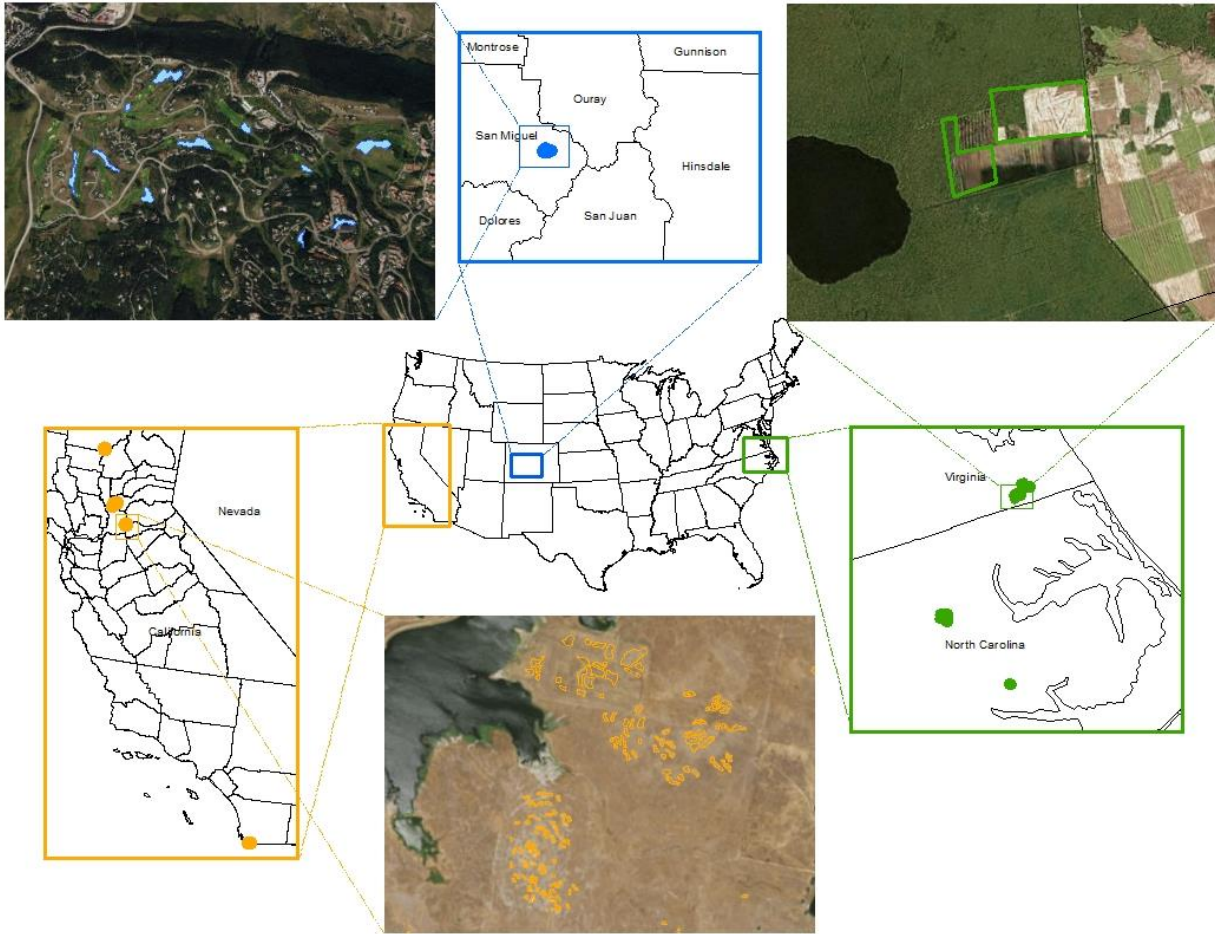


Figure 4.1. Study sites across the United States, including fens and wet meadows in Colorado (blue), vernal pools in California (orange), and forested wetlands in the mid-Atlantic (green). Aerial images show representative projects from each wetland type.

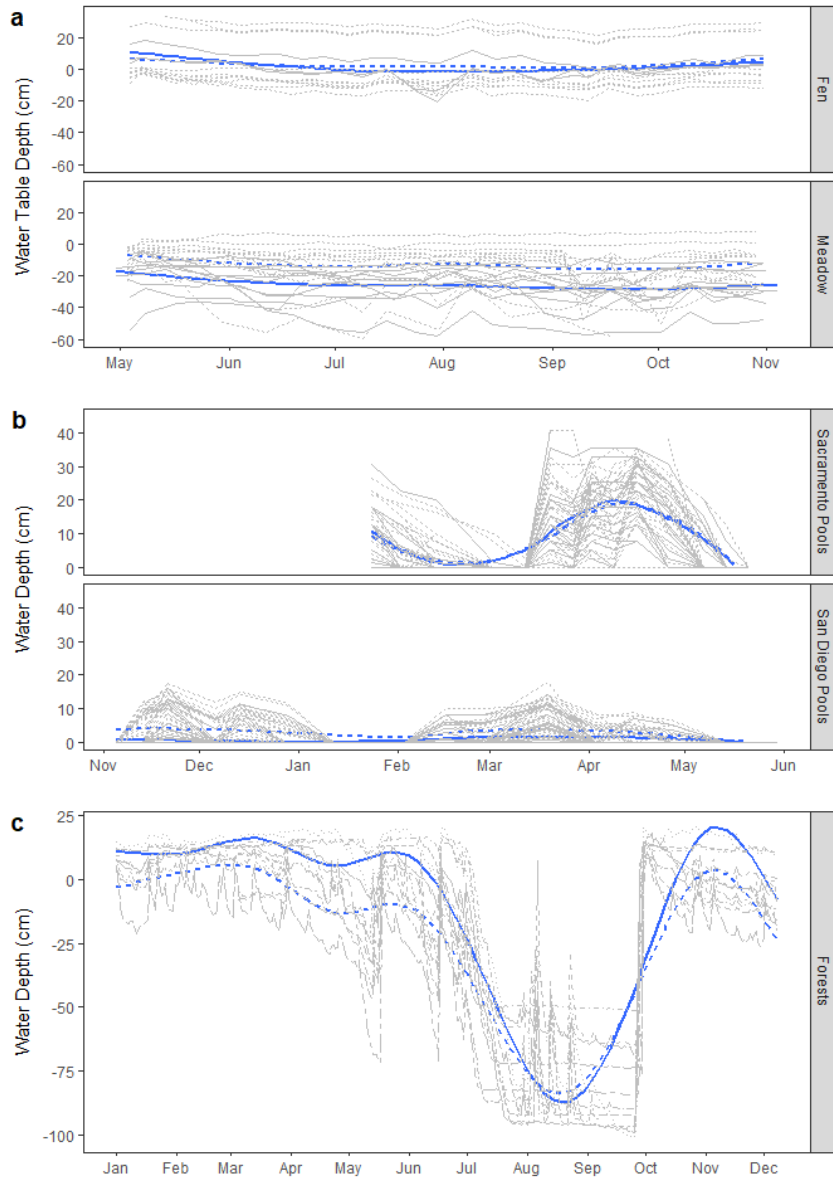


Figure 4.2. Hydrographs for restored (dashed) and reference (solid) fens and wet meadows in 2001 (a), vernal pools in 2009 (b), and non-riverine forested wetlands in 2010 (c). Measured water level at each site is shown in grey, with average water depth shown in blue for restored (dashed) and reference (dashed) sites. Restored fens and wet meadows (a) had a wider range of water table depths than reference sites. Reference fens had consistently higher water tables than reference meadows, though some restored meadows were wetter than restored fens. Vernal pools (b) in Sacramento have higher ponding depths than vernal pools in San Diego. Vernal pools filled between November and February, dried by June, and remained dry the rest of the year (Note compressed x-axis). Restored pools in Sacramento had similar hydroperiods than reference pools, though restored pools in San Diego had higher ponded water depths than reference pools. Water table depths in restored and reference forested wetlands (c) were near the ground surface in the fall and spring, and over 75 cm below ground during the summer. Restored forested wetlands had lower water tables than reference forested wetlands during the fall and spring.

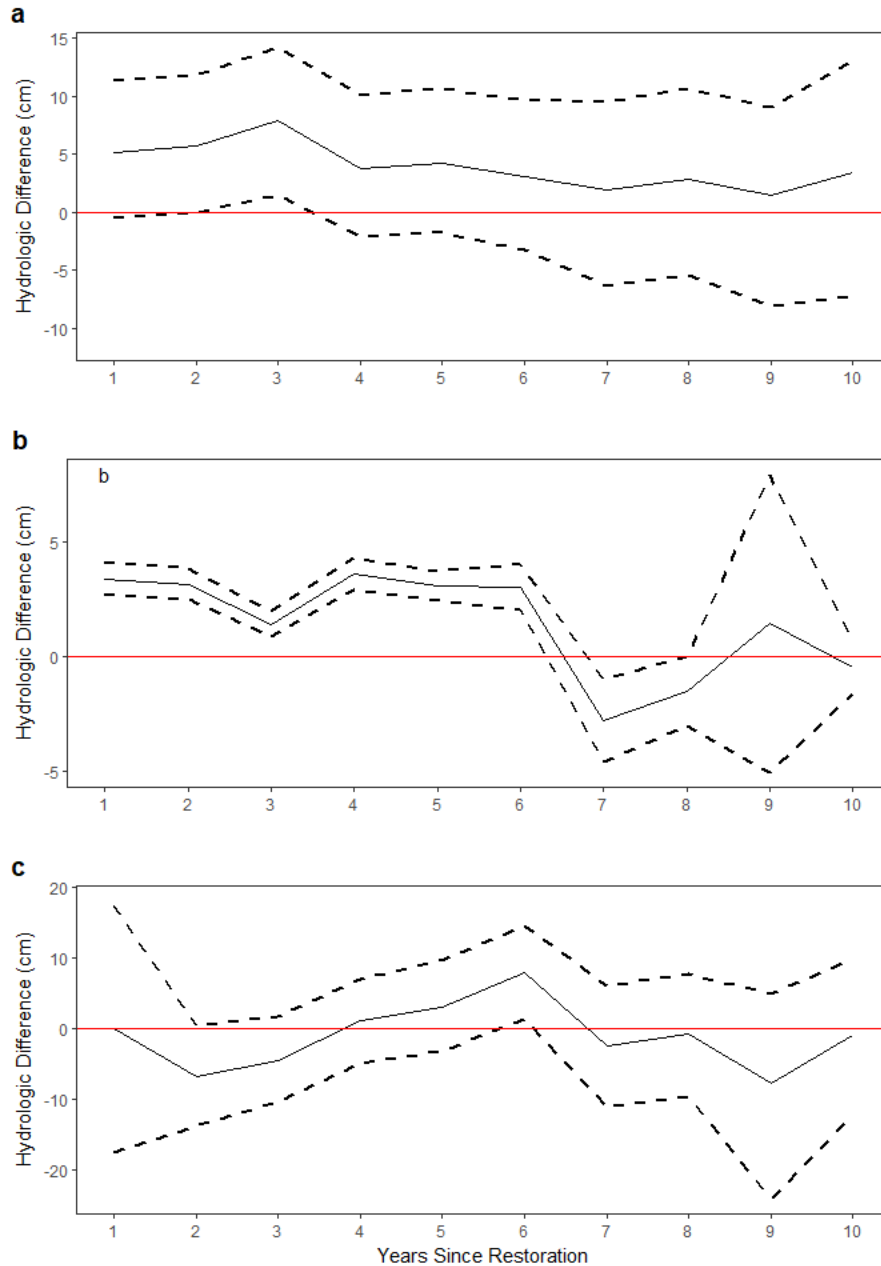


Figure 4.3. Estimated hydrologic difference between restored and reference wetlands for each year following restoration for: (a) fens and wet meadows, (b) vernal pools, and (c) forested wetlands. Average hydrologic difference between restored and reference wetlands (solid line) and 95% credible intervals of the estimate (dashed lines) indicate the restored wetland hydrologic difference from reference water tables through time following restoration. Water tables in restored fens and wet meadows (a) are significantly higher than reference sites for the first three years following restoration, and have no credible difference from reference sites after four years following restoration. Restored vernal pools (b) have greater inundation than reference pools for the first six years, but no credible difference between restored and reference pools after 8 years. Forested wetlands (c) are hydrologically similar to reference wetlands from the first year following restoration.

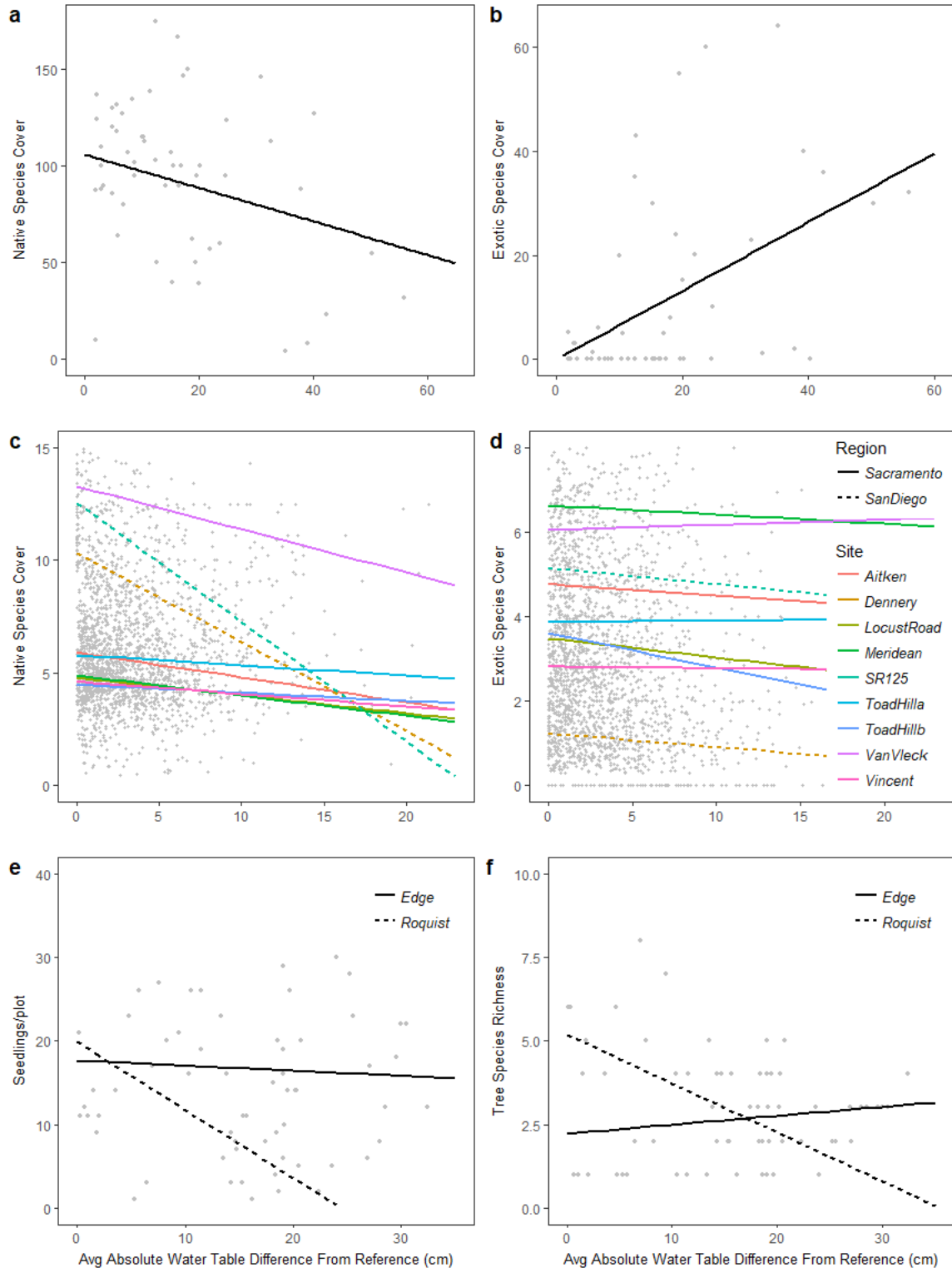


Figure 4.4. Average weekly absolute water table difference between restored and reference wetlands and associated vegetation metrics for fens and wet meadows in Colorado (a, b), vernal pools in California (c, d) from the San Diego region (dashed lines) and Sacramento (solid lines), and mid-Atlantic forested wetlands (e, f). Trendlines for each site are created from the median estimates of β_0 and β_1 from the Bayesian models. Restored fen and wet meadows had higher

native species cover (a) and lower exotic species cover (b) when water tables were similar to reference sites. As restored hydrologic conditions in fens and wet meadows became less similar to reference sites, native species cover decreased (a) and exotic species cover increased (b). Native species cover in three of the eight vernal pool projects was greatest when inundation depths in restored pools were similar to reference pools (c), and decreased as restored vernal pool hydrologic conditions became less similar to reference pools. Vernal pool exotic species cover (d) was independent of the hydrologic similarity between the restored and reference pools in all eight projects. Forest seedling counts (e) and tree species richness (f) was highest when water table levels were similar to reference sites and decreased as water tables differed from reference sites for one of the two forested sites. Seedling counts and tree species richness was not related to hydrologic similarity in the other forested site.

The preceding chapters addressed pressing questions and challenges to wetland restoration by further clarifying the relationship between vegetation and restored water levels. A reciprocal transplant experiment across a restored hydrologic gradient involving two plant species of interest in wetland restoration identified the difference between these species' fundamental and realized niches, highlighting the impact of competitive exclusion in wetland plant species distributions (Chapter 2). An analysis of long-term vegetation composition and hydrologic data in restored wetlands in the San Juan Mountains revealed the convergence in species composition between restored and reference sites when water levels were similar between them (Chapter 3). An evaluation of vegetation and hydrologic data from wetland mitigation projects across the US validated the potential of using reference sites to create hydrologic performance standards for wetland mitigation across wetland types (Chapter 4). These findings are important for future wetland restoration as well as for policy development regarding national wetland mitigation.

My results revealed novel patterns in the plasticity of ecophysiological processes used by plants to conserve water (Chapter 2). Ψ_{mid} and Ψ_{TLP} in both *Carex pellita* and *Typha latifolia* were impacted by transplanting into opposing hydrologic conditions. However, *C. pellita* altered its Ψ_{mid} to a greater degree than *T. latifolia*, with lower Ψ_{mid} when water levels were low and higher Ψ_{mid} when water levels were high. Along with the greater plasticity in Ψ_{mid} in *C. pellita*, this species also adjusted its Ψ_{TLP} through time in response to changing water levels and between the control and cross-boundary transplant. Ψ_{TLP} is often treated as a physiological constant within a species (Bartlett et al. 2012). Only recently has the static nature of this trait been

reconsidered (Bartlett et al. 2014). Wetland plant species can have different water conservation strategies (Touchette et al. 2007), and greater plasticity of Ψ_{TLP} in *C. pellita* may confer a wider hydrologic niche than for species with less plasticity.

Vegetation composition following restoration can be notoriously variable (Laughlin et al. 2017), although I found the vegetation composition in restored wetlands after 15 years of development to better match reference wetlands when the hydrologic conditions between them were similar (Chapter 3). Although the overall correlation between water levels and vegetation composition was low, sites with more similar water levels to reference sites had more similar vegetation composition. Projects that seek to establish a particular suite of species will likely have more success if they match the hydrologic conditions of a nearby reference site. However, caution is warranted in evaluating restoration solely by vegetation, as is the case in many restorations, because many factors can effect vegetation composition through time.

5.1 Sensitivity

My results also identified that the sensitivity of vegetation composition to growing season water levels differed among wetland types. Climate change resilience and sensitivity within plant communities has received increased attention in recent years, although this analysis has been constrained largely to naturally occurring grasslands (Cleland et al. 2013). Hydrologic controls over wetland vegetation have been repeatedly demonstrated in naturally occurring wetlands (Kirkman et al. 2000, Jung et al. 2009, Silvertown et al. 2015) and created wetlands (Cole and Brooks 2000, Kusler 2006, Boers et al. 2007). The sensitivity of wetland vegetation composition to restored water levels has not been evaluated until now. I found the vegetation composition in fens was least sensitive to the restored hydrologic gradient, and riparian wetlands were most sensitive. However, the range in water levels that sustain a particular wetland type is also likely

to be important (Figure 5.1). Fens were the least sensitive to the hydrologic gradient, although they did not have a wide range of water levels. The response of these systems to water levels beyond those evaluated here remains unknown. The level of sensitivity to a hydrologic gradient will also depend on the ecosystem trait being evaluated. Most fens in this study had a similar suite of species regardless of water level, making the sensitivity of their vegetation composition low. However, small changes in water tables can significantly impact other ecosystem traits, such as the carbon sequestration function of fens (Chimner and Cooper 2003). While vegetation sensitivity to different water levels may be low, the sensitivity of other ecosystem traits or processes may be high.

The sensitivity of a wetland to hydrologic alteration may impact its resilience to climate change. Wetlands with a higher resilience to climate change may be those with both a lower rate of change in species composition *and* a wider range of water levels (Figure 5.1). The sensitivity of wetland types to hydrologic alteration and their subsequent climate resilience has implications for conservation and restoration. Ecosystems are threatened as a result of both climate change and local land use changes (Sala and Karl 2013), although many of the environmental challenges ahead are political in nature. Suggestions from the scientific community must therefore provide realistic proposals, balancing the interests of different political constituents, including the environment (Adams 2006). Recognizing the limited resources devoted to conservation and restoration, wetland types that are predicted to be less resilient to climate change *and* more threatened by local land use changes should be prioritized for conservation, preservation, and restoration. However, a significant debate continues regarding this “triage” approach to conservation (Kareiva et al. 2012, Soulé 2013).

5.2 Creating Hydrologic Performance Standards for wetland mitigation

My results show the utility in using monitoring data from reference sites to create hydrologic performance standards to evaluate wetland mitigation (Chapter 4). In a regulatory context, the use of hydrologic performance standards *assumes* the relationship between adequate hydrology and wetland function, but this assumption has not been tested until now. I found restored fens, wet meadows, and vernal pools that had similar water levels as their reference sites had higher cover of native species. Restored forested wetlands with similar water levels as reference sites had higher species richness and more tree seedlings. Although the use of hydrologic performance standards remains uncommon in wetland mitigation, my results promote the use of reference sites to create hydrologic performance standards.

Hydrologic performance standards for wetland restoration can be created using regularly collected water level data from reference sites to identify the naturally occurring range in water table depths each week for the wetland type(s) being evaluated (Figure 5.2). Monitoring water levels in multiple reference sites provides a useful hydrologic characterization for the pre-restoration design and post-restoration evaluation phase (Figure 5.2a). To create a suitable hydrologic performance standard, water levels from reference sites are averaged within each week, and the weekly mean \pm 1 standard deviation in reference water levels are used to create an upper and lower range of acceptable restored water levels (Figure 5.2b). The performance standard can be used to create the restoration design and evaluate restored water levels (Figure 5.2c). Once the hydrologic performance standards are created from reference site data, the concurrently monitored water levels in the mitigation areas can be measured and graphically compared to the performance standard (Figure 5.2d). Water levels within the hydrologic performance standard can be considered successful. Areas with water levels outside of the performance standard should be further evaluated to identify potential issues influencing their

water levels. This method provides a transparent and intuitive approach to evaluate restored wetlands based on the concurrent measurement of water levels in reference wetlands.

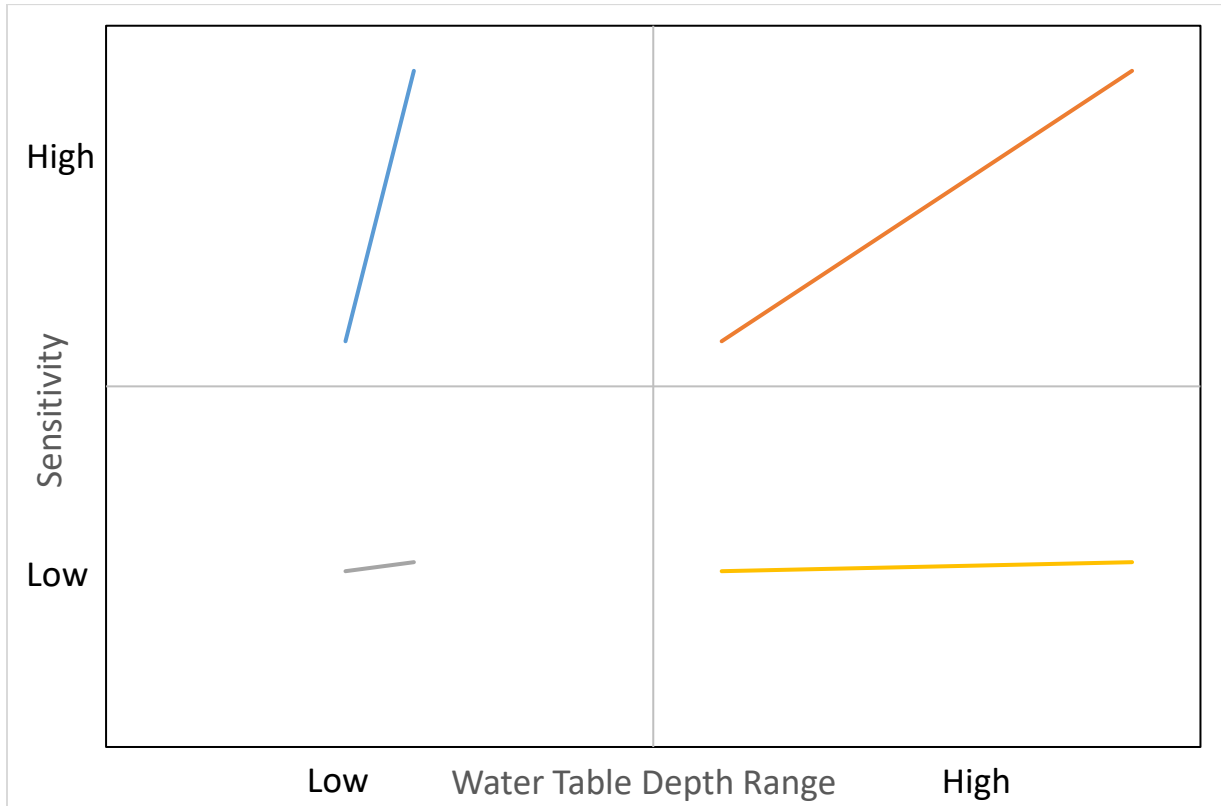


Figure 5.1. Relationship between the sensitivity of vegetation composition to hydrologic variation and the range of hydrologic conditions supporting the wetland type. Communities with low sensitivity and high range will have the greatest success in restoration and the highest resilience to climate change. Communities with high sensitivity and low hydrologic ranges may experience low restoration success and low resilience to climate change.

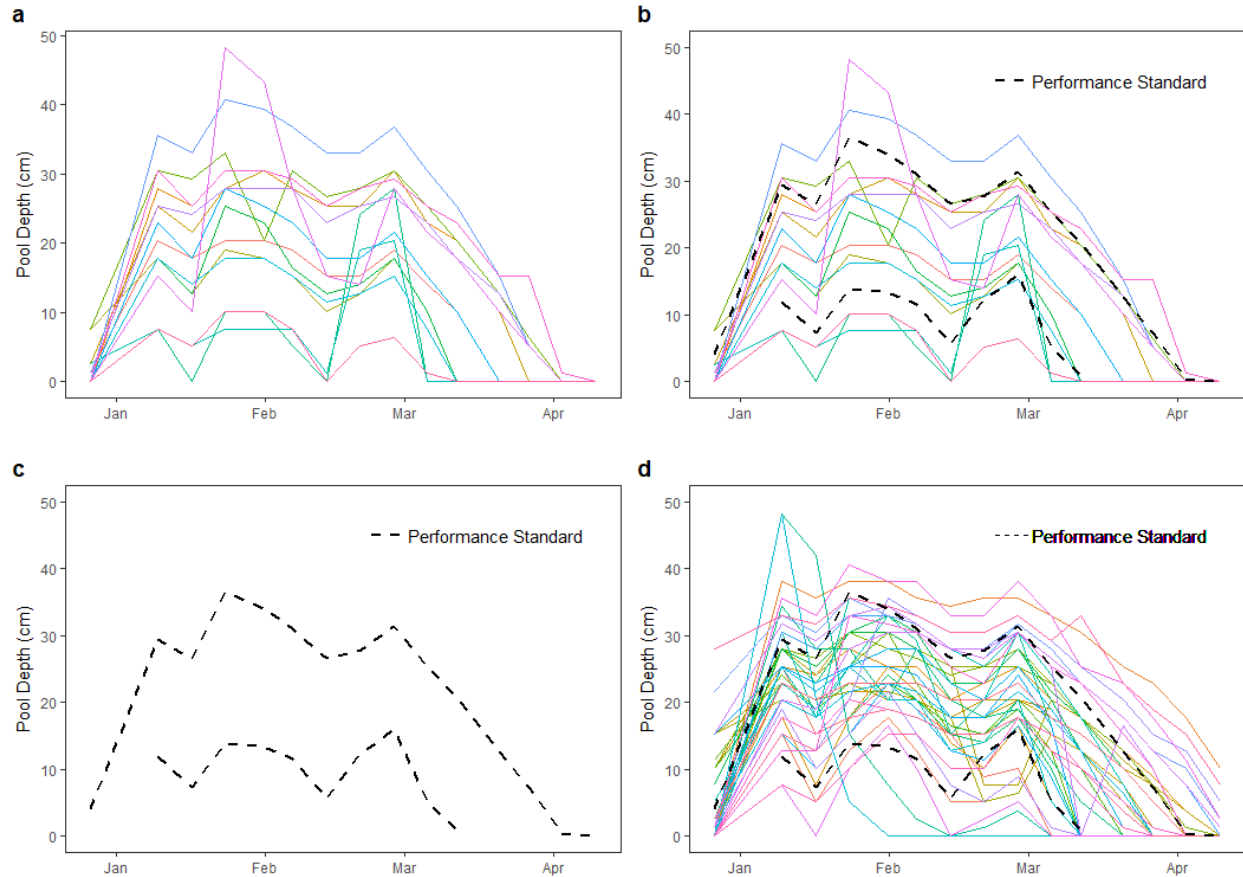


Figure 5.2. The creation of hydrologic performance standards for a vernal pools restoration project using multiple pools (colored lines). Weekly pool depth is plotted for reference sites (a) and hydrologic performance standards are created from the weekly average pool depth from all reference pools buffered above and below by one weekly standard deviation (b). The hydrologic performance standards identify the upper and lower acceptable thresholds for weekly pool depth (c) which is used to evaluate the weekly pool depth measured in the restored pools (d). If the chosen reference pools are representative of the range of naturally occurring pool sizes and depths, hydrologically restored vernal pools should have weekly pool depths within the upper and lower hydrologic performance standard bounds. Most restored pools in this example fall within the hydrologic performance standards. Two noticeably different pools fill more rapidly than reference pools and subsequently drain quicker with a shorter ponding duration than reference pools. The incorrect shape of these pool's hydrographs may indicate the need for adaptive management actions.

6 References

- Acreman, M. C., J. Fisher, C. J. Stratford, D. J. Mould, and J. O. Mountford. 2007. Hydrological science and wetland restoration: some case studies from Europe. *Hydrology and Earth System Sciences Discussions* 11:158–169.
- Adams, W. . 2006. *The Future of Sustainability*. Page (M. Keiner, Ed.). Springer Netherlands, Dordrecht.
- Ambrose, R. F. 2000. Wetland Mitigation in the United States: Assessing the Success of Mitigation Policies. *Wetlands(Australia)* 19(1):1–27.
- Ambrose, R. F., and S. F. Lee. 2007. An Evaluation of Compensatory Mitigation Projects Permitted Under Clean Water Act Section 401 by the California State Water Resources Control Board , 1991-2002 . An Evaluation of Compensatory Mitigation Projects Permitted Under Clean Water Act Section 401:1991–2002.
- Asamoah, S. A., and E. W. Bork. 2010. Drought tolerance thresholds in cattail (*Typha latifolia*): A test using controlled hydrologic treatments. *Wetlands* 30:99–110.
- Baastrup-Spohr, L., K. Sand-Jensen, S. V. Nicolajsen, and H. H. Bruun. 2015. From soaking wet to bone dry: predicting plant community composition along a steep hydrological gradient. *Journal of Vegetation Science* 26:619–630.
- Bartlett, M. K., C. Scoffoni, and L. Sack. 2012. The determinants of leaf turgor loss point and prediction of drought tolerance of species and biomes: A global meta-analysis. *Ecology Letters* 15:393–405.
- Bartlett, M. K., Y. Zhang, N. Kreidler, S. Sun, R. Ardy, K. Cao, and L. Sack. 2014. Global analysis of plasticity in turgor loss point, a key drought tolerance trait. *Ecology Letters* 17:1580–1590.

- Battaglia, L. L., P. R. Minchin, and D. W. Pritchett. 2002. Sixteen years of old-field succession and reestablishment of a bottomland hardwood forest in the Lower Mississippi Alluvial Valley. *Wetlands* 22:1–17.
- Beechie, T. J., D. a. Sear, J. D. Olden, G. R. Pess, J. M. Buffington, H. Moir, P. Roni, and M. M. Pollock. 2010. Process-based Principles for Restoring River Ecosystems. *BioScience* 60:209–222.
- Belyea, L. R., and N. Malmer. 2004. Carbon sequestration in peatland: patterns and mechanisms of response to climate change. *Global Change Biology* 10:1043–1052.
- Bernhardt, E. S., E. B. Sudduth, M. A. Palmer, J. D. Allan, J. L. Meyer, G. Alexander, J. Follstad-Shah, B. Hassett, R. Jenkinson, R. Lave, J. Rumps, and L. Pagano. 2007. Restoring Rivers One Reach at a Time: Results from a Survey of U.S. River Restoration Practitioners. *Restoration Ecology* 15:482–493.
- Bertness, M. D., and A. M. Ellison. 1987. Determinants of Pattern in a New England Salt Marsh Plant Community. *Ecological Monographs* 57:129–147.
- Black, C., and P. Zedler. 1998. An overview of 15 years of Vernal Pool Restoration and Construction Activities in San Diego County, California. Pages 195–205 in C. Witham, E. Bauder, D. Belk, W. Ferren, and R. Ornduff, editors. *Ecology, Conservation, and Management of Vernal Pool Ecosystems - Proceedings from the 1996 Conference*. California Native Plant Society. Sacramento, CA.
- Blom, C. W. P. M., and L. A. C. J. Voesenek. 1996. Flooding: The survival strategies of plants. *Trends in Ecology and Evolution* 11:290–295.
- Boers, A. M., R. L. D. Veltman, and J. B. Zedler. 2007. *Typha x glauca* dominance and extended hydroperiod constrain restoration of wetland diversity. *Ecological Engineering* 29:232–244.
- Van den Bosch, K., and J. W. Matthews. 2017. An Assessment of Long-Term Compliance with

- Performance Standards in Compensatory Mitigation Wetlands. *Environmental Management* 59:546–556.
- Bridgham, S. D., J. P. Megonigal, J. K. Keller, N. B. Bliss, and C. Trettin. 2006. The carbon balance of North American wetlands. *Wetlands* 26:889–916.
- Brinson, M. M., and A. I. Malvárez. 2002. Temperate freshwater wetlands: types, status, and threats. *Environmental Conservation* 29:115–133.
- Brudvig, L. A., R. S. Barak, J. T. Bauer, T. T. Caughlin, D. C. Laughlin, L. Larios, J. W. Matthews, K. L. Stuble, N. E. Turley, and C. R. Zirbel. 2017. Interpreting variation to advance predictive restoration science. *Journal of Applied Ecology* 54:1018–1027.
- Bruland, G. L., and C. J. Richardson. 2005. Hydrologic, edaphic, and vegetative responses to microtopographic reestablishment in a restored wetland. *Restoration Ecology* 13:515–523.
- Caldwell, P. V., M. J. Vepraskas, J. D. Gregory, R. W. Skaggs, and R. L. Huffman. 2011. Linking Plant Ecology and Long-Term Hydrology to Improve Wetland Restoration Success. *Transactions of the ASABE* 54:2129–2137.
- Chapin, F. S., B. H. B. Walker, R. J. R. Hobbs, D. U. D. Hooper, J. H. J. Lawton, O. O. E. Sala, D. Tilman, F. S. Chapin III, B. H. B. Walker, R. J. R. Hobbs, D. U. D. Hooper, J. H. J. Lawton, O. O. E. Sala, and D. Tilman. 1997. Biotic control over the functioning of ecosystems. *Science* 277:500.
- Chapin, F. S., E. S. Zavaleta, V. T. Eviner, R. L. Naylor, P. M. Vitousek, H. L. Reynolds, D. U. Hooper, S. Lavorel, O. E. Sala, S. E. Hobbie, M. C. Mack, and S. Díaz. 2000. Consequences of changing biodiversity. *Nature* 405:234–42.
- Chase, J. M. 2007. Drought mediates the importance of stochastic community assembly. *Proceedings of the National Academy of Sciences* 104:17430–17434.
- Chimner, R. A., and D. J. Cooper. 2003. Influence of water table levels on CO₂ emissions in a

- Colorado subalpine fen: an in situ microcosm study. *Soil Biology and Biochemistry* 35:345–351.
- Cleland, E. E., S. L. Collins, T. L. Dickson, E. C. Farrer, K. L. Gross, L. A. Gherardi, L. M. Hallett, R. J. Hobbs, J. S. Hsu, L. Turnbull, and K. N. Suding. 2013. Sensitivity of grassland plant community composition to spatial vs. temporal variation in precipitation. *Ecology* 94:1687–1696.
- Cole, C. A., and R. P. Brooks. 2000. A comparison of the hydrologic characteristics of natural and created mainstem floodplain wetlands in Pennsylvania. *Ecological Engineering* 14:221–231.
- Cook, B. J., and F. R. Hauer. 2007. Effects of hydrologic connectivity on water chemistry, soils, and vegetation structure and function in an intermontane depressional wetland landscape. *Wetlands* 27:719–738.
- Cooke, S. J., A. M. Rous, L. A. Donaldson, J. J. Taylor, T. Rytwinski, K. A. Prior, K. E. Smokorowski, and J. R. Bennett. 2018. Evidence-based restoration in the Anthropocene—from acting with purpose to acting for impact. *Restoration Ecology* 26:201–205.
- Cooper, D. J., K. M. Kaczynski, J. Sueltenfuss, S. Gaucherand, and C. Hazen. 2017. Mountain wetland restoration: The role of hydrologic regime and plant introductions after 15 years in the Colorado Rocky Mountains, U.S.A. *Ecological Engineering* 101:46–59.
- Dee, S. M., and C. Ahn. 2012. Soil properties predict plant community development of mitigation wetlands created in the Virginia Piedmont, USA. *Environmental Management* 49:1022–1036.
- Duru, M., R. Al Haj Khaled, C. Ducourtieux, J. P. Theau, F. L. F. de Quadros, and P. Cruz. 2009. Do plant functional types based on leaf dry matter content allow characterizing native grass species and grasslands for herbage growth pattern? *Plant Ecology* 201:421–433.

- Dwire, K. a., J. B. Kauffman, and J. E. Baham. 2006. Plant species distribution in relation to water-table depth and soil redox potential in montane riparian meadows. *Wetlands* 26:131–146.
- Eggers, S. 2015. Draft Memorandum: Target hydrology for compensatory mitigation sites. US Army Corps of Engineers, St. Paul District.
- Egler, F. E. 1954. Vegetation science concepts I. Initial floristic composition, a factor in old-field vegetation development with 2 figs. *Vegetatio Acta Geobotanica* 4:412–417.
- Eliceiri, K., C. A. Schneider, W. S. Rasband, and K. W. Eliceiri. 2012. NIH Image to ImageJ : 25 years of image analysis HISTORICAL commentary NIH Image to ImageJ : 25 years of image analysis. *Nature Methods* 9:671–675.
- Environmental Laboratory. 1987. Corps of Engineers Wetlands Delineation Manual. Technical Report Y-87-1. Vicksburg, MS.
- Environmental Law Institute. 2004. Measuring mitigation: a review of the science of compensatory mitigation performance standards.
- Farrer, E. C. E. E. C., and D. E. Goldberg. 2009. Litter drives ecosystem and plant community changes in cattail invasion. *Ecological Applications* 19:398–412.
- Fennessy, S. M., J. K. Cronk, and W. J. Mitsch. 1994. Macrophyte productivity and community development in created freshwater wetlands under experimental hydrological conditions. *Ecological Engineering* 3:469–484.
- Fennessy, S., J. Mack, A. Rokosch, M. Knapp, and M. Micacchion. 2004. Integrated Wetland Assessment Program. Part 5 : Biogeochemical and Hydrological Investigations of Natural and Mitigation Wetlands. Ohio EPA Technical Report WET/2004-5. Ohio Environmental Protection Agency, Wetland Ecology Group, Division of Surface Water, Columbus Ohio.
- Fennessy, S., A. Rokosch, and J. J. Mack. 2007. Developing Performance standards for the

- Assessment of Wetland Mitigation Projects. National Wetlands Newsletter 29.
- Findlay, C. S., and J. Houlihan. 1997. Anthropogenic Correlates of Species Richness in Southeastern Ontario Wetlands. *Correlativos Antropogenicos de la Riqueza de Especies en Humedales del Sureste de Ontario*. *Conservation Biology* 11:1000–1009.
- Fukami, T., T. Martijn Bezemer, S. R. Mortimer, and W. H. Putten. 2005. Species divergence and trait convergence in experimental plant community assembly. *Ecology Letters* 8:1283–1290.
- García-Baquero, G., J. Silvertown, D. J. Gowing, and C. J. Valle. 2016. Dissecting the hydrological niche: Soil moisture, space and lifespan. *Journal of Vegetation Science* 27:219–226.
- Gardner, R. C., J. B. Zedler, A. Redmond, R. E. Turner, C. a Johnston, V. Alvarez, C. a Simenstad, K. L. Prestegard, and W. J. Mitsch. 2009. Compensating for wetland losses under the Clean Water Act (Redux): Evaluating the Federal Compensatory Mitigation Regulation. *Wetlands Newsletter* 31.
- Gerhardt, F., and S. K. Collinge. 2003. Exotic plant invasions of vernal pools in the Central Valley of California, USA. *Journal of Biogeography* 30:1043–1052.
- Gowing, D. J. 2005. Response of Grassland plant communities to altered hydrological management. *Defra 1321* 5:1–21.
- Grace, J. B., and R. G. Wetzel. 1981. Habitat partitioning and competitive displacement in cattails: Experimental field studies. *The American Naturalist* 118:463–474.
- Grinnell, J. 1917. The Niche-Relationships of the California Thrasher. *The Auk* 34:427–433.
- Grissino-Mayer, H. D., W. H. Romme, M. Lisa Floyd, and D. D. Hanna. 2004. Climatic and human influences on fire regimes of the southern San Juan Mountains, Colorado, USA. *Ecology* 85:1708–1724.

- Gutrich, J. J., K. J. Taylor, and M. S. Fennessy. 2009. Restoration of vegetation communities of created depressional marshes in Ohio and Colorado (USA): The importance of initial effort for mitigation success. *Ecological Engineering* 35:351–368.
- Hirzel, A. H., J. Hausser, D. Chessel, and N. Perrin. 2002. Ecological-Niche Factor Analysis: How To Compute Habitat-Suitability Maps Without Absence Data? *Ecology* 83:2027–2036.
- Hobbs, N. T., and M. B. Hooten. 2015. *Bayesian Models: A Statistical Primer for Ecologists*. Princeton University Press.
- Hooper, D. U., F. S. Chapin, J. J. Ewel, A. Hector, P. Inchausti, S. Lavorel, J. H. Lawton, D. M. Lodge, M. Loreau, S. Naeem, B. Schmid, H. Setälä, A. J. Symstad, J. Vandermeer, and D. A. Wardle. 2005. Effects of biodiversity on ecosystem functioning: A consensus of current knowledge. *Ecological Monographs* 75:3–35.
- Hossler, K., V. Bouchard, M. S. Fennessy, S. D. Frey, E. Anemaet, and E. Herbert. 2011. No-net-loss not met for nutrient function in freshwater marshes: recommendations for wetland mitigation policies. *Ecosphere* 2:art82.
- Hubbell, S. 2005. Neutral theory in community ecology and the hypothesis of functional equivalence. *Functional Ecology* 19:166–172.
- Hudson, H., E. Wright, R. B. Atkinson, and J. E. Perry. 2014. *Assessment of Woody Vegetation for Replacement of Ecological Functions in Created Forested Wetlands of the Piedmont Province of Virginia*. Piedmont Wetlands Research Program.
- Hutchinson, G. 1957. Concluding remarks. Cold Spring Harbor Symposium. *Quantitative Biology* 22:415–427.
- Johnson, W. C. 2000. Tree recruitment and survival in rivers: Influence of hydrological process. *Hydrological Processes* 14:3051–3074.

- Johnson, Y. Ben, T. H. Shear, and A. L. James. 2012. Identifying ecohydrological patterns in natural forested wetlands useful to restoration design. *Ecohydrology* 5:368–379.
- Johnson, Y. Ben, T. H. Shear, and A. L. James. 2014. Novel ways to assess forested wetland restoration in North Carolina using ecohydrological patterns from reference sites. *Ecohydrology* 7:692–702.
- Jung, V., L. Hoffmann, and S. Muller. 2009. Ecophysiological responses of nine floodplain meadow species to changing hydrological conditions. *Plant Ecology* 201:589–598.
- Kareiva, P. M., M. A. Marvier, and R. Lalasz. 2012. Conservation in the Anthropocene: Beyond Solitude and Fragility. <http://thebreakthrough.org/index.php/journal/past-issues/issue-2/%20conservation-in-the-anthropocene/>.
- Keddy, P. 1999. Wetland restoration: The potential for assembly rules in the service of conservation. *Wetlands* 19:716–732.
- Keddy, P. A. 1992. Assembly and response rules: two goals for predictive community ecology. *Journal of Vegetation Science* 3:157–164.
- Kercher, S. M., and J. B. Zedler. 2004. Flood tolerance in wetland angiosperms: A comparison of invasive and noninvasive species. *Aquatic Botany* 80:89–102.
- Kirkman, L., P. Goebel, L. West, M. Drew, and B. Palik. 2000. Depressional wetland vegetation types: a question of plant community development. *Wetlands* 20:373–385.
- Konar, M., M. Jason Todd, R. Muneeppeerakul, A. Rinaldo, and I. Rodriguez-Iturbe. 2013. Hydrology as a driver of biodiversity: Controls on carrying capacity, niche formation, and dispersal. *Advances in Water Resources* 51:317–325.
- Kotowski, W., W. Thorig, R. Van Diggelen, and M. J. Wassen. 2006. Competition as a factor structuring species zonation in riparian fens - a transplantation experiment. *Applied Vegetation Science* 9:231–240.

- Kusler, J. 2006. Developing Performance Standards for the Mitigation and Restoration of Northern Forested Wetlands. Association of State Wetland Managers, Inc.
- Laughlin, D. C., R. T. Strahan, M. M. Moore, P. Z. Fulé, D. W. Huffman, and W. W. Covington. 2017. The hierarchy of predictability in ecological restoration: are vegetation structure and functional diversity more predictable than community composition? *Journal of Applied Ecology* 54:1058–1069.
- Levin, S. A. 1992. The Problem of Pattern and Scale in Ecology: The Robert H. MacArthur Award Lecture. *Ecology* 73:1943–1967.
- Lhotsky, B., B. Kovács, G. Ónodi, A. Csecserits, T. Rédei, A. Lengyel, M. Kertész, and Z. Botta-Dukát. 2016. Changes in assembly rules along a stress gradient from open dry grasslands to wetlands. *Journal of Ecology* 104:507–517.
- Lovell, J. T., and E. Menges. 2013. Dominant species responses to drought in seasonal wetlands: evidence from reciprocal transplants across a moisture gradient 1. *The Journal of the Torrey Botanical Society* 140:157–169.
- Lu, J., G. Sun, S. G. McNulty, and N. B. Comerford. 2009. Sensitivity of Pine Flatwoods Hydrology To Climate Change and Forest Management in Florida, Usa. *Wetlands* 29:826–836.
- Magee, T. K., and M. E. Kentula. 2005. Response of wetland plant species to hydrologic conditions. *Wetlands Ecology and Management* 13:163–181.
- Martin, L. M., K. A. Moloney, and B. J. Wilsey. 2005. An assessment of grassland restoration success using species diversity components. *Journal of Applied Ecology* 42:327–336.
- Matthews, J. W., A. L. Peralta, D. N. Flanagan, P. M. Baldwin, A. Soni, A. D. Kent, and A. G. Endress. 2009. Relative influence of landscape vs. local factors on plant community assembly in restored wetlands. *Ecological Applications* 19:2108–2123.

- McCune, B., and J. Grace. 2002. *Analysis of Ecological Communities*. MjM Software Design.
- Meinzer, F. C., D. R. Woodruff, D. E. Marias, K. A. McCulloh, and S. Sevanto. 2014. Dynamics of leaf water relations components in co-occurring iso- and anisohydric conifer species. *Plant Cell and Environment* 37:2577–2586.
- Mitsch, W. J., and R. F. Wilson. 1996. Improving the Success of Wetland Creation and Restoration with Know-How, Time, and Self-Design. *Ecological Applications* 6:77–83.
- Moorhead, K. K. 2013. A Realistic Role for Reference in Wetland Restoration. *Ecological Restoration* 31:347–352.
- Moreno-Mateos, D., P. Meli, M. I. Vara-Rodríguez, and J. Aronson. 2015. Ecosystem response to interventions: lessons from restored and created wetland ecosystems. *Journal of Applied Ecology* 52:1528–1537.
- Moreno-Mateos, D., M. E. Power, F. A. Comín, and R. Yockteng. 2012. Structural and Functional Loss in Restored Wetland Ecosystems. *PLoS Biology* 10:e1001247.
- Mouquet, N., Y. Lagadeuc, V. Devictor, L. Doyen, A. Duputié, D. Eveillard, D. Faure, E. Garnier, O. Gimenez, P. Huneman, F. Jabot, P. Jarne, D. Joly, R. Julliard, S. Kéfi, G. J. Kergoat, S. Lavorel, L. Le Gall, L. Meslin, S. Morand, X. Morin, H. Morlon, G. Pinay, R. Pradel, F. M. Schurr, W. Thuiller, and M. Loreau. 2015. REVIEW: Predictive ecology in a changing world. *Journal of Applied Ecology* 52:1293–1310.
- National Research Council. 2001. *Compensating for wetland loss under the Clean Water Act*. National Academy Press, Washington, DC.
- Oksanen, J., F. G. Blanchet, M. Friendly, R. Kindt, P. Legendre, D. McGlenn, P. R. Minchin, R. B. O'Hara, G. L. Simpson, P. Solymos, M. H. H. Stevens, E. Szoecs, and H. Wagner. 2017. *vegan: Community Ecology Package*. R package version 2.4-3.
- Olden, J. D., and N. L. Poff. 2003. Redundancy and the choice of hydrologic indices for

- characterizing streamflow regimes. *River Research and Applications* 19:101–121.
- Petru, B. J., G. M. Chescheir, and C. Ahn. 2014. Assessment of water budgets and the hydrologic performance of a created mitigation wetland-A modeling approach. *Ecological Engineering* 71:667–676.
- Pezeshki, S. R. 2001. Wetland plant responses to soil flooding. *Environmental and Experimental Botany* 46:299–312.
- Poff, N. L., and J. V. Ward. 1989. Implications of Streamflow Variability and Predictability for Lotic Community Structure: A Regional Analysis of Streamflow Patterns. *Canadian Journal of Fisheries and Aquatic Sciences* 46:1805–1818.
- Price, J., A. Heathwaite, and A. Baird. 2003. Hydrological processes in abandoned and restored peatlands: An overview of management approaches. *Wetlands Ecology and Management* 11:65–83.
- Purinton, C. 1897. Description of the Telluride quadrangle.
- R Core Team. 2016. R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria.
- Richter, B. D., J. V Baumgartner, J. Powell, and D. P. Braun. 1996. A method for assessing hydrologic alteration within ecosystems. *Conservation Biology* 10:1163–1174.
- Sala, O. E., F. S. Chapin, J. J. Armesto, E. L. Berlow, J. Bloomfield, R. Dirzo, E. Huber-Sanwald, L. F. Huenneke, R. B. Jackson, A. Kinzig, R. Leemans, D. M. Lodge, H. A. Mooney, M. Oesterheld, N. L. Poff, M. T. Sykes, B. H. Walker, M. Walker, and D. H. Wall. 2000. Global biodiversity scenarios for the year 2100. *Science* 287:1770–4.
- Sala, O. E., and J. W. Karl. 2013. Land degradation and climate change: A sin of omission? *Frontiers in Ecology and the Environment* 11:283.
- Sanderson, J. S., N. B. Kotliar, and D. A. Steingraeber. 2008. Opposing environmental gradients

- govern vegetation zonation in an intermountain playa. *Wetlands* 28:1060–1070.
- Schimelpfenig, D. W., D. J. Cooper, and R. A. Chimner. 2014. Effectiveness of Ditch Blockage for Restoring Hydrologic and Soil Processes in Mountain Peatlands. *Restoration Ecology* 22:257–265.
- Schlatter, K. J., A. M. Faist, and S. K. Collinge. 2016. Using performance standards to guide vernal pool restoration and adaptive management. *Restoration Ecology* 24:145–152.
- van Seters, T. E., and J. S. Price. 2002. Towards a conceptual model of hydrological change on an abandoned cutover bog, Quebec. *Hydrological Processes* 16:1965–1981.
- Sieben, E. J. J., C. D. Morris, D. C. Kotze, and A. M. Muasya. 2010. Changes in plant form and function across altitudinal and wetness gradients in the wetlands of the Maloti-Drakensberg, South Africa. *Plant Ecology* 207:107–119.
- Silvertown, J., Y. Araya, and D. Gowing. 2015. Hydrological niches in terrestrial plant communities: a review. *Journal of Ecology* 103:93–108.
- Silvertown, J., M. E. Dodd, D. J. G. Gowing, and J. O. Mountford. 1999. No Title. *Nature* 400:61–63.
- Snow, A. A., and S. W. Vince. 1984. Plant Zonation in an Alaskan Salt Marsh: II. An Experimental Study of the Role of Edaphic Conditions. *The Journal of Ecology* 72:669.
- Soulé, M. 2013. The “new conservation.” *Conservation Biology* 27:895–897.
- Steyer, G. D., C. E. Sasser, J. M. Visser, E. M. Swenson, J. A. Nyman, and R. C. Raynie. 2003. No Title. *Environmental Monitoring and Assessment* 81:107–117.
- Suding, K. N. 2011. Toward an Era of Restoration in Ecology: Successes, Failures, and Opportunities Ahead. *Annual Review of Ecology, Evolution, and Systematics* 42:465–487.
- Suganuma, M. S., and G. Durigan. 2015. Indicators of restoration success in riparian tropical forests using multiple reference ecosystems. *Restoration Ecology* 23:238–251.

- Sun, G., S. S. G. McNulty, J. P. J. Shepard, D. M. Amatya, H. Riekerk, N. B. Comerford, W. Skaggs, and L. Swift. 2001. Effects of timber management on the hydrology of wetland forests in the southern United States. *Forest Ecology and Management* 143:227–236.
- Tilman, D. 1999. The ecological consequences of changes in biodiversity: A search for general principles. *Ecology* 80:1455–1474.
- Toogood, S. E., C. B. Joyce, and S. Waite. 2008. Response of floodplain grassland plant communities to altered water regimes. *Plant Ecology* 197:285–298.
- Touchette, B. W., L. R. Iannacone, G. E. Turner, and A. R. Frank. 2007. Drought tolerance versus drought avoidance: A comparison of plant-water relations in herbaceous wetland plants subjected to water withdrawal and repletion. *Wetlands* 27:656–667.
- Tyree, M. T., and H. T. Hammel. 1972. The Measurement of the Turgor Pressure and the Water Relations of Plants by the Pressure-bomb Technique. *Journal of Experimental Botany* 23:267–282.
- USACE and USEPA. 2008. Compensatory mitigation for losses of Aquatic Resources; Final rule. 73 Federal Registry 19594, 19595:1–113.
- Wetzel, P. R., W. M. Kitchens, J. M. Brush, and M. L. Dusek. 2004. Use of a reciprocal transplant study to measure the rate of plant community change in a tidal marsh along a salinity gradient. *Wetlands* 24:879–890.
- White, P. S., and J. L. Walker. 1997. Approximating Nature's Variation: Selecting and Using Reference Information in Restoration Ecology. *Restoration Ecology* 5:338–349.
- Young, T. P., D. A. Petersen, and J. J. Clary. 2005. The ecology of restoration: historical links, emerging issues and unexplored realms. *Ecology Letters* 8:662–673.
- Zedler, J. B. 1996. Ecological Issues in Wetland Mitigation: An Introduction to the Forum. *Ecological Applications* 6:33–37.

Zedler, J. B., and J. C. Callaway. 1999. Tracking Wetland Restoration: Do Mitigation Sites Follow Desired Trajectories? *Restoration Ecology* 7:69–73.