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The Influence of Climate and Seed Dispersal on Restoration in the San
Francisco Bay

By

Dylan Edward Chapple

A dissertation submitted in partial satisfaction of the requirements for the degree of Doctor of
Philosophy in Environmental Science, Policy, and Management in the Graduate Division of
the University of California, Berkeley

Committee in charge:

Professor Adina M. Merenlender, Chair

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Summer 2017

The influence of climate and seed dispersal on restoration in the San Francisco Bay

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Abstract

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Doctor of Philosophy in Environmental Science, Policy and Management

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Professor Adina Merenlender, Chair

Ecosystem restoration is increasingly used as a tool to offset the contemporary loss of habitat or help address past ecosystem destruction. However, given the complex, interconnected nature of ecosystem processes, restoration outcomes are notoriously variable. In certain ecosystems, minimal intervention may be able to produce desired restoration outcomes, but in others even high levels of intervention may not achieve restoration goals. Significant uncertainties remain about restoration trajectories over time and space. In order to effectively deliver the benefits these projects purport to offer, a detailed scientific understanding of restoration trajectories is necessary to inform the practice of ecological restoration moving. To better understand the factors influencing restoration trajectories in California's San Francisco Bay (SF Bay), I compare change in vegetation over time at an older restoration and reference site using field data, explore rates of change at a recently established wetland restoration site in the context of a historic drought using remote sensing of satellite imagery, and compare seed dispersal across three restoration and two reference sites. Addressing these questions will aid in the management of these projects and design of future project which will help improve conservation outcomes and address impacts associated with sea level rise and increased climate variability.

While ecosystem development can take decades if not centuries, most restoration projects are minimally monitored, and a five-year window for assessment is often the best-case funding scenario. This means that detailed temporal studies of restoration projects are rare, which is particularly problematic in variable areas where climate cycles proceed at decadal scales. To

address this gap, I worked with a vegetation field data set collected most years between 1990 and 2005 at an established restoration site initiated in 1975 (Muzzi Marsh) and a historical reference wetland (China Camp) in Marin County, CA. To determine the factors influencing reference and restoration trajectories, I examined changes in plant community identity in relation to annual salinity levels in the SF Bay, annual rainfall, and tidal channel structure. Over the entire study period, both sites experienced significant directional change away from the 1990 community. Community change was accelerated following low salinity conditions that resulted from strong El Niño events in 1994–1995 and 1997–1998. Overall rates of change were greater at the restoration site and driven by a combination of dominant and sub-dominant species, while change at the reference site was driven by sub-dominant species. Sub-dominant species first appeared at the restoration site in 1996 and incrementally increased during each subsequent year, whereas sub-dominant species cover at the reference site peaked in 1999 and subsequently declined.

In addition to the later-stage restoration dynamics highlighted above, climate variability may also influence the early stages of restoration site development. At a developing restoration site in the SF Bay, I use object-based image analysis (OBIA) and change analysis of high-resolution IKONOS and WorldView-2 satellite imagery to explore whether mean annual rates of change from mudflat to vegetation are lower during drought years with higher salinity (2011–2015) compared to years with lower salinity (2009–2011). I found that vegetation increased at a mean rate of 1979 m²/year during California's historic drought, 10.4 times slower than the rate of 20580 m²/year between 2009 and 2011 when the state was not in drought. Vegetation was significantly concentrated in areas in closer to channel edges, where salinity stress is ameliorated, and the magnitude of the channel effect increased in the 2015 image.

Seed dispersal is another critical but understudied mechanism driving restoration site development. Where and when seeds arrive at a restoration site can have major implications for how a restoration project proceeds. In my final chapter, I explore seed dispersal over a chronosequence of three restoration sites and two reference sites at Eden Landing Ecological Reserve (Hayward, CA), part of the South Bay Salt Pond Restoration Project. I find that seeds of wetland species in the restoration sites were significantly aggregated in areas with vegetation cover above 30%, and that many study plots were completely devoid of wetland seeds. Vegetation cover was significantly related to channel proximity and relative elevation at the

sites. Reference sites contained significantly more seeds than restoration sites, but density was low overall at the reference sites. The oldest restoration site had statistically equivalent seed density compared to one of the reference sites. Across all sites, the pioneer dominant species *Salicornia pacifica* was the most common seed species, and sub-dominant species were only found in a single plot in the restoration sites and in overall low densities in the reference sites. These results highlight the fact that seeds or seedlings may need to be added to developing restoration sites, and that manipulating elevation and channel structure may be important for accelerating the rate of vegetation development.

Table of Contents

| | |
|--------------------------|-----------|
| Table of contents | i |
| Acknowledgements | ii |
| Introduction | 1 |
| References | 8 |
| Chapter One | 13 |
| Abstract | 13 |
| Introduction | 14 |
| Methods | 17 |
| Results | 23 |
| Discussion | 27 |
| References | 30 |
| Appendix | 35 |
| Chapter Two | 37 |
| Abstract | 37 |
| Introduction | 38 |
| Methods | 42 |
| Results | 47 |
| Discussion | 51 |
| References | 55 |
| Chapter Three | 62 |
| Abstract | 62 |
| Introduction | 63 |
| Methods | 66 |
| Results | 69 |
| Discussion | 73 |
| References | 77 |
| Tables | 82 |
| Conclusion | 84 |
| References | 88 |

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Dissertation Introduction

As the footprint of human activities expands worldwide, ecosystem restoration is increasingly pursued as a means of enhancing natural areas to improve their value as habitat and their ability to provision ecosystem services. Restoration seeks to return ecological function and form to degraded ecosystems. The field is generally divided into two components: the practice of restoration on the ground (ecological restoration) and the study of the ecological interactions that determine restoration trajectories/outcomes (restoration ecology). As both of these fields develop, it is increasingly clear that ecosystem responses to restoration vary widely based on a number of factors including the degree of ecosystem alteration, abiotic conditions at a site, invasive exotic species and more. While high levels of variability in restoration outcomes are not surprising given the complexity of natural systems, they make understanding restoration trajectories challenging, which has major implications for the science and the practice of restoration. In order to better understand how restoration unfolds over time, detailed, often system-specific studies are needed, but extended monitoring and science-based inquiry are rarely part of restoration project funding. This information is critical for returning ecosystems to functional states in the most cost-effective manner. For restoration to effectively deliver on its promise of offsetting ecosystem loss in a changing world, science and practice must continue intertwining to produce the information needed to move the field forward.

Restoration in Practice

The process of ecological restoration takes a wide variety of forms throughout the world depending on the needs of the ecosystem, the funding structure of the work, and the follow-up integrated into the process. Depending on the extent of alteration from the original state, restoration may require relatively little work (Holl and Aide, 2011) or extensive, perpetual efforts to create and maintain the desired ecosystem state (Brown et al., 2013; Norgaard et al., 2009). Early restoration concepts were largely based around the theory of ecological succession, where ecosystems recover from disturbance along a predictable sequence of different habitat types before reaching a final state, or climax community (Connell and Slayter 1977). While this may be the case in some ecosystems, restoration projects are highly likely to proceed along non-linear pathways (Suding et al., 2004a; Zedler et al., 2012). During the process of recovery, the

context of a given project may stall ecosystems in intermediate levels of development until they reach a critical threshold point that moves them towards the desired state (Peters et al., 2004; Scheffer et al., 2009). These critical transitions can come in the form of management interventions, stochastic events such as floods or fires, species interactions or environmental conditions. To understand how restoration proceeds, it is essential to understand how spatial and environmental conditions interact with management efforts to structure restoration outcomes.

Interpretations of restoration trajectories are often based on how different parameters compare between *restoration sites* and *reference sites* (Moreno-Mateos et al., 2012; Moss, 2015). Reference sites are more intact, less perturbed ecosystems with a set of physical and biotic conditions that restoration projects aim to emulate. Due to a variety of factors described below, it often takes decades for these conditions at restoration sites to reach reference levels (Moreno-Mateos et al., 2012). Unfortunately, monitoring efforts are rarely sufficient or executed over a long enough time span to provide comparisons between restoration and reference sites and quantify restoration outcomes (Bernhardt et al., 2007; Kondolf et al., 2007; Palmer et al., 2010; Suding et al., 2015). This mismatch between monitoring practices subject to institutional and financial barriers and the ecological timeframes that determine restoration outcomes is a major issue in the field.

In ecosystems with variable climate regimes, data taken from reference sites at a single point in time may not capture high inherent system variability, which may confound interpretations of restoration outcomes (Chapple et al., 2017; Cleland et al., 2013). Given that increased variability is a projected outcome of climate change, the need for more robust temporal and spatial monitoring is likely to become more relevant across a range of ecosystems in coming years. The standard (yet still rare in practice) five-year window for project monitoring is likely to be insufficient for capturing the full range of dynamics in ecosystem restoration efforts worldwide (Zedler et al., 2012). This highlights the need to expand both the collection and interpretation of restoration data.

Compelling arguments have been made that moving away from definitions of “success” that depend on matching reference conditions may be one way to move restoration forward (Hobbs et al., 2014; Kueffer et al., 2010; Zedler, 2007; Zedler et al., 2012). However, the inherent risk in this approach is that accepting these alternative pathways may accelerate the rate of destruction by permitting incomplete restoration efforts (Murcia et al., 2014). To forge a

middle ground between these two approaches, more empirical data on the rate and nature of restoration development are needed to guide how interventions are selected. While there are examples of projects that are able return to pre-disturbance conditions with minimal intervention (Hobbs et al., 2014), the majority of restoration practitioners are faced with systems where some, if not most, aspects have been pushed outside of the natural range of variability (Funk et al., 2008; Hobbs et al., 2014; Jackson and Hobbs, 2009; Stanford, 2013; Stralberg et al., 2011; Suding et al., 2004b). Expanding knowledge about restoration project trajectories is critical for selecting the appropriate means of restoring ecological function and form to a site.

Restoration interventions can take many forms depending on the needs of the project. Generally, these approaches are conceptualized along a continuum from passive restoration, where a key stressor is removed from the landscape and the desired ecosystem type returns with little or no additional intervention, to active restoration, where multiple human interventions are needed to bring back the desired ecological conditions (Holl and Aide, 2011). Restoration of tropical forest from areas converted to pasture are an example of a system where passive restoration has proved to be particularly successful (Aide et al., 2000). A combination of the increased rate of vegetation growth due to warm temperatures and water availability, an abundance of seed dispersing birds and generally close proximity to relatively intact habitats drive this process. On the other end of the spectrum, prairie grassland is an example of a system where active restoration is required to meet restoration goals. In these cases, seeds and the proper dispersers are often unavailable due to extensive alteration of the habitat matrix and regular fire regimes may need to be implemented to maintain the characteristic prairie structure (Rowe, 2010). In practice, most restoration projects pursue a combination of passive and active strategies based on site context and available resources (Funk et al., 2008). Ecosystem-level generalizations are often highly variable from site to site, and continued assessment of restoration projects are needed to develop robust predictive strategies for restoration planning (Brudvig 2011). Combining detailed understandings of on the ground outcomes and ecological theory is necessary to help improve restoration outcomes.

Community Assembly Theory in Restoration

The sequence of interactions that interact to form ecological communities are typically described as the process of *community assembly*. Ultimately, community identity following a

disturbance is constrained by three broad *ecological filters*: dispersal filters, abiotic filters, and biotic interactions (Suding et al., 2016). Understanding how these factors interact to structure plant communities is essential for selecting restoration management approaches that address the central filters impeding the development of a site (Matthews et al., 2009). Interactions where changes in one system component has effects on another are known as *feedbacks*, and can have positive or negative implications for restoration project development (Larsen and Harvey, 2010; Suding et al., 2004b). While research on these topics is developing steadily, the context dependence of restoration outcomes and extended time periods needed to fully discern restoration outcomes necessitates the continued exploration of the mechanisms driving restoration project trajectories.

Dispersal, or the movement of a species from one area to another, is a primary determinant of which species reach an area. Dispersal strategies vary widely between species, and a plant's dispersal traits can greatly influence where and when it is found (Myers and Harms 2009). *Priority effects* occur if an early arriving species has either positive or negative consequences for species arriving subsequently (Connell and Slatyer, 1977). These effects are often related to the spatial location and configuration of a site. The appropriate propagules to drive the restoration process may or may not be available at a site based on its location in relation to source habitats, which can influence site development (Brudvig et al., 2009; Collinge et al., 2013; Matthews et al., 2009). These spatial interactions can also influence the temporal development of a site, with sites closer to source populations exhibiting faster rates of convergence with reference sites (Helsen et al., 2013). In many cases, extensive alterations of the habitat matrix lead to the widespread proliferation of invasive exotic species. Arrival of these species can drastically alter restoration trajectories. Lack of native propagule sources and abundance of invasive propagule sources mean that dispersal is commonly managed by the addition of native species and the removal of invasive species. Understanding where and when to manage dispersal effectively is a key step in producing desired restoration outcomes (Holl and Aide, 2011).

Abiotic factors, broadly defined as the physical, chemical, and climatic attributes of an ecosystem, often determine which species can establish and persist following dispersal. For example, tidal wetlands species are highly constrained by the salinity regime at the site, proximity to channels and elevation, determines the degree to which species are inundated

(Callaway et al., 2007; Callaway and Sabraw, 1994; Sanderson et al., 2000). Human alterations like the removal of topsoil during mining can change the abiotic context of a site to such a degree that returning historic habitat types requires extensive interventions like re-creating historic soil conditions (Ballesteros et al., 2012). Historic disturbance regimes such as fire or flooding may also be key abiotic factors necessary for effective restoration (Suding et al. 2016). In some cases, the extent of alteration may be so extreme that restoring to historical baselines may not be possible. Human-induced increases in soil nitrogen interact with extreme fire regimes to favor invasive species over native species in southern California grasslands (Larios et al., 2013), highlighting the potential for various abiotic factors to interact and determine restoration outcomes. Regional and local climate are also key determinants of ecosystem dynamics (Carr 2012, Favier 2012) that determine restoration trajectories (Holmgren et al., 2006; Holmgren and Scheffer, 2001). Projected increases in climate variability and shifts in climate regimes worldwide are likely to have large impacts on restoration outcomes, and better understanding how climate influences restoration will be essential for effectively managing projects into the future.

Following arrival via dispersal and establishment contingent on abiotic filters, biotic filters, determined by species interactions, often play a role in what is able to establish at a site. Biotic interactions can take many forms, notably competition, facilitation and predation. Due to the heavily interconnected nature of ecosystems, each of these forms can drive interactions that ripple across trophic levels (Painter et al., 2015; Peters et al., 2004). Competition can influence restoration outcomes if target species are unable to effectively acquire resources when other species are competing for the same resources (Armitage et al., 2006). This can be a particularly important in heavily invaded systems with abundant propagules for strong competitors (Hultine et al., 2010). Predator/prey interactions can have a wide variety of impacts on ecosystems. Direct exploitation, like preferential browsing of juvenile riparian plants by deer or cows, can negatively affect target organisms and compromise the restoration process. On the other hand, indirect effects of predation may help promote desired management outcomes, as in the case of wolf reintroduction in Yellowstone National Park, where expanding wolf populations led to decreases in elk populations that correlated with the recovery of target riparian ecosystems (Painter et al., 2015). However, manipulation of predator/prey food web relationships may also negatively impact target organisms. In the Great Lakes region of the United States, carp species

were introduced in the 1970's and 1980's to control algal blooms, but ended up also having major negative impacts on native fish species (Suding et al., 2016). Facilitation occurs when a species alters conditions at a site in ways that facilitate the establishment of other species. In restoration, this is often seen in the planting of nurse plants, which help ameliorate harsh conditions and allow for the establishment of target species that would otherwise not be able to persist (Padilla and Pugnaire, 2006).

A crucial aspect of these three categories of ecological filters is that they do not operate independently of each other (Matthews et al., 2009). In many cases, feedbacks, whereby changes in system states either promote or constrain restoration outcomes, emerge and drive the restoration process. In river systems, patterns of riparian vegetation alter hydrologic flow, which in turn influences the geomorphology of the system. Plant species dispersal and establishment is determined by these geomorphic patterns, and the resulting vegetation patterns further influence how the river system develops (Corenblit et al., 2009; Gurnell et al., 2004). In tidal wetlands, intertidal species trap mineral sediments and produce organic matter, creating positive feedbacks that maintain the appropriate surface elevation for plant growth. This allows these systems to persist under moderate increases in sea level rise (D'Alpaos et al., 2012; Morris et al., 2002). Feedbacks can also have negative consequences for ecosystem development. In a grassland system, plots with vegetative cover below 20% vegetative cover are more susceptible to erosion and are unable to maintain soil fertility, rendering the system unable to attain target vegetation density without intervention (Gao et al., 2011).

Tidal wetland restoration in the San Francisco Bay

Tidal wetlands are inundated by high tide events twice daily and exist at the interface between rapidly rising oceans and upland areas that are often densely populated. They provide protection from storm surges that can be more efficient than conventional levee systems, and their management and restoration will be an essential aspect of sea level rise adaptation worldwide (Goals Project, 2015). They also filter pollutants from urban and agricultural runoff, provide nursery habitat for a wide variety of organisms and serve as important stopping points on avian migration routes. These systems are among the most productive ecosystems on earth but have experienced substantial losses due to human impacts (Zedler and Kercher, 2005). Early efforts to protect these ecosystems from development began in the late 1950's in California's San

Francisco (SF) Bay. Early efforts to fill the Bay began in what is now San Francisco's financial district, with streets developing around ships that were intentionally stranded in the intertidal zone. To exclude tidal waters and allow for human use, soil, construction debris, and other materials were placed on top of wetlands and mudflats, raising these areas above the tide line. To create land for agriculture, salt harvesting and other industrial uses, wetlands were diked to prevent tidal flow. From the first wave of gold-rush arrivals to the area in the 1850s through the mid 20th century, tidal wetlands dwindled from 190,000 acres to fewer than 40,000 acres. In the 1950s, plans for Bay fill projects threatened to destroy nearly all of the remaining acreage, and the Save the Bay movement emerged as an attempt to halt Bay fill. The movement succeeded and in many ways set the template for the modern regulation of environmental issues. The passage of the McAtter-Petris Act in 1965 created the Bay Conservation and Development Commission, which took a regional approach to regulating Bay fill and effectively halted the destruction of wetlands in the region (BCDC 2010).

From 1970 to 2009, over 17,000 acres were restored to tidal wetlands and over 30,000 additional acres of restoration are planned from 2009 to 2030 (Goals Project, 2015). With a variety of large scale projects underway and an established history of restoration efforts, tidal wetlands in the SF Bay are an excellent opportunity to study the restoration process and integrate research into the project planning process. Much of the research in this dissertation was performed in the South Bay Salt Pond Restoration Project (SBSRP), a 15,000 acre, multi-agency effort led by the California Coastal Conservancy to restore industrial salt ponds to a mosaic of tidal wetlands and managed tidal habitats. The project is managed under an adaptive management framework, which is designed to incorporate scientific research into the management process in an iterative manner. The project is performed in distinct phases, with each phase testing a variety of management approaches, collecting data on the outcomes, interpreting the results, and using the conclusions to inform the subsequent steps of the restoration process (Trulio et al., 2007). This science-based approach aims to improve restoration outcomes by using data to shift priorities as the project evolves, a process that has emerged as the most robust, if still imperfect, approach to restoration (Fabricius and Cundill, 2014; Gregory et al., 2006).

Restoration in the SF Bay is constrained by a range of interacting ecological filters. Physical abiotic factors, particularly elevation and tidal channel structure, determine which

species establish where, with higher elevation areas and locations closer to channel edges being hotspots for vegetation development. These physical abiotic factors interact with ambient salinity levels in tidal waters, which are determined by both landscape position (proximity to fresh vs. salt water) (Callaway et al. 2007) and interannual precipitation variability. Once species have established, early colonizing species such as *Salicornia pacifica* (pickleweed) and the invasive exotic hybrid *Spartina alterniflora* (cordgrass) can lead to strong biotic effects for other colonizing species (Armitage et al., 2006). Projects are also heavily dependent on “eco-geomorphic” feedbacks between biotic and abiotic components that maintain the elevation of the marsh surface when plants produce biomass and trap sediments that increase elevation, which in turn increases primary productivity and further raises the marsh surface (Da Lio et al., 2013). The interactions between these factors over time shape restoration trajectories in SF Bay tidal wetlands.

Dissertation Overview

This dissertation aims to fill key knowledge gaps about ecological filters influencing restoration outcomes. The first two chapters focus on the influence of two abiotic filters on vegetation development: climate (represented by Bay salinity) and geomorphology (represented by tidal channel structure). Chapter three explores seed dispersal patterns across a chronosequence of three restoration projects and two reference sites.

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Chapter 1: Climate Variability Structures Plant Community Dynamics in Mediterranean Restored and Reference Tidal Wetlands

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Abstract: In Mediterranean regions and other areas with variable climates, interannual weather variability may impact ecosystem dynamics, and by extension ecological restoration projects. Conditions at reference sites, which are often used to evaluate restoration projects, may also be influenced by weather variability, confounding interpretations of restoration outcomes. To better understand the influence of weather variability on plant community dynamics, we explore change in a vegetation dataset collected between 1990 and 2005 at a historic tidal wetland reference site and a nearby tidal wetland restoration project initiated in 1976 in California's San Francisco (SF) Bay. To determine the factors influencing reference and restoration trajectories, we examine changes in plant community identity in relation to annual salinity levels in the SF Bay, annual rainfall, and tidal channel structure. Over the entire study period, both sites experienced significant directional change away from the 1990 community. Community change was accelerated following low salinity conditions that resulted from strong El Niño events in 1994-1995 and 1997-1998. Overall rates of change were greater at the restoration site and driven by a combination of dominant and sub-dominant species, whereas change at the reference site was driven by sub-dominant species. Sub-dominant species first appeared at the restoration site in 1996 and incrementally increased during each subsequent year, whereas sub-dominant species cover at the reference site peaked in 1999 and subsequently declined. Our results show that frequent, long-term monitoring is needed to adequately capture plant community dynamics in variable Mediterranean ecosystems and demonstrate the need for expanding restoration monitoring and timing restoration actions to match weather conditions.

Introduction

The practice of restoring native plant communities aims to facilitate transitions between degraded and ecologically functional landscapes by manipulating abiotic (Boyer and Thornton; Brand et al., 2012; Williams and Orr, 2002a) and biotic conditions (Silliman et al., 2015). However, transitions from a degraded state to a desirable state depend not only on actions taken at discrete sites, but also on regional climate and weather (Holmgren et al., 2006; Holmgren and Scheffer, 2001a; Vaughn and Young, 2010). Research on the impacts of spatial and environmental determinants of restoration outcomes has developed steadily (Grman et al., 2013, 2015; Matthews et al., 2009), but detailed temporal studies that capture interannual dynamics in highly variable climates are still under-represented in the literature (Brudvig, 2011; Vaughn and Young, 2010). Restored sites can take many years to match conditions at reference sites (Moreno-Mateos et al., 2012), which may have impacts on the conservation benefits that restoration projects purport to offer (Moreno-Mateos et al., 2015; Zedler and Callaway, 1999). Understanding the role of climate and weather in determining plant community dynamics will be essential for managing restoration projects into the future.

Mediterranean climates and other arid and semi-arid systems around the world are characterized by high interannual weather variability (high coefficient of variation for precipitation) (Dettinger et al., 2011; Dettinger and Cayan, 2003; Holmgren and Scheffer, 2001a), which may impact plant species dynamics (Bêche et al., 2009; Cleland et al., 2013), and by extension, restoration outcomes (Sitters et al., 2012). These changes in weather can lead systems down different trajectories depending on where and when projects are initiated (Suding et al., 2004a). Without long-term data, it is challenging to know whether observed changes at restoration sites are true trends or simply transient effects (Bagchi et al., 2012). For example, initial increases in native plant diversity following restoration may decline over time (Collinge et al., 2013), leading to false interpretations of restoration outcomes if too short an evaluation window is assessed. These spurious conclusions may influence restoration management and policy (Vaughn and Young, 2010). While theory in this regard has gained acceptance, the consideration of temporal variability in weather when implementing and evaluating restoration has lagged behind (Brudvig, 2011; Vaughn and Young, 2010).

Integrating contingencies related to climate into planning and monitoring efforts has high potential to improve management outcomes. For most restoration projects, a 5-year monitoring

plan is the best case scenario, and monitoring may not even be part of the project funding structure (Bernhardt et al., 2007; Kondolf et al., 2007b; Zedler et al., 2012). However, wet and dry years may exist consecutively, with extended periods of drought interspersed with pockets of heavy rainfall. Ecological communities may also respond in subsequent (lag) years or be further influenced by species interactions that are contingent on weather (Dudney et al., 2016). The uncertainty and variability of weather and its influence on ecological communities may create mismatches between project timing and weather conditions that would favor success (Sitters et al., 2012). Despite a pressing need to understand these dynamics, a recent meta-analysis identified a lack of studies using long-term data to investigate the influence of interannual variability on restoration outcomes (Brudvig, 2011).

Our study explores tidal marsh plant community dynamics at a restoration and a reference site in California's San Francisco (SF) Bay over a 15-year period. Mediterranean ecosystems like the SF Bay are defined by dry summers and intermediately wet winters, with a high coefficient of variation for precipitation from year to year (Dettinger, 2005; Dettinger et al., 2011). In tidal systems in California, salinity is influenced by drought conditions that can significantly reduce the amount of precipitation delivered and El Niño events that can increase rainfall and snowpack (Dettinger and Cayan, 2003). Work from the Tijuana Estuary in southern California demonstrated that primary productivity of the tidal wetland co-dominant *Spartina foliosa* increases during periods of higher freshwater flows related to El Niño events and declines in years with higher salinity (Zedler, 1983a; Zedler et al., 1986). Other studies show the importance of lowered salinity for seed emergence in high marsh species (Noe and Zedler, 2001), increased abundance of salt sensitive species following experimental freshwater addition (Callaway and Sabraw, 1994; Shumway and Bertness, 1992), and the importance of periods of high rainfall in structuring tidal marsh restoration outcomes (Zedler et al., 2003). Historic analyses of pollen samples in a tidal wetland in the south SF Bay show that species composition can vary markedly across time, likely in response to freshwater dynamics (Watson, 2004). El Niño events have been shown to influence densities of microbenthic organisms in California marshes by homogenizing community composition across reference and restored marshes (Levin and Talley, 2002). These types of shifts can impact food web dynamics for faunal communities that subsequently interact with plant distributions (Bertness, 1985; Bortolus et al., 2002; Nomann and Pennings, 1998), underscoring the fact that changes in plant distributions have the potential

to impact a range of other tidal wetland organisms. This highlights the importance of understanding plant community responses to weather variability, which may be a central factor controlling restoration trajectories in Mediterranean ecosystems (Holmgren and Scheffer, 2001b; Sitters et al., 2012). These areas are expected to be hotspots of climate change over the coming century, increasing uncertainty and variability (Callaway et al., 2007). While Mediterranean ecosystems are relatively rare globally, increased variability is a projected outcome of the changing climate across the globe (Pachauri et al., 2014) and the lessons learned from these regions will only become increasingly relevant in a variety of ecosystems worldwide.

In our study, we focus on California tidal wetlands, where salinity (Callaway et al., 2007; Callaway and Sabraw, 1994), channel structure (Morzaria-Luna et al., 2004; Sanderson et al., 2000), species dynamics (Armitage et al., 2006), and elevation (Watson, 2004) interact to influence species composition, and shifts in salinity can alter productivity (Zedler, 1983a) and species composition (Callaway and Sabraw, 1994). Furthermore, since plant community restoration in the SF Bay is largely driven by passive seed dispersal via tidal waters (hydrochory) (Diggory and Parker, 2011), dynamics at restoration sites may be related to the dynamics in adjacent reference sites (Brudvig et al., 2009). In the SF Bay, a complex set of upstream interactions in the Sierra Nevada and Central Valley determine salinity levels, which are generally higher in areas closer to the Pacific Ocean and vary throughout the year in response to snowmelt, human diversions, and other factors (Dettinger and Cayan, 2003). Consequently, variation in Bay salinity levels may be a better predictor of plant community transitions than local rainfall, which may only minimally influence salinity in sites inundated by the tide twice daily (Callaway et al., 2007).

To better understand the influence of interannual weather variability on restoration outcomes, we analyzed a long-term data set of plant community composition collected at one reference and one restoration site between 1990 and 2005. These studies were initially set up as part of an effort by the California Coastal Conservancy to better understand restoration trajectories over time in order to plan and manage future projects (Phillip Williams and Associates, LTD and P.M. Faber, 2004a). To our knowledge, this data set is one of the longest continuous data sets comparing a tidal wetland reference and restoration site. To explore how regional salinity, local rainfall, and site topography influence plant community trajectories, we look at SF Bay salinity adjacent to the sites, rainfall, and channel structure.

Methods

Sites

The San Francisco Bay (SF Bay; 37°50'37N, 122°21'46S) is a tidal estuary in central California, USA whose watershed drains the majority of the western side of the Sierra Nevada through the Central Valley (Dettinger and Cayan, 2003). The area is characterized by a Mediterranean climate, with a wet season extending from October through April and a dry season extending from May through September (Dettinger and Cayan, 2003). Beginning in the mid-1800s, widespread land conversion led to the destruction of approximately 79% of historic wetlands, and since the early 1970s, over 17,000 acres have been restored (Goals Update 2015). We collected data at a tidal wetland reference site (China Camp State Park, San Rafael, CA, USA; 38°00'36N 122°30'25S; Figure 1, now part of the SF Bay National Estuarine Research Reserve) and restoration site initiated in 1976 (Muzzi Marsh, Corte Madera, CA, USA; 37°55'36N 122°30'25S; Figure 1, now part of the Corte Madera State Ecological Reserve) (Phillip Williams and Associates, LTD and P.M. Faber, 2004a; Williams and Faber, 2001). China Camp State Park is an approximately 5000 year old tidal salt marsh (Phillip Williams and Associates, LTD and P.M. Faber, 2004a). The site is notable for its intact transitions from wetland to upland, a rarity in the heavily altered SF Bay. Due to the low amount of alteration at the site, it is commonly used as a reference for pre-disturbance tidal wetland conditions in the area (Phillip Williams and Associates, LTD and P.M. Faber, 2004b; Williams and Faber, 2001). Muzzi Marsh is one of the earliest tidal marsh restoration projects in the SF Bay (Williams and Faber, 2001), and our data collection began 14 years after the initial restoration actions. Roughly half of the study area was filled with dredge material prior to tidal breaching, and the remainder of the area increased in elevation through passive sedimentation. Tidal channels were slow to form in the filled area, an insight that led to abandoning the idea of filling sites with material prior to breaching levees for restoration (Phillip Williams and Associates, LTD and P.M. Faber, 2004a). Neither site has significant direct links to upland freshwater outflow, with China Camp at approximately 1400 m and Muzzi Marsh at approximately 1700 m from the nearest major freshwater source.



Figure 1. North SF Bay (San Francisco Bay) and study sites. Study sites: Reference site (China Camp) is approximately 5000 years old and is the most commonly used reference site in the SF Bay for tidal salt marshes. Restoration site (Muzzi Marsh) is the second oldest intentional restoration project in the SF Bay, initiated in 1976. Salinity sampling station 15 is a stop on the bi-monthly US Geological Survey (USGS) water quality cruise. Wetland layer shows other wetland habitats in the region.

Field Data Collection

Study plots were established in 1990 to better understand how reference and restoration site conditions change over time, and preliminary work on the data can be found in Williams and Faber 2004 (Phillip Williams and Associates, LTD and P.M. Faber, 2004a). At each site, a series of consecutive 15.2 m (50 ft) linear plots were established, extending from the upland transition edge to the end of the marsh plain (Figure 2). Plots were marked with plastic pipes for repeat surveys, nearly all of which were present when we re-visited the sites in 2015. Vegetation composition was collected by stretching a meter tape between the markers at the beginning and end of each plot and determining the percent vegetation cover of each species along the linear section of the meter tape (Phillip Williams and Associates, LTD and P.M. Faber, 2004a). Elevation was surveyed in 2005 using a total station related to a permanent benchmark at each site and elevation data was converted from the National Geodetic Vertical Datum (NGVD 1927)

to the North American Vertical Datum (NADV 1988) (Figure 2). To determine the elevation of the marsh plain at each site, we excluded tidal channels from the data and calculated the mean. The number of tidal channels crossing through each plot was also determined for inclusion in statistical models. Each year, vegetation was sampled in late June or early July to capture peak biomass and species composition. Due to differences in site size, data was collected from 33 plots at the reference site and 45 plots at the restoration site for most years between 1990 and 2005. Due to funding restrictions, species composition data was not taken in 1991, 1993, 1997, 2000, or 2001 at the reference site or in 1991, 1993, or 2000 at the restoration site. Our methodologies for working with the missing years is detailed in the Data Analysis section below. To determine how the sites had progressed since 2005, we collected data at both sites in September of 2015, following 4 years of historic drought in the area.

Salinity and Rainfall

Bay salinity in parts per thousand (PPT) was taken from the US Geological Survey (USGS) water quality cruises initiated in 1990 (Cloern and Schraga, 2016). Salinity is a primary determinant of species distributions in the SF Bay, and is likely to be significantly influenced in both timing and magnitude by climate change (Callaway et al., 2007). Bay salinity is determined by stream and river flow from the Sierra Nevada, and to a certain extent by upstream management of flows (Dettinger and Cayan, 2003). Our salinity data was taken from Station 15 of the USGS San Francisco Bay water quality cruise data set (Figure 1) (US Geological Survey). Due to the close proximity of this sampling station to the sites and the lack of direct freshwater flow into either site, this data is an adequate proxy for site-level salinity. To determine monthly averages, mean salinity was taken from the two upper sampling depths. For most months, two sampling dates were available to determine the monthly mean. If only one sampling date was available, it was used as the monthly mean. We calculated rainfall for each rain year using National Oceanic and Atmospheric Administration (NOAA) weather station data from Muir Woods National Monument in Mill Valley, Marin County, CA, USA (US National Oceanic and Atmospheric Administration, 2017). This data set was the only local data set that encompassed the entire study period without significant gaps, and was roughly equidistant from the two sites, so it was used for both sites. Daily precipitation was collected in mm, summed to produce monthly totals, and was then used to determine rain year means. To determine the annual salinity

and rainfall means, we aggregated data by rain year, stretching from October to September of each set of consecutive years. Years are referred to by vegetation sampling date, (e.g., 1995) for time periods encompassing the previous rain year (e.g., October 1994–September 1995). These two data sources provide relatively high-temporal resolution that is necessary for interpreting community change over time. Notably, our study period begins at the end of a major drought (1990–1992) and includes 2 major El Niño years (winters 1994–1995 and 1997–1998) that brought above average precipitation at the local and watershed scale, and subsequently lowered salinity levels in the SF Bay.

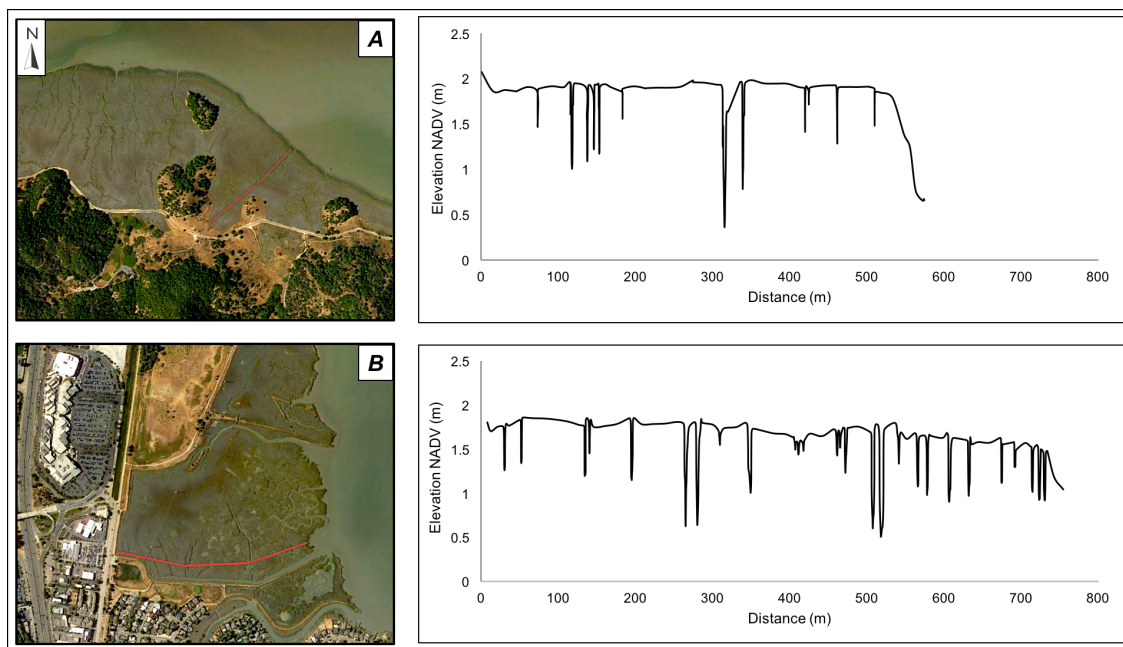


Figure 2. Google Earth aerial imagery for China Camp (A, reference site) and Muzzi Marsh (B, restoration site). The total transect length was 574 m at China Camp and 754 m at Muzzi Marsh. Mean elevation of the marsh plain (excluding channels) was 1.850 m (NADV 88) at China Camp and 1.68 m (NADV 88) at Muzzi Marsh. Sampling at both sites began in 1990 and was performed for most years through 2005. Both sites are tidal and receive no substantial freshwater from the surrounding landscape. The study area at China Camp is part of the China Camp State Park and is surrounded by protected oak woodland and grassland, while the study area at Muzzi Marsh is part of the Corte Madera Ecological Reserve and is surrounded largely by urban development.

Data Analysis

To assess change in sub-dominant species between years, we calculated the total percent cover of sub-dominant species each year and subtracted the previous year's total cover. The species included in this analysis are *Frankenia salina* (Alkali Heath), *Distichlis spicata* (Saltgrass), *Jaumea carnosa* (Fleshy Jaumea), and *Grindelia stricta* (Marsh Gumplant). These species are more sensitive to salinity (Callaway et al., 2007; Zedler et al., 2003) and less abundant in restoration sites compared to the dominant species *Salicornia pacifica* (Pickleweed) and *Spartina foliosa* (Pacific Cordgrass) (Phillip Williams and Associates, LTD and P.M. Faber, 2004a), so they provide valuable insight into community dynamics. Because tidal wetland restoration in the SF Bay is largely driven by seed arrival through hydrochory (Diggory and Parker, 2011), sub-dominant species were not actively planted at either site. To account for missing years, the sub-dominant change was divided by the number of missing years (for example, a change of 2% from 1992 to 1994 with 1993 missing was divided into a 1% change per year). We took the means of salinity and rainfall for the years in question (for example, for assessing change between 1992 and 1994, we took the mean of salinity during the 1993 and 1994 rain years) and used these in our models to avoid over-weighting the adjusted data for missing years. In our resulting models, change over missing periods is included as a single data point per plot. We ran models with and without the additional years included, and it did not change the significance of the outputs, so we elected to present results from the more conservative approach.

To determine community change across time, we used a Bray-Curtis dissimilarity metric to examine plot-level species turnover at each site (Cleland et al., 2013). These metrics sum the absolute value of species abundance differences between year A and year B and divide this sum by the total abundance of species found in each plot across both years (McCune et al., 2002). We removed bare ground from our cover data, calculated the relative abundance of each species in each plot, log transformed the data, and used the Vegan package in R (Oksanen et al., 2013) to determine the change relative to the initial (1990) community and for each combination of pairwise years (e.g., 1994–1995). For change from the initial community, we did not estimate values for the missing year averages since we were interested in directional trends, which are discernable without the replacement of missing years. For change between pairwise years, we divided the dissimilarity value for the available pairwise combination (e.g., 1992–1994) by the number of years to generate the mean annual change for that year. We elected not to use overall

species diversity as a metric for this analysis, because the reference site did not include significant amounts of *Spartina foliosa* or *Salicornia depressa*, which heavily influenced the diversity analysis.

To determine the influence of salinity and rainfall on sub-dominant species, we first used generalized additive models to look at the influence of mean annual salinity and rainfall on the change in sub-dominant species abundance. We elected to use this non-parametric approach because salinity and rainfall data were correlated and collected from the same location across multiple years and thus were not truly independent. For each site, the mean change in sub-dominant abundance for pairwise years was the dependent variable, and log transformed mean salinity and rainfall were the independent variables. Generalized additive models were fit using the GAM package in R (Hastie, 2013).

To explore the change over time relative to the initial community across time, we divided the data into three periods based on the influence of the major 1995 and 1998 El Niño events on Bay salinity: period 1 (1990–1994; mean salinity = 22.92 ppt), period 2 (1995–1999; mean salinity = 16.28 ppt), and period 3 (1999–2005; mean salinity = 22.79 ppt). 1990–1992 encompassed the end of a major drought in California (Figure 3). To determine differences in salinity levels between the three periods, we used linear mixed models with year and salinity sample depth as random effects, and time period as the fixed effect.

For each of these three periods, we explored directional change over time, with plant community dissimilarity compared to the 1990 community as the dependent variable, year and channel as the fixed variables, and plot as the random variable, resulting in a model structure similar to a mixed-effects broken-stick linear regression model. The same analysis was used to explore changes in percent cover of the sub-dominant species over the different periods. Since many wetland species are clonal perennials, abundance is an appropriate means of determining species dynamics. For all linear mixed effects analyses, separate models were run for the two sites. Linear mixed effects models were performed using the lme4 package in R (Bates et al., 2016). Change in sub-dominant cover between 2005 and 2015 was assessed using a non-parametric Wilcoxon Rank Sum test in R. We did not use elevation in the models, because the regularly spaced and linear nature of the sample plots was not conducive to a single elevation measurement that reflected the entire distribution of the plant species in each plot. Results are

reported below, with China Camp referred to as the “reference” site and Muzzi Marsh as the “restored” site.

Results

At the reference site, *Salicornia pacifica* was dominant, comprising between 99 and 67 percent of total cover depending on the year. At the restoration site, *Salicornia pacifica* was dominant in all years except for 1997-1999 when *Spartina foliosa* became dominant. Subsequent to this period of dominance, *Spartina foliosa* comprised a higher proportion of cover than it did from 1990-1996. The annual pioneer species *Salicornia depressa* was present in intermediate densities at the reference site in 1990, but steadily declined to nearly zero by 2005 (Figure 3). At both sites, sub-dominant cover was largely comprised of the clonal perennial *Distichlis spicata* and the woody wetland shrub *Grindelia stricta*, with *Distichlis* comprising a higher proportion at the restoration site. The clonal perennial species *Frankenia salina* and *Jaumea carnosa* were also present in lower abundances at both sites. *Bolboschoenus maritimus* (Alkali Bulrush) was present in very low abundance (maximum 2.35%) at the reference site only. Full information for species cover across years can be found in Table S1 in the Supplemental Materials. Mean sub-dominant species cover per plot at the reference site comprised 12.86% in 2005 and 5.63% of species cover in 2015, a notable but non-significant ($p = 0.079$, $W = 533$) net loss of 7.23%. At the restoration sites, mean sub-dominant species cover per plot comprised 7.01% of species cover in 2005 and 7.33% in 2015, a non-significant change.

Salinity levels during period 2 (1995–1999) were significantly lower than during period 1 (1990–1994; $p = 0.005$, $t = -3.881_{df=7.706}$), and period 3 (2000–2005; $p = 0.000$, $t = 4.496_{df=111}$), and salinity levels during period 1 and period 3 were not significantly different from each other ($p = 0.366$, $t = -0.953_{df=8.637}$) (Figure 3). Sub-dominant species increased in cover over the entire study period for both reference ($p < 0.000$, $t = 4.981_{df=5}$) and restored sites ($p < 0.000$, $t = 8.084_{df=5}$). Looking at change across the three time periods, sub-dominant species did not increase significantly at the reference site during period 1 ($p = 0.570$, $t = 0.565_{df=5}$). They did, however, increase significantly during period 2 ($p < 0.000$, $t = 6.361_{df=5}$), and then decreased significantly during period 3 ($p = 0.015$, $t = -2.461_{df=5}$). At the restoration site, sub-dominant species did not appear in the transect until 1996 (Figure 3). Subsequent to appearing in the transect at the restoration site, significant positive change over time was observed for these

species during period 2 ($p < 0.000$, $t = 3.954_{df=5}$) and period 3 ($p < 0.00$, $t = 3.865_{df=5}$). Across both sites, greater densities of sub-dominant species were found in plots with channels over the study period (reference: $p < 0.000$, $t = 4.981_{df=5}$; restoration: $p < 0.007$, $t = 2.747_{df=5}$). In 2005, plots with channels at the reference site supported mean sub-dominant cover of 15.436% compared to 0.31% sub-dominant cover in plots without channels. In 2005 at the restoration site, plots with channels supported mean sub-dominant cover of 17.033% compared to 0.071% in plots without channels. Full information for the above models can be found in Table S2 in the Supplementary Materials.

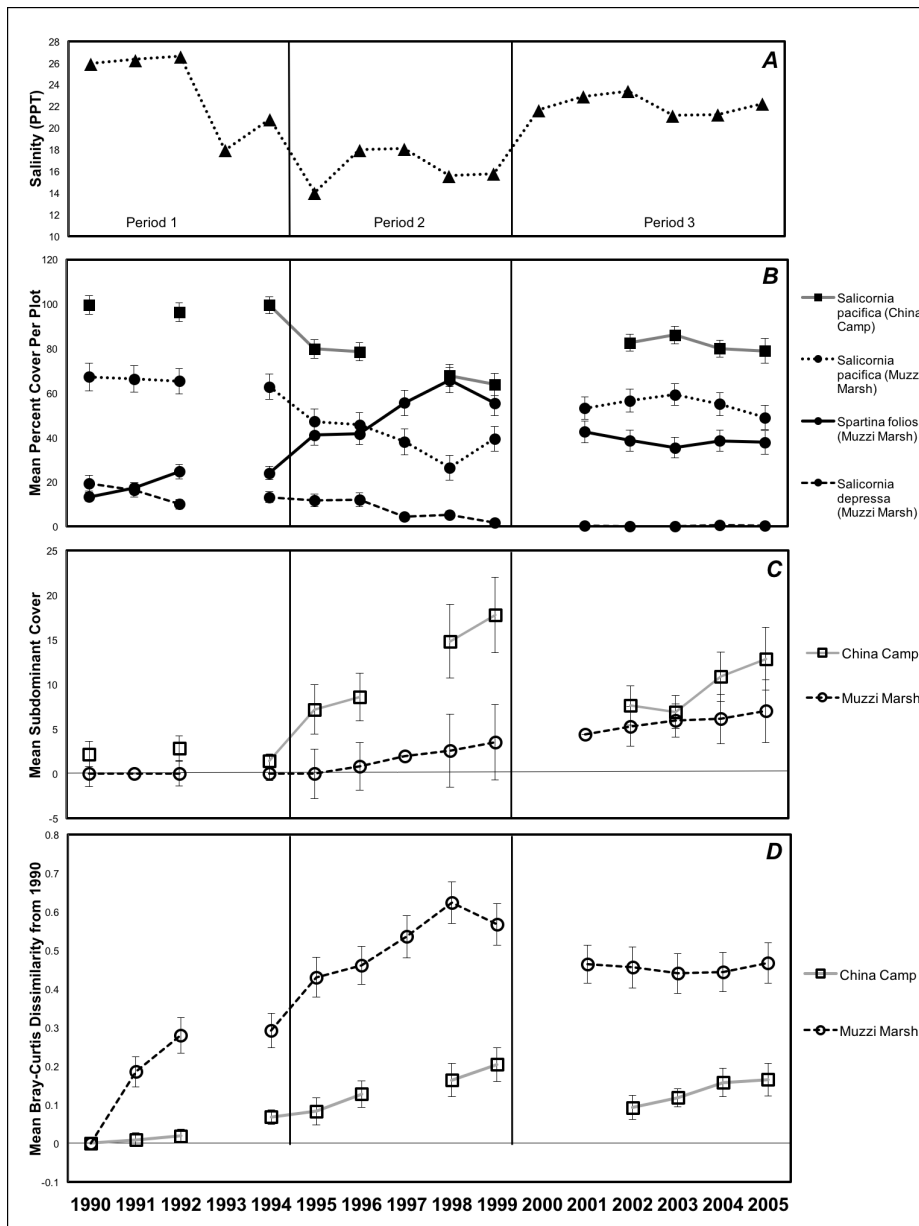


Figure 3. (A) Salinity from USGS Station 15. Data was collected bi-monthly for most months throughout the study period in parts per thousand (PPT); (B) Mean cover of pioneer/dominant species at reference and restoration sites. Throughout the study period, *Salicornia pacifica* was dominant at the reference site, with minimal abundance of *Spartina foliosa*, which is not represented here because it never comprised more than 5.3% of mean cover per plot. At the restoration site, *Salicornia pacifica* was dominant most years, with *Spartina foliosa* becoming dominant from 1997 to 1999 during the extended period of low salinity. *Salicornia depressa*, a salt tolerant, early colonizing annual species begins at intermediate cover in 1990 but declines to less than 1% by 2005, indicating directional change; (C) Mean sub-dominant cover per plot at the reference and restoration sites. Following low cover in the high salinity period one, cover begins to significantly increase at both sites during the low salinity period two. At the reference site, sub-dominant cover peaks in 1999, then declines overall during period three, while cover increases incrementally every year at the restoration site; (D) Mean community change per plot relative to the initial community (1990) at the reference and restored sites. At both sites, change is greatest during period two, when salinity is low. At the reference site, the change is lower overall, driven largely by the relative abundance of sub-dominant species and begins to decline following the peak of sub-dominant cover in 1999. At the restoration site, change is driven by the dynamics of the three pioneer species and sub-dominant species abundance. Change is significant over all three time periods (positive change during periods one and two, negative change during period 3) but strongest during period two. Error bars reflect the standard error of the mean.

At the reference site, the change in sub-dominant cover between pairwise years was significantly related to mean annual salinity ($p = 0.012$, $f = -9.894_{df=1}$), with sub-dominant cover increasing during the years with lower salinity and declining or remaining static during the period of higher salinity (Figure 4). At the restoration site, salinity was not a significant predictor of change in sub-dominant species cover between pairwise years ($p = 0.453$, $f = -0.611_{df=1}$) (Figure 4). Rainfall was not a significant predictor at the reference ($p = 0.466$, $f = -0.581_{df=1}$) or restoration site ($p = 0.739$, $f = 0.117_{df=1}$).

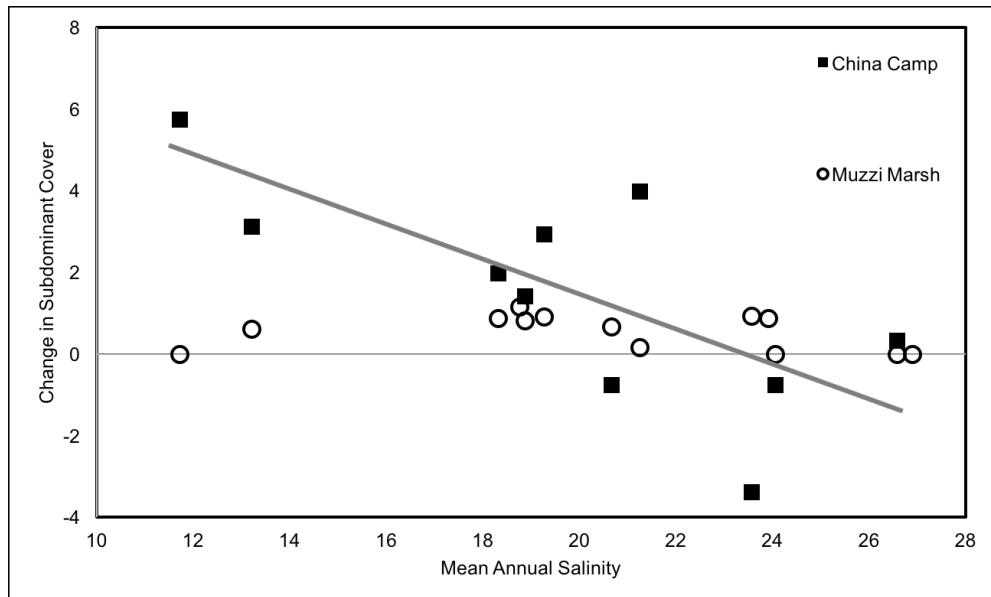


Figure 4. Sub-dominant change over mean annual salinity. We computed change in the sub-dominant community by subtracting the previous year’s total cover of sub-dominant species from the percent cover in the subsequent year. The relationship was significant at the reference site ($p = 0.012$, $f = -9.894_{df=1}$), but not significant at the restoration site ($p = 0.453$, $f = -0.611_{df=1}$). The line represents the fit for a univariate linear model but reported statistics in the text are for non-parametric generalized additive models.

Change over time relative to the 1990 community was significant over the whole study period (1990–2005) for both sites (reference: $p < 0.000$, $t = 5.776_{df=5}$; restoration: $p < 0.000$, $t = 16.456_{df=5}$). The changes observed at both sites were also significantly related to channel density (reference: $p < 0.001$, $t = 3.310_{df=5}$; restoration: $p < 0.034$, $t = 2.115_{df=5}$) (Figure 3). At the reference site, the mean dissimilarity between 1990 and 2005 was 0.227 in plots with channels and 0.113 in plots without channels. At the restoration site, the mean dissimilarity between 1990 and 2005 was 0.540 in plots with channels and 0.427 in plots without channels. Looking at the change over the three periods (Figure 3), change at the reference site was only significant during period 2 ($p < 0.000$, $t = 5.934_{df=5}$), when salinity was significantly lower than in the other periods. At the restoration site, directional change away from the 1990 community was significantly positive over the first two periods and stronger during period 2 (Period 1: $p < 0.000$, $t = 7.854_{df=5}$; Period 2: $p < 0.000$, $t = 11.420_{df=5}$), and then significantly declined between 1999 and 2005 ($p < 0.000$, $t = -4.180_{df=5}$). Full model results are available in Table S3 in the Supplemental Materials.

Discussion

At both sites, sub-dominant plant species abundance and community dissimilarity from the 1990 community significantly changed over the study period, illustrating that neither reference nor restoration sites are static over time. At the reference site during the lower salinity period three, plot-level sub-dominant species abundance significantly, peaking at over 17 percent in 1999 after five consecutive years of low salinity. However, abundance stayed static during period one and declined during period three, both periods of higher salinity compared to period two (Figure 3). At the restoration site, sub-dominant species were not present (0% cover) until 1996, and steadily increased during each subsequent year. At both sites, sub-dominant species and the overall community showed directional change from the 1990 baseline, where low diversity was likely due to high salinity resulting from the drought of 1988–1992.

At the restoration site, change was largely driven by transitions between the two dominant species, *Salicornia pacifica* and *Spartina foliosa*, and the salt-tolerant annual early colonizer *Salicornia depressa*, which had approximately 20 percent mean cover in 1990 but declined to zero by 2005. Both *Spartina foliosa* and *Salicornia depressa* are common early colonizers of low elevation areas in restoration sites, which likely explains their higher abundance at the lower elevation Muzzi Marsh (Figure 2). Abundance of *Spartina* peaked in 1998, likely since it is able to take advantage of the increased tidal heights and lowered salinity that result from the extreme El Niño events (Ward et al., 2003; Zedler, 1983a). Notably, non-*Spartina* sub-dominant density increased from roughly one percent in 1995 to more than seven percent at the reference site between 1994 and 1995, after the first major El Niño event. Following this increase at the reference site, we observed the first sub-dominant species appear at the reference site in 1996. This change occurred twenty years after the initial restoration actions, pointing to the necessity of long-term data collection to understand restoration trajectories. Given the importance of seed dispersal via hydrochory for the restoration process (Diggory and Parker, 2011), this may indicate that increased sub-dominant abundance following the first strong El Niño event at the reference sites initiated spillover effects, where seeds dispersed to the restoration site via hydrochory (Brudvig et al., 2009), but we were unable to test this with our data.

Our results clearly show that we can detect the influence that changes in salinity have on plant community transitions at tidal wetland reference and restoration sites. Local rainfall may

still be important especially for the seed establishment phase and for species in uplands directly adjacent to tidal wetlands (Noe and Zedler, 2001), but we were not able to detect its influence on the change in sub-dominant abundance at these sites. This is likely because the mix of runoff from the Sierra Nevada and tidal inundation are the primary sources of water in tidal wetlands in the SF Bay, and these tidal waters have a bigger impact on plant community identity than local rainfall patterns (Callaway et al., 2007). While other similar studies in different ecosystems have explored rainfall as a key climate driver (Cleland et al., 2013; Holmgren and Scheffer, 2001a), our results highlight how the overarching influences of weather and climate are likely to be system specific. In the case of the SF Bay, salinity is linked to precipitation and snowmelt cycles throughout the interior of California, but also to diversions for agriculture and urban uses farther up in the watershed (Callaway et al., 2007; Dettinger and Cayan, 2003), meaning that both natural and human responses to climate variability have the ability to shift reference and restoration conditions. In the Mediterranean climate of the SF Bay, variability is likely to spur or slow key transitions and state changes that impact how restoration projects develop (Scheffer et al., 2009; Suding and Hobbs, 2009). Without high resolution temporal data, it is challenging to interpret trajectories of change at reference and restoration sites, because transient effects may be incorrectly identified as directional change (Bagchi et al., 2012).

Interannual variability in precipitation is expected to increase under climate change (Pachauri et al., 2014). Restoration and conservation projects will need to adapt to shifting climate regimes to meet targets, particularly as systems are pushed out of their twentieth century stable states (Suding et al., 2004a; Suding and Hobbs, 2009). Consecutive years of drought or precipitation may lead to species shifts that go beyond simple annual effects and may be additive over many years (Watson, 2004). Site physical attributes are likely to interact with climate effects, evidenced by the fact that sub-dominant species density in our study is influenced by tidal channels in addition to salinity. Channel proximity can improve survivorship of planted sub-dominant species (O'Brien and Zedler, 2006), likely due to lower salinity as a result of tidal flushing (Sanderson et al., 2000). These overlaps between weather and landscape topography may be a crucial means of targeting future restoration efforts in areas where species diversity is most likely to be buffered against climate variability.

Importantly, our study is only able to explore these trends at one of each site type. This potentially limits our ability to draw broad conclusions, but our results are consistent with

shorter-term studies on tidal wetland species dynamics throughout California, with regards to salinity (Callaway et al., 2007; Callaway and Sabraw, 1994; Zedler, 1983a; Zedler et al., 1986) and channel structure (Sanderson et al., 2000; Zedler et al., 1999), so we expect them to be widely applicable in the region. Furthermore, since our data is observational, it is challenging to discern the precise mechanisms underlying the trends we observed. Notably, our data do not include information on soil porewater salinity, which has been shown to influence both the germination (Noe and Zedler, 2001) and distribution of tidal wetland species (Sanderson et al., 2000). However, it is likely that the salinity of tidal waters measured in the SF Bay relates to soil salinity at the sites. While China Camp is the most commonly used reference site in the region, Muzzi Marsh is situated next to another historic marsh in the Corte Madera Ecological Reserve that may have different species dynamics. When we returned to the sites in 2015 (40 years after initial restoration actions), the total sub-dominant cover across all plots was higher at the restoration site than the reference site, but *Spartina foliosa* was still co-dominant with *Salicornia pacifica*, in contrast to the single species dominance of *Salicornia pacifica* at the restoration site. This indicates that convergence has not fully occurred between the reference and restoration conditions. However, it is worth noting that *Spartina foliosa* provides a critical habitat for the federally endangered Ridgway's Rail (*Rallus obsoletus*) (Goals Project, 2015), meaning that the restoration site may provide a better endangered species habitat. This highlights that convergence with reference conditions may not always be the most effective means of judging restoration outcomes (Moss, 2015; Zedler, 2007; Zedler et al., 2012). Furthermore, the maintenance of sub-dominant species cover at the restoration site between 2005 and 2015 parallel to the decline of these species at the reference site indicates that the series of low salinity years in between 1995 and 1999 may have initiated a directional community change at the restoration site that is more resistant to the effects of drought than the reference community.

A series of insightful papers have posited that restoration actions should be timed with climate events, a notion that our findings support (Holmgren et al., 2006; Holmgren and Scheffer, 2001a; Sitters et al., 2012). Other authors have pointed to the insufficiency of the majority of restoration monitoring efforts (Bernhardt et al., 2007; Zedler et al., 2012). Our results show that even the best-case-scenario five year monitoring plan is likely to miss key developments in the restoration process, and that studies that compare two points in time may miss key stochastic developments that occur in the years between (Levine et al., 2014). For

instance, if our sites were only monitored in 1994 with sub-dominant abundance as a key metric, one might conclude that the restoration site had adequately converged with the conditions observed in the reference site, since cover was at or near zero at both sites. However, revisiting the site in 1995 would reveal a seven-fold increase at the reference site with no change at the restored wetland site. Furthermore, significant directional change away from the initial community was observed at both sites over the study period, and these dynamics may influence the biotic response ratios used to compare the reference and restored sites (Moreno-Mateos et al., 2012). This is especially pressing in areas where restoration is used as mitigation for habitat conversion, as shorter term trends might be interpreted as directional change, but diversity may in fact decrease following initial actions (Collinge et al., 2013). The findings presented here from a long-term monitoring effort have significant implications for how restoration projects should be managed in variable climates.

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Appendix:

Table A1. Species cover over the study period. Values below reflect the total percent cover for each species over the entire study area for each year, and thus may not be equivalent to the percentages reported in the results, which reflect mean density per plot. Species abbreviations are as follows: SADE = *Salicornia depressa*, SPFO = *Spartina foliosa*, SAPA = *Salicornia pacifica*, DISP = *Distichlis spicata*, JACA = *Jaumea carnosa*, FRSA = *Frankenia salina*, GRST = *Grindelia stricta*, BOMA = *Bolboschoenus maritimus*. Note that 2015 data is included at the end, with a 10-year gap between 2005 and 2015.

| Site | SADE | | SPFO | | SAPA | | DISP | | JACA | | FRSA | | GRST | | BOMA | | Sub Dom Total | |
|------|------|-------|------|-------|-------|-------|------|------|------|------|------|------|------|------|------|------|---------------|------|
| | CC | MM | CC | MM | CC | MM | CC | MM | CC | MM | CC | MM | CC | MM | CC | MM | CC | MM |
| 1990 | 0.00 | 19.46 | 3.53 | 13.35 | 94.19 | 67.19 | 1.13 | 0.00 | 0.54 | 0.00 | 0.59 | 0.00 | 0.03 | 0.00 | 0.00 | 0.00 | 2.28 | 0.00 |
| 1991 | 0.00 | 16.43 | | 17.30 | | 66.27 | | 0.00 | | 0.00 | | 0.00 | | 0.00 | | 0.00 | | 0.00 |
| 1992 | 0.00 | 10.04 | 3.83 | 24.67 | 93.64 | 65.29 | 1.04 | 0.00 | 0.60 | 0.00 | 0.89 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 2.53 | 0.00 |
| 1994 | 0.00 | 13.21 | 4.41 | 24.04 | 94.15 | 62.76 | 0.40 | 0.00 | 1.05 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 1.44 | 0.00 |
| 1995 | 0.00 | 11.75 | 4.55 | 41.06 | 89.14 | 47.19 | 4.91 | 0.00 | 0.65 | 0.00 | 0.28 | 0.00 | 0.48 | 0.00 | 0.00 | 0.00 | 6.31 | 0.00 |
| 1996 | 0.00 | 11.98 | 3.83 | 41.56 | 88.06 | 45.64 | 3.78 | 0.82 | 1.11 | 0.00 | 0.28 | 0.00 | 2.22 | 0.00 | 0.72 | 0.00 | 7.39 | 0.82 |
| 1997 | 0.00 | 4.47 | | 55.61 | | 38.06 | | 1.81 | | 0.00 | | 0.00 | | 0.05 | | 0.00 | | 1.86 |
| 1998 | 0.00 | 5.24 | 4.34 | 65.73 | 81.35 | 26.40 | 9.52 | 2.08 | 1.12 | 0.00 | 0.22 | 0.00 | 3.44 | 0.55 | 0.00 | 0.00 | 14.31 | 2.63 |
| 1999 | 0.00 | 1.64 | 3.18 | 55.50 | 79.51 | 39.39 | 8.17 | 2.95 | 2.21 | 0.00 | 0.53 | 0.00 | 4.04 | 0.53 | 2.35 | 0.00 | 14.95 | 3.48 |
| 2001 | 0.00 | 0.37 | | 42.57 | | 53.17 | | 2.69 | | 0.00 | | 0.18 | | 1.01 | | 0.00 | | 3.88 |
| 2002 | 0.00 | 0.11 | 3.83 | 38.65 | 89.53 | 56.51 | 1.41 | 3.14 | 2.03 | 0.13 | 0.59 | 0.25 | 2.59 | 1.21 | 0.00 | 0.00 | 6.63 | 4.73 |
| 2003 | 0.00 | 0.11 | 5.31 | 35.36 | 88.08 | 59.21 | 2.30 | 3.24 | 2.24 | 0.26 | 0.61 | 0.34 | 1.19 | 1.48 | 0.28 | 0.00 | 6.33 | 5.32 |
| 2004 | 0.00 | 0.71 | 2.61 | 38.55 | 87.08 | 55.06 | 3.17 | 4.60 | 3.03 | 0.18 | 0.92 | 0.20 | 2.20 | 0.71 | 1.00 | 0.00 | 9.31 | 5.68 |
| 2005 | 0.00 | 0.31 | 3.01 | 41.01 | 87.20 | 53.01 | 2.34 | 3.77 | 2.90 | 0.13 | 0.14 | 0.67 | 2.73 | 1.11 | 1.67 | 0.00 | 8.12 | 5.68 |
| 2015 | 0.00 | 0.00 | 2.71 | 31.67 | 94.49 | 61.45 | 0.36 | 4.94 | 1.44 | 1.43 | 0.46 | 0.24 | 0.55 | 0.27 | 0.00 | 0.00 | 2.81 | 6.88 |

Table A2. Sub-dominant plant species abundance change over time. At the reference site, abundance significantly increases during period 2 (low salinity) and subsequently significantly decreases when salinity rises in period 3. At the restoration site, sub-dominant species are not

present in period 1 and increase significantly during periods 2 and 3. At both sites, change in sub-dominant cover is increased in plots containing channels. * connotes significant results.

| Period | | <i>p</i> | Estimate | SE | <i>t</i> | Df |
|---------------------------------------|---------|----------|----------|-------|----------|----|
| Reference Site (China Camp) | | | | | | |
| 1 (1990–1994) | Year | 0.570 | –0.002 | 0.003 | –0.565 | 5 |
| | Channel | 0.959 | –0.001 | 0.023 | –0.050 | 5 |
| 2 (1994–1999) | Year | <0.000 * | 0.031 | 0.005 | 6.361 | 5 |
| | Channel | 0.006 * | 0.163 | 0.058 | 2.839 | 5 |
| 3 (1999–2005) | Year | 0.015 * | –0.009 | 0.004 | –2.461 | 5 |
| | Channel | 0.006 * | 0.166 | 0.059 | 2.809 | 5 |
| Total (1990–2005) | Year | <0.000 * | 0.006 | 0.001 | 4.981 | 5 |
| | Channel | 0.006 * | 0.129 | 0.046 | 2.823 | 5 |
| Restoration Site (Muzzi Marsh) | | | | | | |
| 1 (1990–1994) | Year | na | na | na | na | 5 |
| | Channel | na | na | na | na | 5 |
| 2 (1994–1999) | Year | <0.000 * | 0.0076 | 0.002 | 3.954 | 5 |
| | Channel | 0.0847 | 0.025 | 0.015 | 1.713 | 5 |
| 3 (1999–2005) | Year | <0.000 * | 0.006 | 0.002 | 3.865 | 5 |
| | Channel | 0.0032 * | 0.105 | 0.035 | 3.025 | 5 |
| Total (1990–2005) | Year | <0.000 * | 0.005 | 0.001 | 8.084 | 5 |
| | Channel | 0.007 * | 0.05148 | 0.019 | 2.747 | 5 |

Table A3. Plant community dissimilarity from the initial year. For each period, the change is analyzed using the last year of the previous period as the starting point. Dissimilarity is calculated relative to the 1990 community to discern directional change over time. Both reference and restoration sites exhibit significant directional change over time, but the magnitude of change is higher at the restoration site. Change is only significant during period 2 (low salinity) at the reference site, but is significant over all three periods at the restoration site. Over all periods at the reference site, change is concentrated in plots containing channels because sub-dominant diversity is driving community change, while at the restoration site, where change is driven by the interactions between three pioneer species in addition to sub-dominant species, the channel is only significant when considering the entire study period. * connotes significant results.

| Period | | <i>p</i> | Estimate | SE | <i>t</i> | Df |
|---------------------------------------|---------|----------|----------|--------|----------|----|
| Reference Site (China Camp) | | | | | | |
| 1 (1990–1994) | Year | 0.089 | 0.034 | 0.020 | 1.694 | 5 |
| | Channel | 0.014 * | 0.047 | 0.019 | 2.455 | 5 |
| 2 (1994–1999) | Year | <0.000 * | 0.155 | 0.0287 | 5.394 | 5 |
| | Channel | 0.022 * | 0.127 | 0.055 | 2.312 | 5 |
| 3 (1999–2005) | Year | 0.650 | 0.023 | 0.007 | 3.381 | 5 |
| | Channel | 0.046 * | 0.104 | 0.055 | 1.871 | 5 |
| Total (1990–2005) | Year | <0.000 * | 0.055 | 0.010 | 5.776 | 5 |
| | Channel | 0.001 * | 0.085 | 0.026 | 3.31 | 5 |
| Restoration Site (Muzzi Marsh) | | | | | | |
| 1 (1990–1994) | Year | <0.000 * | 0.212 | 0.027 | 7.854 | 5 |
| | Channel | 0.453 | 0.030 | 0.041 | 0.742 | 5 |
| 2 (1994–1999) | Year | <0.000 * | 0.370 | 0.032 | 11.42 | 5 |
| | Channel | 0.519 | 0.053 | 0.084 | 0.632 | 5 |
| 3 (1999–2005) | Year | <0.000 * | –0.199 | 0.048 | –4.18 | 5 |
| | Channel | 0.636 | 0.040 | 0.087 | 0.464 | 5 |
| Total (1990–2005) | Year | <0.000 * | 0.174 | 0.011 | 16.456 | 5 |
| | Channel | 0.034 * | 0.085 | 0.040 | 2.115 | 5 |

Chapter 2: Tidal wetland restoration project development during a historic drought: a remote sensing approach

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Abstract

Tidal wetland restoration efforts can be challenging to monitor in the field due to unstable local conditions and poor site access. However, understanding how restored systems evolve over time is essential for future management of their ecological benefits, many of which are related to vegetation dynamics. Physical attributes such as elevation and distance to channel play crucial roles in governing vegetation expansion in developing tidal wetlands. However, in Mediterranean ecosystems, drought years, wet years and their resulting influence on salinity levels may also play a crucial role in determining the trajectory of restoration projects, but the influence of weather variability on restoration outcomes is not well understood. Here, we use object-based image analysis (OBIA) and change analysis of the high-resolution IKONOS and WorldView-2 satellite imagery to explore whether mean annual rates of change from mudflat to vegetation are lower during drought years with higher salinity (2011-2015) compared to years with lower salinity (2009-2011) at a developing restoration site in California's San Francisco Bay. We found that vegetation increased at a mean rate of 1979 m²/year during California's historic drought, 10.40 times slower than the rate of 20580 m²/year between 2009 and 2011 when the state was not in drought. Vegetation was significantly concentrated in areas in closer to channel edges, where salinity stress is ameliorated, and the magnitude of the effect increased in the 2015 image. In our image analysis, we found that different distributions of water, mud and algae between years led to different segmentation settings for each set of images, highlighting the need for more robust and reproducible OBIA strategies in complex wetlands. Our results demonstrate that adaptive monitoring efforts in variable climates should take into account the influence of weather on tidal wetland ecosystems, and that high-resolution remote sensing can be an effective means of assessing these dynamics.

Introduction

Tidal wetland ecosystems worldwide are threatened by a range of human activities (Erwin, 2009; Klemas, 2013; Zedler and Kercher, 2005) and have been in steady decline for the last 150 years in California (Goals Project, 2015). In recent years, significant efforts have been undertaken to reverse this widespread loss and alteration. To effectively implement and plan restoration efforts, detailed understandings of system dynamics are necessary for driving adaptive management approaches (Spencer et al., 2016). To date, studies of restoration projects have focused more on the physical aspects of vegetation development and how they relate to sediment supply, initial elevation and landscape context (Brand et al., 2012; Kelly et al., 2011; Williams and Orr, 2002). However, due to a variety of interacting factors, restoration projects may not proceed in a simple linear manner over time (Chapple et al., 2017; Holmgren et al., 2006; Holmgren and Scheffer, 2001a; Peters et al., 2004; Scheffer et al., 2009; Sitters et al., 2012). Rates of restoration change over time and the factors that influence these transitions are critical yet understudied aspects of the restoration process. Since restoration projects increasingly use iterative, data-driven adaptive management strategies to plan projects, an improved understanding of how systems change over longer time periods is necessary.

Due to its Mediterranean-type climate and variable weather between years, California's San Francisco Bay (SF Bay) is an interesting location to study how climate variability influences restoration projects (Chapple et al., 2017). Between 2011 and 2015, California experienced an extreme drought event with an essentially incalculable return period (Robeson, 2015). This extended dry period has led to changes in other plant communities across the state (Asner et al., 2016; Copeland et al., 2016), and has likely influenced restoration project trajectories (Chapple et al., 2017; Holmgren and Scheffer, 2001a). At the broad scale, plant communities in SF Bay tidal wetlands are primarily influenced by the salinity of tide waters (Callaway et al., 2007; Malamud-Roam and Ingram, 2004), which are influenced by snowpack levels and a complex series of upstream interactions across the state (Dettinger and Cayan, 2003). Anthropogenic sources of atmospheric carbon appear to be contributing to reduced snow pack in the state, which is expected to continue declining (Berg and Hall, 2017). These shifts will likely have major impacts on salinity and plant community dynamics throughout the estuary (Callaway et al., 2007; Malamud-Roam and Ingram, 2004) and will play a role in determining how restoration trajectories progress (Chapple et al., 2017). An improved understanding of how extreme events

like California's historic drought impact restoration efforts is essential for future management (Callaway et al., 2007; Holmgren et al., 2006; Holmgren and Scheffer, 2001a; Sitters et al., 2012; Zedler et al., 2012), given that increased climate variability is a major projected outcome of climate change (Pachauri et al., 2014).

In the SF Bay, the restoration of tens of thousands of acres of tidal wetland are planned or in process (Goals Project, 2015). Tidal wetlands in the area are inundated twice daily by tidal water, and the ambient salinity of Bay water is the primary determinant of tidal wetland plant community structure at the broad scale (Callaway et al., 2007; Chapple et al., 2017). At the site-level scale, salinity interacts with tidal channel structure and elevation to determine vegetation patterns (Chapple et al., 2017; Sanderson et al., 2000; Schile et al., 2011a). Previous studies on the role of freshwater dynamics in California's tidal wetlands have focused on field-collected data, finding that salinity can play a pronounced role in plant productivity and community dynamics (Callaway and Sabraw, 1994; Chapple et al., 2017; Zedler, 1983b). To improve management outcomes, understanding vegetation trends at larger scales is critical, and remote sensing of aerial imagery provides a cost-effective means of monitoring tidal wetland sites where access may be challenging. In particular, object-based image analysis (OBIA) is a promising technique for monitoring tidal salt marshes (Dronova, 2015), and has been applied to looking at vegetation across spatial scales in these ecosystems (Moffett and Gorelick, 2013, 2016; Tuxen and Kelly, 2008), but has only recently been used to explore change over time (Campbell et al., 2017). Previous geospatial work using aerial imagery has largely taken place in the North SF Bay, where freshwater river runoff buffers Bay salinity (Tuxen et al., 2008; Tuxen and Kelly, 2008). While large-scale manipulation of freshwater in restoring tidal wetlands is not feasible, remotely sensed data allows for retrospective consideration of how drought has influenced restoration trajectories.

Ecological trends are often hard to predict in heavily modified restoration sites (Suding et al., 2004a; Zedler, 2007), which makes monitoring a crucial aspect of iterative restoration design (Bernhardt et al., 2007; Chapple et al., 2017; Kondolf et al., 2007a; Zedler et al., 2012). These uncertainties are compounded by climate variability, but the influence of year-effects on restoration outcomes is under-represented in the literature (Vaughn and Young, 2010). Site conditions in developing tidal wetlands can be particularly challenging for ground surveys owing to tides, mud and limited access options (Diggory and Parker, 2011; Watson, 2008). Remote

sensing of satellite imagery allows for the monitoring of large wetland areas at a fraction of the cost and time associated with field monitoring, but it is still under-utilized as a restoration tool (Klemas, 2013). To effectively track the fine scale trends required by most tidal wetland restoration projects, high resolution (<4m) imagery is needed to analyze surface trends (Dronova, 2015).

High-resolution satellite imagery also presents certain challenges for accurately characterizing restoration targets such as vegetation cover. Due to high spatial complexity caused by fine-scale patterning of water, algae, topography and other features, high-resolution imagery can be challenging to interpret. Often, pixel-based approaches are hampered by their inability to consider both the pixel identity and spatial context in classifying landscapes (Tuxen and Kelly, 2008). To account for these issues, object-based approaches are increasingly used to categorize heterogeneous landscapes like tidal wetlands (Campbell et al., 2017; Dronova, 2015; Moffett and Gorelick, 2013, 2016; Tuxen and Kelly, 2008; Wang et al., 2004). In tidal wetland restoration projects, sediment is highly dynamic over time, and imagery must be gathered at low tide for optimal visualization while surface water and debris can vary greatly between images (Fulfrust, 2012; Tuxen and Kelly, 2008). Further, vegetation patches may be heterogeneous, leading to salt-and-pepper speckle artifacts that confuse delineation and interpretation of cover types (Moffett and Gorelick, 2013). By smoothing local noise and allowing for supervised classification for each year, OBIA can help address some of these issues (Dronova, 2015), but it has rarely been used for monitoring restoration outcomes (but see Campbell et al., 2017). OBIA methods are effective because they rely on multi-scale interpretations of images instead of simple pixel measures (Schiewe et al., 2001). By nature, pixels represent a fixed area of the ground surface, defined by the pixel size, or resolution. Object-based approaches integrate pixel information with spatial information, as pixels closer together in space are more likely to be related (Blaschke and Hay, 2001). Further, the shape of objects can be incorporated and controlled in the OBIA process flow, allowing for more detailed pattern analysis (Blaschke et al., 2000; Schiewe et al., 2001). A comparison of pixel-based and object based analyses of IKONOS imagery in a tidal system found that object-based methods repeatedly outperformed pixel-based methods (Wang et al., 2004).

Object-based methods rely on a mix of the parameter classes listed above to segment images for analysis. Scale and shape parameters capture the spatial attributes of the study system,

while spectral bands from the imagery capture variation in visual and often infrared sensor bands (Dronova, 2015). The process of segmentation incorporates user-specified weights for each of these parameters and divides the images into discrete objects. Based on how well these objects capture variation across the landscape, the user varies parameters to arrive at an appropriate set of objects (Moffett and Gorelick, 2013). Once the appropriate objects are defined, the user classifies a subset of objects into classes. This subset of points is then used to classify the entire image.

Despite its strong potential, change analysis is less frequently implemented in tidal wetland ecosystems using OBIA. The most frequent use of this technique has been in mapping mangrove ecosystems (Conchedda et al., 2008; Gaertner et al., 2014; Son et al., 2015), where Conchedda *et al.* found that increases in mangrove ecosystems in Senegal may be attributable to increased precipitation in the region over the study period (Conchedda et al., 2008). Campbell et al. were able to track the influence of Hurricane Sandy on vegetation dynamics across a range of wetlands in New York (Campbell et al., 2017). These studies highlight the potential to use these methods to discern the influence of weather variability on vegetation change.

Tidal wetland restoration has been underway in the SF Bay since the mid-nineteen seventies (Williams and Faber, 2001). Early projects showed that the proper elevation range was crucial for plant establishment, but that pre-filling sites to their target elevations prevented the development of tidal channels, leading to inferior quality habitat (Williams and Faber, 2004; Williams and Faber, 2001). As such, tidal wetlands in the SF Bay are typically restored through a hybrid process, whereby topography is sculpted before returning tidal influence to insure proper drainage, but the mudflats accrete sediment passively from the tide over time to reach target elevations for vegetation development (Brand et al., 2012; Kelly et al., 2011; Williams and Orr, 2002). This allows for the development of tidal channel networks that convey tidal waters in and out of these sites. Both channel structure and elevation play key roles in determining vegetation patterning, largely due to the reduction of salinity in higher elevation areas and areas closer to channel edges (Brand et al., 2012; Sanderson et al., 2000; Tuxen et al., 2011). Channel proximity also influences salinity levels: poorly drained areas in the interior of the marsh exhibit lower biomass production when ambient salinity levels are higher, while channel edges appear to buffer the negative influences of ambient salinity, allowing for similar levels of biomass production across different salinity levels in areas adjacent to channels (Schile et al., 2011a).

Biomass production influences the speed of restoration, which in turn influences the resilience of developing restoration projects to sea level rise (Goals Project, 2015); it is thus critical to understand how restoration sites change over time.

Despite a developed conceptual framework on the spatial development of marshes from mudflats based on sediment and elevation, the influence of weather variability and extreme events like drought over time is less well understood. In California tidal salt marshes, freshwater added by El Nino events (Chapple et al., 2017; Zedler, 1983) and experimental manipulations (Callaway and Sabraw, 1994; Schile et al., 2011b; Woo and Takekawa, 2012) has been shown to influence biomass production and species identity. Freshwater impacts can also influence plant dynamics at restoration sites (Chapple et al., 2017), but these impacts have not been explored at larger spatial scales. To better understand the influence of drought on vegetation development over time, we performed change analysis at a developing restoration site in the South Bay Salt Pond Restoration Project (SBSRP) in Hayward, CA during California's historic drought (2011-2015) and a period of average precipitation (2009-2011). In the SF Bay, earlier change detection efforts have largely relied on using spectral indicators such as NDVI to track restoration site changes over time (Fulfrust et al., 2012; Kelly et al., 2011; Tuxen et al., 2008). The goals of our study are three-fold: **1)** compare rates of annual vegetation change during the drought period to a period with greater freshwater influence (2009-2011) **2)** assess how channel structure influences vegetation patterning across different years and **3)** discern the utility of OBIA classification and change analysis to detect changes in a tidal wetland restoration project.

Methods

Study area

Our study focused on a single marsh (North Creek Marsh, 37°36'40.20"N, 122°6'43.94"W) at Eden Landing Ecological Reserve in Hayward, CA, part of the South Bay Salt Pond Restoration Project (Figure 1). The SBSRP is an adaptively-managed effort to restore over 15,000 acres of former salt-evaporation ponds to a mosaic of tidal wetlands and managed ponds (Trulio et al., 2007). North Creek Marsh is a 37.32 ha restoration site initiated in 2006. The site was historically tidal wetland that was converted to industrial salt-evaporation in the late 19th century (Stanford, 2013). Tidal influence was returned to the area by breaching a levee at the southern end of the site. The restoration process is driven by tidal transport of sediment building

the marsh plain to the appropriate level (Brew and Williams, 2010), then seed dispersal via tidal hydrochory driving the development of vegetation (Diggory and Parker, 2011). In addition to the passive restoration process via seed dispersal, the Invasive Spartina Project actively planted selected portions of the site with the native cordgrass *Spartina foliosa*, *Distichlis spicata* (saltgrass) and *Grindelia stricta* (marsh gumplant) (Hammond, 2016).

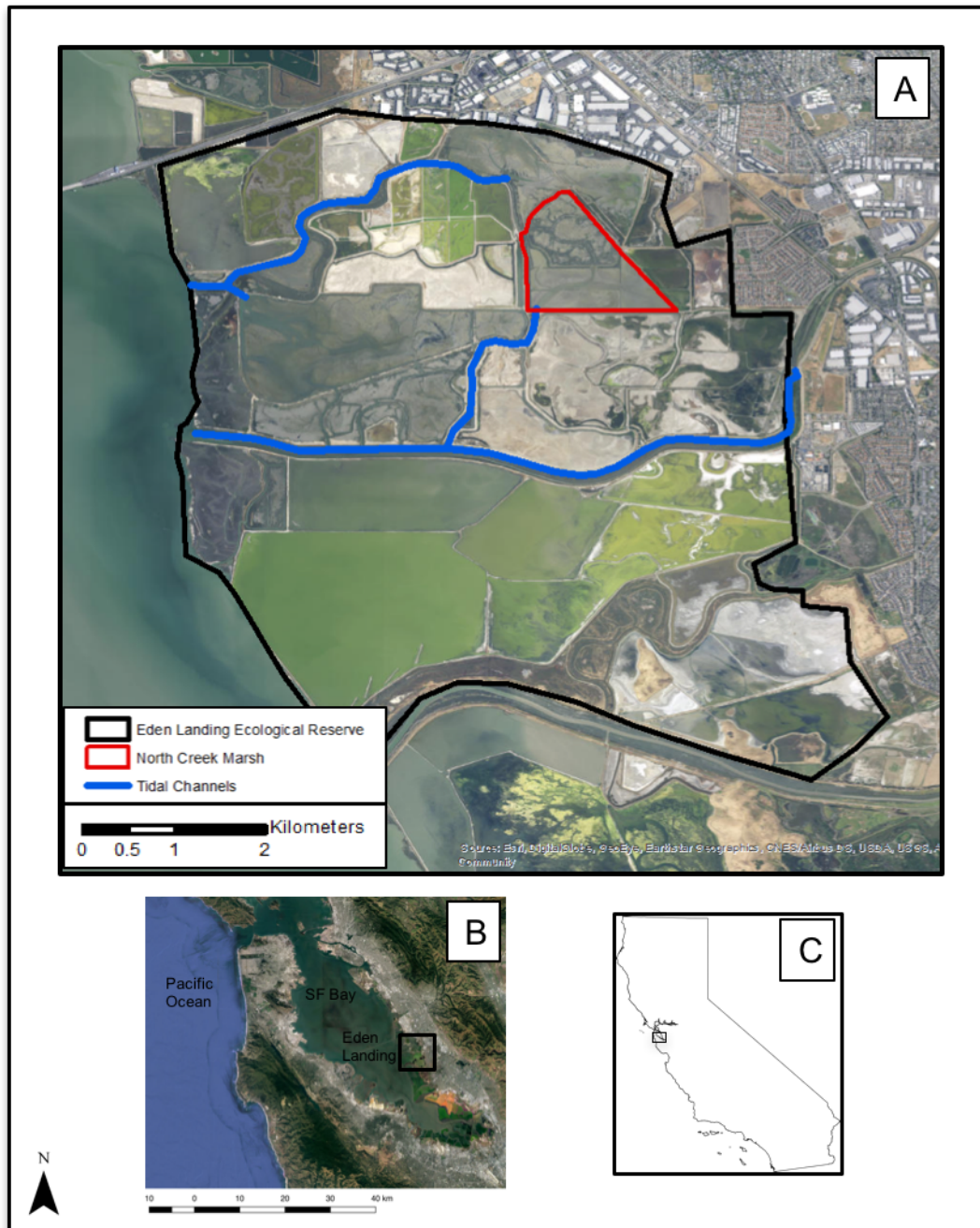


Figure 1: A) Eden Landing Ecological Reserve (CA Dept. Fish and Wildlife), Hayward, California, USA. **B)** South San Francisco Bay, Eden Landing Ecological Reserve outlined. **C)** San Francisco Bay Aerial images reproduced with permission from ©Google, 2017.

Salinity data analysis

We determined mean annual salinity for each rain year (October-September) between 2009 and 2015 using Station 30 from the USGS SF Bay water quality archive (Cloern and Schraga, 2016). To explore potential differences between tidal heights, we determined mean higher high water (MHHW) and monthly maximum tide from the NOAA Redwood City Tide Gauge, the closest tide station with continuous data over the study period (<https://tidesandcurrents.noaa.gov/>). For salinity and MHHW, we subset the data for rain years 2009-2011 and 2012-2015 to correspond to the dates of our imagery and California's historic drought. To determine differences between the two periods, we performed a non-parametric Kruskal-Wallis test for salinity, MHHW and monthly maximum tide. To determine directional trends in salinity during the two periods, we used non-parametric generalized additive models to analyze salinity levels over time using the *gam* package in R (Hastie, 2013). Non-parametric tests were used due to non-normality of salinity data.

Remote sensing data and image pre-processing

For 2009 and 2011, we obtained 0.8-m pan sharpened IKONOS imagery of the South Bay Salt Pond Restoration Project from the San Francisco Estuary Institute (© Digital Globe Inc., 2011). For 2015, we obtained 0.5-m WorldView-2 imagery (© Digital Globe Inc., 2015). Each set of imagery contained 4 spectral bands: red, green, blue and near-infrared (NIR). To ensure phenological continuity between collection dates, all images were collected near peak biomass (June 23 2009, July 7 2011, and June 21 2015) at low tide to ensure maximum visibility of vegetation. The timing of collection is essential because tidal water frequently covers landscape features, such as vegetation patches, essential to change detection. To double check that intermediate years at our site did not exhibit anomalous vegetation growth that is not accounted for in our analysis, we reviewed Google Earth imagery (© Google, 2017) for all available dates between June 2009 and June 2015.

To prepare the images for analysis, we re-projected the 2009 image from the GCS 1984 datum to the NAD 1983 datum to match the 2011 and 2015 images. We down-sampled all images to 0.8-m pixel resolution to match the lowest resolution images. We then geocorrected all images, resulting of an offset of 0.5-pixel maximum. Images were imported into eCognition (© Trimble Inc.) software to perform object-based image analysis. To allow for the most effective interpretation of vegetation patches, bands 4, 3 and 2 were visualized as RGB, respectively, and the Histogram Equalization stretch was applied across the image.

Object-based image classification

Object-based analyses were performed in eCognition Developer software version 8.8 (© Trimble Inc.). As a first step, we generated primitive image objects as spatial units for wetland classification using the Multiscale Resolution Segmentation (MRS) tool which requires the parameters of scale, shape and compactness to control object size and heterogeneity. For all images, we used the red, green, blue, and infrared bands to classify imagery. To determine their values for our objectives, we worked through a series of scale parameter values in increments of 5, and both shape and compactness parameters in increments of 0.1. We assessed each combination of settings by trial and error to determine which combination of parameters best matched the visual distribution of vegetation at the site. Notably, due to the differences in the original resolution of image datasets, we had to individually adjust their MRS parameters to obtain primitive objects of comparable size. For the 2011 image, using a scale of 10 resulted in unrealistically small objects. Using scales of 40 and above did not capture enough of the surface variation, and after comparison of incremental steps, we determined that a scale of 30 most effectively captured the vegetation patterning on the marsh surface. We selected a scale of 25 for the 2015 image and a scale of 6 for the 2009 image. For all images, shape was given low weight (0.1) in the final classification, as shapes in wetland vegetation are highly dependent on patch size and do not conform to regular patterns across the marsh surface (Moffett and Gorelick, 2013). Compactness was given a medium weight (0.5). For all images, the 4 bands were given equal weight.

Following the segmentation process, we manually identified at least 50 training samples for each of the 3 main categories: Water/Channels, Mudflat and Vegetation. Vegetation is included as a simple category since the majority of vegetation at the site consists of *Salicornia*

pacifica, an early-colonizing marsh dominant (Krause, 2016). *Jaumea carnosa* (Fleshy Jaumea), *Frankenia salina* (Alkali Heath), the annual *Salicornia europaea* (common glasswort), *Grindelia stricta* (marsh gumplant) and *Spartina foliosa* (California cordgrass) are present in lower densities due to natural recruitment (Krause, 2016) and planting (Hammond, 2016), but our imagery did not allow for differentiation between species. Samples were selected by examining the imagery and cross-referencing these observations with checks of Google Earth (©2015 Google) imagery to verify vegetation patterns. This information was combined with expert knowledge on vegetation patterns from field visits conducted between 2013 and 2015. Once samples were selected, images were classified by including a supervised nearest neighbor process algorithm with the mean brightness, mean near-infrared and standard deviation of the red band selected as class-discriminating features. We initially included the Normalized Difference Vegetation Index (NDVI), which uses the red and infrared bands to detect green vegetation, as a classification parameter. However, this led to spurious identification of algae as vegetation and misclassified vegetated areas with apparent mud-films as mudflat, so we elected not to include it in the final process decision tree. Following sample selection and implementation of the nearest neighbor algorithm, images from all years were separately classified into the three categories using the classification algorithm in eCognition. Once images from each year had been classified, the resulting classifications were imported into ENVI to perform change detection analysis via simple spatial overlay. Images were masked to include only the marsh-plain area.

To perform accuracy assessment, we used the Random Points tool (Standard C Rand function) in ArcGIS v. 10.3 (Esri Inc.) to select between 54 and 87 points per category per year, excluding training samples, and visually identified cover categories. Samples that fell along object edges were excluded from the random point selection. Google Earth images (©2015 Google) from each year were used to manually verify sample collection points. These points were imported as Regions of Interest (ROI) into ENVI v.5.2 (Harris Geospatial Inc.) software to perform accuracy analysis. The ROIs were used to populate the Confusion Matrix tool, which calculates standard accuracy metrics (overall accuracy, kappa, user's and producer's accuracies for different classes) of a classified image based on verified samples.

Following classification, we analyzed vegetation patch dynamics. To determine the relationship between vegetation presence and channel structure, we digitized a vector of the major channels at the site, then created a distance raster using the Euclidean Distance tool in

ArcGIS v. 10.3 (Esri Inc.). This tool calculates the distance from a specified feature and outputs a continuous raster with corresponding values. We generated 1000 random points using the Random Points tool in ArcGis and extracted the vegetation layer from our classification for each year. Based on this data we used vegetation presence (1) and absence (0) to run a generalized linear model with a binomial distribution using the lme4 package in R (Bates et al., 2017). To determine changes in patch configuration across the 3 images, we ran patch statistics using FragStats v. 4 (McGarigal et al., 2015).

Results

Salinity and Tides

Our results show that salinity was significantly higher during California's historic drought, and the magnitude of mean annual vegetation change was 10.40 times slower during this period compared to the lower salinity period that preceded it (Figure 2, 3). Mean salinity was 25.64 ppt for 2009-2010, 23.99 ppt for 2010-2011, with an overall mean of 24.82 ppt (CV=0.198) between 2009 and 2011. Mean salinity was 26.08 ppt for 2011-2012, 28.18 ppt for 2012-2013, 30.12 ppt for 2013-2014 and 29.50 ppt for 2014-2015, with a mean salinity of 28.47 ppt (CV=0.10) between 2011 and 2015 (Figure 5). Salinity was significantly different between these two periods ($p < 0.000$, $\chi^2 = 18.40$). Salinity significantly decreased between 2009 and 2011 ($p < 0.001$, $F = 18.69$) and significantly increased between 2011 and 2015 ($p < 0.001$, $F = 16.50$). Neither MHHW ($p = 0.354$, $\chi^2 = 0.86$) nor monthly maximum tide was significantly different between the two periods ($p = 0.354$, $\chi^2 = 43.87$) (Figure 2).

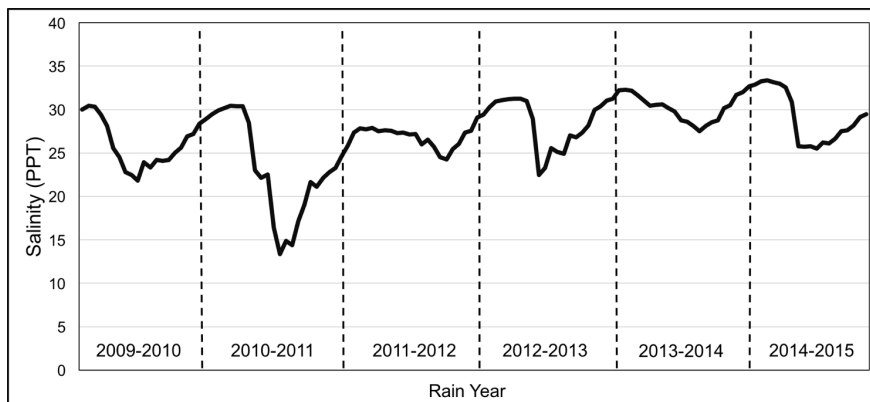


Figure 2: SF Bay Salinity, rain years 2009-2015. Data were taken from Station 30 of the bi-monthly USGS Water Quality Cruise (Cloern and Schraga, 2016).

Remote sensing classification accuracy

We obtained high classification accuracy for each of our cover categories in each year. For 2009, we obtained an overall accuracy of 92.42% and a Kappa Coefficient of 0.88. For 2011, we obtained an overall accuracy of 95.02% and a Kappa Coefficient of 0.92. For 2015, we obtained an overall accuracy of 96.83% and a Kappa Coefficient of 0.95. The lower overall accuracy in the 2009 image was due to overestimating the coverage of water on the marsh surface (Table 1). Vegetation, the focal target of post-restoration monitoring, was consistently classified with high user's and producer's accuracy exceeding 92% at all times (Table 1). It was most commonly misclassified with water in 2009 and 2015 and mudflat in 2011. Some of the overall classification error also occurred due to misclassification of water and mudflats that did not correspond to vegetation per se and thus was of lower concern for our objectives.

Table 1: Accuracy assessment for each cover category for 2009, 2011 and 2015.

| Class | 2009 | | 2011 | | 2015 | |
|----------------|--------------------------|--------|--------------------------|--------|--------------------------|--------|
| | Producer's | User's | Producer's | User's | Producer's | User's |
| | Overall accuracy: 92.42% | | Overall accuracy: 95.02% | | Overall accuracy: 96.83% | |
| Channels/Water | 96 | 82.76 | 94.12 | 96 | 91.8 | 98.25 |
| Vegetation | 98.08 | 94.44 | 95.89 | 92.11 | 98.67 | 96.1 |
| Mudflat | 87.5 | 97.67 | 94.81 | 98.65 | 98.82 | 96.55 |

Changes in vegetation cover and distribution

Total vegetation cover increased from 58154 m² of the study area to 99315 m² from 2009 to 2011, an increase of 70% at a mean rate of 20580 m²/year. In contrast, vegetation cover increased from 99315 m² in 2011 to 107232 m² in 2015, a 7.97% change from the 2011 cover at a mean rate of 1979 m²/year (Figure 3, 4). For all years, vegetation presence was significantly related to distance from channel, with areas closer to channel more likely to support vegetation, but the magnitude of the effect was notably larger in the 2015 image (2009: p<0.000, z=-3.49; 2011: p=0.002, z=-2.98; 2015: p<0.000, z=-6.33). In the 2011 image, we observed some vegetation colonization of interior mudflat areas that did not persist in the 2015 image (Figure 4, 5). The overall number of patches decreased from 2009 (394 patches) to 2011 (282 patches) and

increased in 2015 (473 patches). Mean patch area was the largest in 2011 (352 m²), intermediate in 2015 (226 m²) and smallest in 2009 (147 m²) (Table 2).

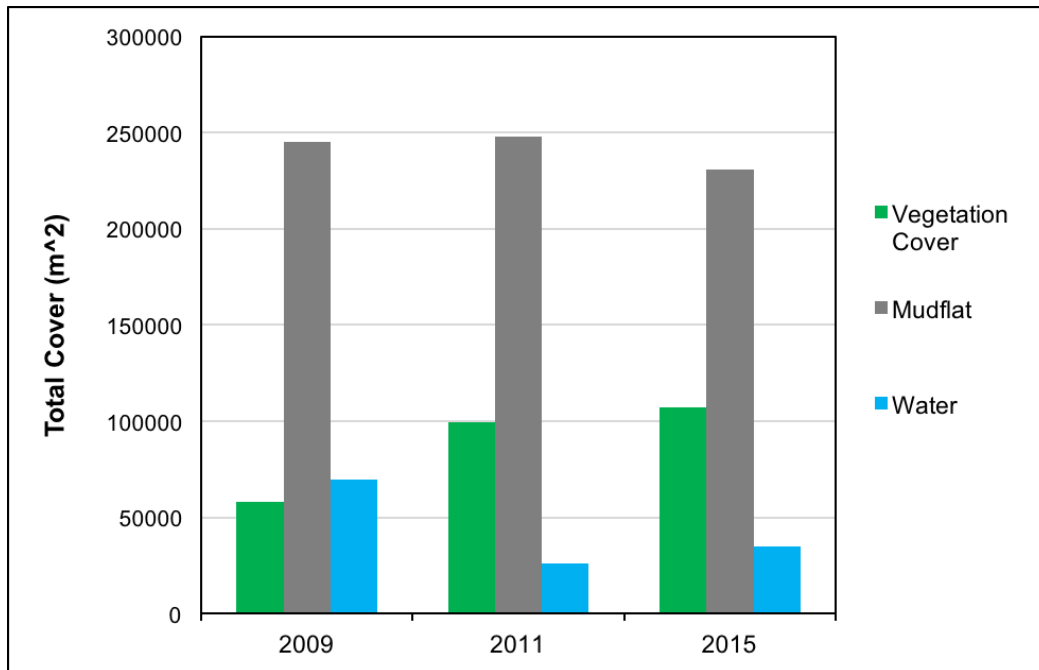


Figure 3: Cover type change. Mudflat was the dominant cover type across all 3 years. Vegetation increased at a rate of 20580 m²/year between 2009 and 2011, and 1979 m²/year between 2011 and 2015.

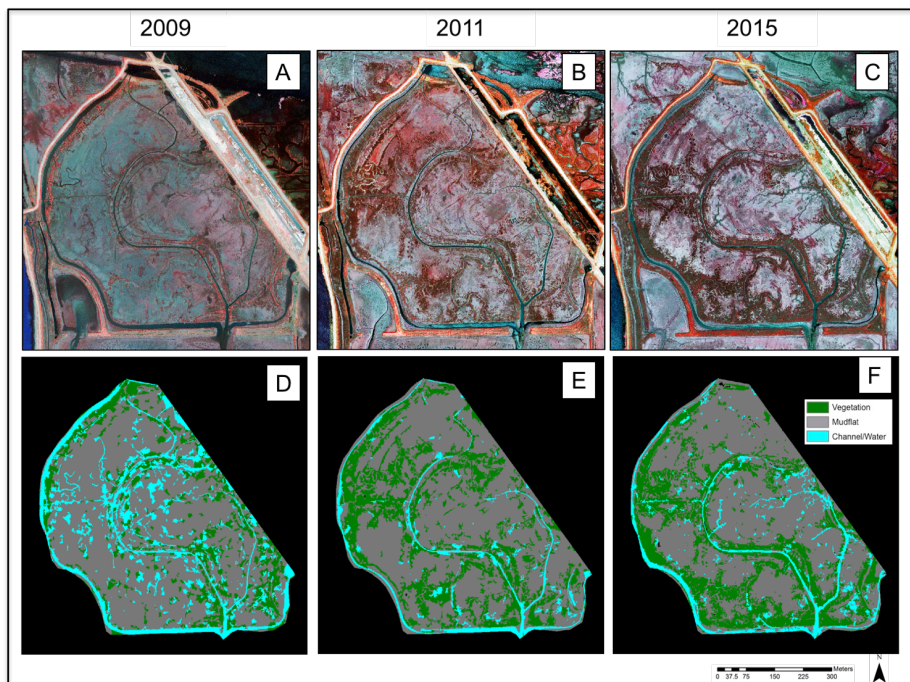


Figure 4: Change over time at North Creek Marsh. A-C) False color imagery for 2009, 2011 and 2015. D-F) Classifications of cover types for 2009, 2011, and 2015. Aerial images reproduced with permission from ©DigitalGlobe, 2017.

Among non-vegetated surfaces, mudflats were the most prevalent cover class across all years, declining slightly in 2015, with total cover of 245413 m² in 2009, 247685 m² in 2011 and 230752 m² in 2015. Since the amount of water in aerial images is highly dependent on the timing of image, tidal phase, and other stochastic factors, changes in water coverage should be interpreted with caution. In our images, water accounted for 69764 m² in 2009, 26188 m² in 2011, and 34787 m² in 2015 (Figure 3, 4).

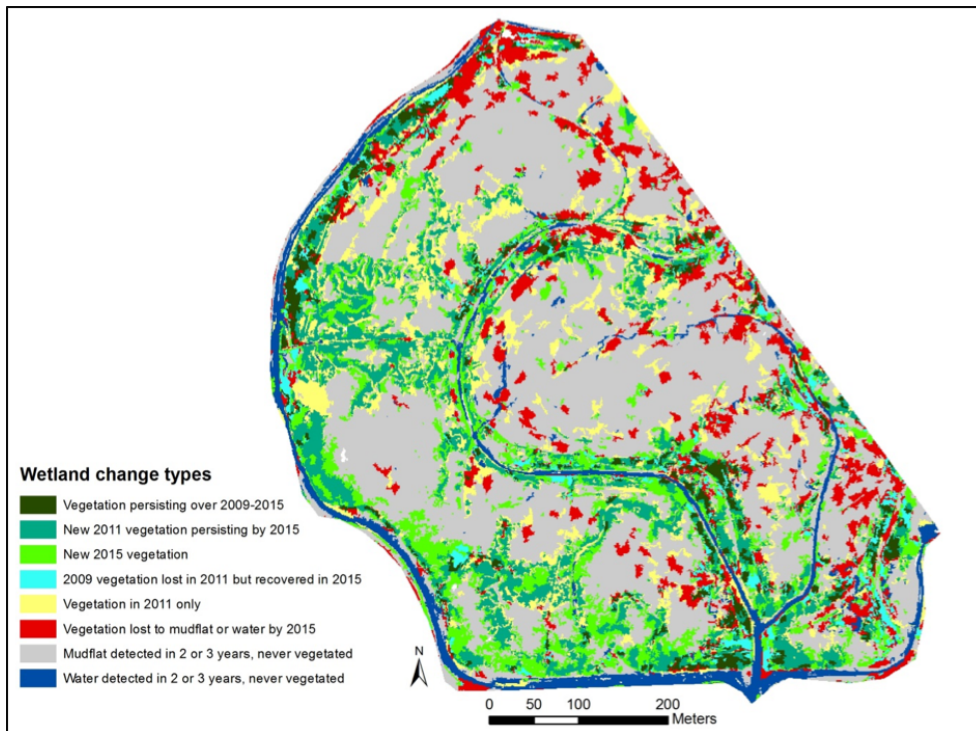


Figure 5: Change detection image at North Creek Marsh, 2009-2011. Vegetation is largely concentrated along channel edges. Interior areas are largely persistent mudflat over the entire study period. Some interior areas away from channels contain vegetation in the 2011 classification only that is subsequently lost in 2015.

Table 2: Patch statistics for 2009, 2011 and 2015.

| Year | Number of patches | Mean patch area, m ² | Maximum patch area, m ² | Standard deviation patch area, m ² | Coefficient of variation |
|------|-------------------|---------------------------------|------------------------------------|---|--------------------------|
| 2009 | 394 | 147.6 | 4682.24 | 385.79 | 2.61 |
| 2011 | 282 | 352.18 | 25623.7 | 1641.05 | 4.66 |
| 2015 | 473 | 226.71 | 21194.9 | 1351.44 | 5.96 |

Discussion

Post-restoration vegetation dynamics in tidal wetlands

Our results demonstrate that drought may impact vegetation change rates in Mediterranean-type tidal wetland restoration projects, leading to non-linear recovery patterns. At North Creek Marsh, vegetation cover increased from 2009 to 2011 and from 2011 to 2015, but the mean annual rate of change during the first period, when Bay salinity was lower, was almost ten times as rapid as change during the second period, when historic drought conditions elevated salinity levels in the Bay. By employing remotely sensed imagery to study this progression, we were able to scale up from previous field efforts that demonstrated the effect of lowered salinity on plant productivity (Schile et al., 2011; Woo and Takekawa, 2012; Zedler, 1983a), and restoration trajectories (Chapple et al., 2017). Previous work from Southern California documented increased rates of *Spartina foliosa* establishment in response to increased sedimentation rates brought on by El Nino events (Ward et al., 2003) and increased *Spartina* biomass and structure in response to lowered salinity brought on by El Nino events (Zedler, 1983a; Zedler et al., 1986, 198). Our results show that freshwater availability may also influence the rate of vegetation expansion in recently restored wetlands dominated by *Salicornia pacifica*. These larger-scale observations are supported by experimental results that demonstrate that increased salinity levels reduced *Salicornia pacifica* biomass production (Schile et al., 2011; Woo and Takekawa, 2012). In contrast to our site, a similar restoration project in a more freshwater marsh without a notable drought period reached 90% vegetated over a 10 year period, with no evidence of slowing pace after initial gains (Tuxen et al., 2008). This indicates that restoration projects in higher salinity regions may exhibit more variable, less linear trajectories due to interannual variability in salinity. While increased inundation during periods of higher rainfall could be another factor influencing vegetation change, we found no significant difference in MHHW or monthly maximum tide between the two periods.

Our results also demonstrate that channel structure is a key determinant of where vegetation establishes, and may be even more important during periods of elevated salinity. Vegetation was significantly associated with channel proximity for all years, but between 2011 and 2015, the strength of the interaction between vegetation presence and channel proximity nearly doubled. We also visually observed establishment of new vegetation patches in interior marsh areas in 2011 (Figure 4), but these patches did not persist in 2015. Channels drive the

restoration process by improving drainage across the marsh surface and lowering salinity (O'Brien and Zedler, 2006; Sanderson et al., 2000; Wallace et al., 2005; Williams and Orr, 2002). Biomass production of *Salicornia pacifica* is significantly influenced by elevated salinity in in poorly drained areas, but salinity has no effect in well-drained areas adjacent to channels (Schile et al., 2011). Our results indicate that salinity levels likely interact with the channel structure at the site, allowing vegetation to persist and expand in areas adjacent to channels but precluding development in poorly drained interior areas. Under projected climate change scenarios, increased prevalence of drought is likely to reduce snowpack and increase salinity. This may slow the overall rate of vegetation change and increase the importance of channel structure in the restoration process.

The potential of OBIA for wetland monitoring and future research needs

Our results also show how object-based image analysis can be used to overcome some of the challenges with high resolution data to map vegetation change over time in developing tidal wetlands. The dynamic nature of tidal processes mean that images are often different from each other based on how mud and water appear in the image, which can present problems for comparing images from different years (Campbell et al., 2017; Dronova, 2015). Furthermore, local noise and spectral variation, especially pronounced at higher spatial resolution, pose considerable challenges for delineating wetland cover type patches as semantic entities (Moffett and Gorelick, 2013), particularly at early post-restoration stages with higher spatial heterogeneity (Tuxen and Kelly, 2008; Tuxen et al., 2008; Kelly et al., 2011). By using object-based methods, we were able to create realistic objects for our cover types that produced high levels of accuracy, allowing for comparison between years at high spatial resolution. While NDVI has historically been employed as a means of detecting vegetation, we found that classification parameters that relied too heavily on NDVI led to classification of areas with green algae on the mudflat surface as vegetation. By also taking into account spatial parameters, our object-based approach minimized spurious mapping of vegetation that may occur when using pixel-based change methods. Our results highlight the distinct benefit of using OBIA in assessing early stages of restoration project development to capture fine scale change and to streamline semi-automated vegetation detection despite some degree of required specificity of methods and parameters at individual dates. Although OBIA benefits in wetland analyses have long been recognized (Tuxen

and Kelly, 2008; Dronova, 2015), this methodology is still under-utilized in the context of restoration monitoring (Klemas 2013) and offers powerful opportunities for cost-effective, spatially comprehensive and repeated characterizations of vegetation development and landscape structure.

Notably, different algorithm parameters were needed for each image to produce images with the highest accuracy. We were able to attain a high level of accuracy across all three images, but accuracy was slightly lower in the in the 2009 imagery, when algae and surface water led to more confusion between classes, highlighting the importance of date-specific conditions on wetland surface analysis in tidal systems. Distributions of water and mud across the landscape were mapped differently in different years, due to different tidal heights at the time of collection and evolving morphology of landscape topography that likely led to retention of water in different areas across the years. We suggest that changes between mudflat and water should be interpreted with caution, since they are highly temporally variable and sensitive to when imagery was collected. While vegetation increased overall, there were also notable areas of localized vegetation loss (particularly in areas farther from channels), which indicates that the site is still evolving. We expect that efforts to monitor multiple restoration sites will likely need to create separate classifications for each site to minimize the impact of unique surface conditions at a given tidal stage and surface variability on classification effectiveness.

Limitations and Future Directions

In addition to the effects of wet years and drought, the trends we observed are likely influenced by a combination of other factors. In the commonly accepted models of tidal wetland development, sedimentation rates are expected to slow as the marsh plain reaches equilibrium with tidal inundation (D'Alpaos et al., 2012; Morris et al., 2002; Schile et al., 2014; Williams and Orr, 2002b), which could explain the observed decrease in the rate of vegetation expansion we observed. However, sedimentation data collected at the site shows that annual sedimentation rates between the breach date in 2006 and 2013 were marginally slower (1.21cm/year) than between 2013 and 2016 (1.33cm/year), when drought conditions persisted (Krause, 2016). This indicates that the decreased rate of vegetation expansion is not due to decreased rates of sedimentation. Further, between 2012 and 2015, *Spartina foliosa* was planted across the study site, (Hammond, 2016). Since these plantings were largely adjacent to areas of existing

vegetation, they may have contributed to the expansion we observed, which means that rates of natural expansion during the drought years may have been even lower than our results indicate. Lastly, our analysis of tidal height data shows that differences in tidal inundation did not differ between the wet and dry periods.

The inability to detect species-level trends is an important limitation of our study. In addition to the *Spartina foliosa* plantings, the tidal wetland sub-dominant species *Frankenia salina* (Alkali Heath) and *Jaumea carnosa* (Fleshy Jaumea) were also present at the site in very low densities (Krause, 2016). Work from older restoration and reference sites in the north SF Bay indicate that Bay salinity can also influence the dynamics of sub-dominant species (Chapple et al., 2017), which may be a promising direction for future studies in these areas. However, *Salicornia pacifica* is the dominant species in the early stages of restoration in the area, and is responsible for the majority of vegetation cover. One of the major implications of rates of vegetation change is the ability of developing restoration projects to keep pace with sea level rise (Goals Project, 2015), so for the purposes of our study understanding overall rates of vegetation change is appropriate. Advancing this OBIA-based monitoring framework to develop a capacity to detect species-level transitions in the future is an important research need that could benefit from the advances in high-resolution hyperspectral platforms (Lucieer et al., 2014; Santos et al., 2011).

Implications for restoration and adaptive management

Our results demonstrate that considering non-linear post-restoration site development trajectories that are dependent on climate may be crucial for structuring adaptive management decisions in variable climates. A detailed understanding of how weather interacts with site geomorphology to influence outcomes is important for planning effective restoration efforts (Chapple et al., 2017; Holmgren and Scheffer, 2001a; Sitters et al., 2012; Vaughn and Young, 2010). Importantly, slower progress of vegetation is not entirely negative, as the intermediate habitat mosaic of vegetation, mudflat and water provides habitat for a number of avian species (Moss, 2015). However, given that the rapid re-vegetation of tidal wetland restoration projects is considered to be one of the best means of allowing developing sites to keep pace with sea-level rise (Goals Project, 2015), understanding the role of weather in determining these rates will be essential for managing projects that are resilient to climate change.

Developing reproducible remote sensing techniques is a promising, potentially cost-effective means of monitoring change in these projects over time. Future efforts should explore change over multiple sites to discern how generalized these weather-dependent trends are and how transferable image classification settings are between sites. Sampling restoration sites across a range of salinity levels in the SF Bay would allow for an exploration of how the spatial context of sites might influence their temporal development. Since field sampling is limited by time, scale, funding and spatial resolution, remotely sensed products hold high promise for addressing these issues.

From a restoration management perspective, our findings supported other work demonstrating that channel edges are hotspots of vegetation development (O'Brien and Zedler, 2006; Sanderson et al., 2000; Wallace et al., 2005). Attempts to add diversity into developing marshes should focus on these areas, a practice which is already in place in the SF Bay (Hammond, 2016). Since we show that interior mudflat areas away from channels may be slow to develop vegetation, proactive manipulation of elevation in these areas prior to restoring tidal access may be one way to speed vegetation development. Further, efforts to actively manipulate channel structure may also help speed the development of vegetation establishment. These actions are likely to be more necessary in areas where salinity levels are currently higher, but may become necessary across a range of sites as climate change shifts salinity distributions in the SF Bay (Callaway et al., 2007). Proactive geomorphic intervention is likely to make these projects more resilient to the impacts of sea level rise.

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Chapter Three: Bio-physical interactions determine seed dispersal patterns in the South Bay Salt Pond Restoration Project

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Abstract

Restoration projects often rely on un-assisted (passive) seed dispersal to restore native plant communities. In tidal wetland restoration efforts in California's San Francisco (SF) Bay, seed transport via tidal flow (hydrochory) is the primary driver of vegetation development in restoration projects. To better understand how native halophyte seed dispersal interacts with physical and biotic factors at restoration sites, I explore seed bank and seasonal seed rain over two years at three restoration sites of different ages and two reference sites in the South Bay Salt Pond Restoration Project. I measured elevation, vegetation cover, distance from channel and soil salinity across these sites to discern how these factors interact with seed distributions. Reference sites had significantly more vegetation cover, seed bank and seed rain compared to the restoration sites. Vegetation patterns at the restoration sites were determined by distance from channel, elevation, and site age. At the restoration sites, halophyte seed bank density was low overall and significantly aggregated around areas with higher vegetative cover, but was not directly related to distance from channel, relative elevation or site age. Seasonal seed rain was significantly related to vegetation cover, relative elevation, and site age, but not distance from channel. Comparing seed densities between individual sites, the oldest restoration site had significantly higher vegetation cover and seed rain density than the two younger restoration sites, and statistically similar seed rain density to the reference sites. These results show that vegetation patches play a key role in building the seed bank, and that seeds appear to not be retained or dispersed into lower elevation areas without vegetation cover. Since transitioning bare areas to vegetated is a key step in mitigating the negative impacts of sea level rise, management efforts should consider manipulating abiotic conditions to increase elevation heterogeneity or biotic conditions through planting or adding seeds to speed development in these areas.

Introduction

Tidal wetlands provide critical ecosystem services (Barbier et al. 2011), and widespread degradation has made them a high priority for restoration efforts (Zedler & Kercher 2005; Silliman et al. 2015). However, various interactive factors may slow (Moreno-Mateos et al. 2012) or prevent restored ecosystems from matching conditions at reference sites (Zedler & Callaway 1999). The complex interactions between biological and physical ecosystem properties that create and maintain inter-tidal vegetation are key in the tidal wetland restoration process (D'Alpaos et al. 2012; Da Lio et al. 2013). Vegetation in these systems is strictly constrained by the physical environment, largely due to the negative effects of salinity on plant primary productivity and species diversity (O'Brien & Zedler 2006). Both elevation (Bertness & Hacker 1994; Crain et al. 2004; Brand et al. 2012) and proximity to tidal channel (Sanderson et al. 2000; Williams & Faber 2001; Williams & Orr 2002; Chapple and Dronova 2017) ameliorate salinity and aid in vegetation development, which drives the restoration process. However, many tidal wetland restoration projects are driven by passive dispersal via the tidal transport of seeds (hydrochory), and it is less well understood how the dispersal process interacts with vegetation and abiotic factors at sites across time.

Dispersal of plant species is a key step in the restoration of vegetation communities (Suding et al. 2004; Wolters et al. 2005; Morzaria-Luna & Zedler 2007; McConkey et al. 2012; O'Connell et al. 2013). Restoration sites can take many decades to reach conditions at reference sites (Moreno-Mateos et al. 2012; Moreno-Mateos et al. 2015), and understanding seed dispersal patterns is essential for effectively planning restoration interventions. Seed dispersal occurs in two broad phases: the initial spread of a propagule to a location (seed rain) and the retention of a propagule in the soil at a location (seed bank) (McConkey et al. 2012). Project managers employ either passive restoration methods, where plant propagules arrive via the available ambient dispersal mode (e.g. water, wind or animals) or active restoration methods, where seed or other plant material is purposefully introduced to restore native plant communities (Holl & Aide 2011; Zahawi et al. 2014; Suding 2011). Following passive or active introduction, propagules are faced with a series of biotic and abiotic establishment filters that influence plant community composition and fine-scale species distribution patterns (Grman et al. 2015). Understanding the

interactions between dispersal patterns and the biotic and abiotic conditions at restoration sites can help improve restoration outcomes.

In the majority of tidal wetland restoration projects in coastal California, seeds arrive passively via hydrochory and interact with site conditions to form initial patches of pioneer vegetation that drive site development. However, the diversity and density of seeds in these developing projects lag behind those in reference sites (Morzaria-Luna & Zedler 2007; Diggory & Parker 2011). Tidal wetland species germination is primarily a function of salinity, which must drop below a certain level for species to effectively establish (Janousek 2014, etc.). High soil salinities (Zedler et al. 2003; Janousek & Folger 2013) and seed loss (Huiskies et al. 1995; Diggory and Parker 2011) can preclude seed establishment (Zedler et al. 2003). In an upper intertidal marsh in Southern California, seed germination was influenced by the timing and intensity of rainfall events that lowered salinity, opening up a window of opportunity for species to establish (Noe and Zedler 2001). In brackish marshes in the north San Francisco Bay, seed dispersal was high in restoration sites, but many key halophytes were missing in the seed bank and seed rain, and much of the seeds initially dispersed into the restoration sites was lost due to tidal flushing (Diggory and Parker 2011). Further, the strongest predictor of species presence in the seed bank was its presence in the standing vegetation, which indicates that non-dominant species are likely to be under-represented in tidal wetland restoration project seed banks (Diggory and Parker 2011). In natural tidal wetlands in California, clonal growth is the most common means of reproduction, which drives the majority of re-vegetation following disturbance in natural wetlands (Allison 1996). In the early stages of tidal wetland restoration, the initial establishment of vegetation patches on mudflats is key for fostering the subsequent clonal growth that vegetates the site. In this study, I explore how seed dispersal is influenced by biotic and abiotic system components across 3 developing tidal wetland restoration projects of different ages and 2 reference sites.

The establishment of vegetation at a tidal wetland restoration site drives the restoration process by initiating a series of interactions between abiotic geomorphic conditions and vegetation. Vegetation influences elevation and channel stability by raising surface elevation through the below-ground production of organic matter and the trapping of mineral sediment by slowing tidal flow, further reducing soil salinity, and allowing for greater production of biomass (Morris et al. 2002; Mudd et al. 2010; D'Alpaos et al. 2012; Kirwan & Mudd 2012). In natural

systems, these feedback cycles allow sites to keep pace with moderate rates of sea level rise (SLR) (Da Lio et al. 2013; Morris et al. 2002). In restoration projects, the rapid development of vegetation will help buffer sites against drowning due to accelerated rates of SLR (Goals Project 2015). Since passive dispersal is key to the speed and nature of restoration project development, an improved understanding of the process will aid managers tasked with sustaining restoration projects in the context of SLR. While overall seed density may be high in brackish systems with higher biomass production (Diggory and Parker 2011), more saline areas may have low rates of seed production and dispersal (Morzaria-Luna and Zedler 2007), making the retention of seeds even more important for producing desired outcomes.

Seed loss due to tidal flushing occurs when seeds are suspended by rising waters and subsequently exported from the vegetated marsh plain, and is a common occurrence in tidal systems (Huiskies et al. 1995, Rand 200, Diggory and Parker 2011). Tide can also create flow-divergence patterns when it interacts with vegetation or geomorphic features like channel edges that slow water flow locally, but increases flow in adjacent areas, intensifying sediment scour (Bouma et al. 2007; Temmerman et al. 2012; Vandenbruwaene et al. 2013). Because seeds in wetland restoration projects are largely transported via hydrochory, flow divergence may also play a role in determining dispersal patterns. In actively planted restoration sites, increasing vegetation clump size in areas can reduce the rates of flow-induced erosion, increasing biomass of planted individuals and improving restoration outcomes (Silliman et al. 2015). Vegetated areas can in-turn trap more seeds (Gurnell et al. 2004) and influence geomorphology by modulating flow, producing belowground organic matter and trapping sediments (Morris et al. 2002; Corenblit et al. 2009; D'Alpaos 2011; Da Lio et al. 2013; Thorne et al. 2014). In vegetated areas, positive feedbacks can increase the rate of biomass development, while in bare areas, negative feedbacks related to flow and elevation can maintain an un-vegetated state (Gurnell et al. 2004). While experiments have confirmed the importance of these interactions in actively planted tidal wetland areas (O'Brien & Zedler 2006; Silliman et al. 2015), it is not clear how vegetation, geomorphology and seed dispersal interact in passively restored systems.

To explore the interactions between seed dispersal, biotic and abiotic factors in tidal wetland restoration, we explore how geomorphology and vegetation influence seed distributions and soil salinity at three restoration and two reference sites in California's San Francisco (SF) Bay, where approximately 30,000 acres of tidal wetland are slated for restoration over the

coming decades (Goals Project 2015). The sites are located on former salt evaporation ponds. Salinity levels in the South Bay are elevated due to their distance from North Bay delta freshwater flows and low levels of freshwater input from local watersheds. Since local plant communities are highly constrained by salinity, we expect that overall seed densities will be lower than densities in North Bay brackish communities (Diggory and Parker 2011). We predict that 1) reference sites have higher seed densities than restoration sites, 2) vegetation patterns at restoration sites are determined by geomorphic factors, and 3) seed rain and seed bank density for wetland species are related to abiotic factors and vegetation.

Methods

Field Study

The study was conducted at Eden Landing Ecological Reserve in Hayward, CA (Figure 1), which is part of the larger South Bay Salt Pond Restoration Project (SBSRP), a 50 year, adaptively managed project to restore over 15,000 acres of former industrial salt pond built on historic wetlands to a mosaic of tidal habitats (Trulio et al. 2007). To restore tidal habitat, managers manipulate the geomorphology of former salt ponds and return tidal flow thus allowing for the arrival of tidal sediment (Brew & Williams 2010) and seed (Diggory & Parker 2011) to drive ecosystem development. We examined 3 restoration sites breached to allow tidal influence: North Creek Marsh (NCM; breached in 2006), Mount Eden Creek (MEC; breached in 2009) and E9 (breached in 2012) (Figure 2). For comparative purposes, we also studied two established marshes in the same area which are both 100+ years old (Callaway et al. 2012), Old Alameda Creek (OAC) and Whale's Tail (WT). Lastly, we sampled a third reference marsh in a less saline area adjacent to the outflow of Old Alameda Creek. We did not include this data in our main analysis, for reasons detailed below. At each site, we established a grid consisting of 3 rows of 5 plots spaced 30 m apart ($n=15$ plots/site) (Figure 2). We used this approach for two reasons: first, to explore the influence of channel morphology on dynamics (Hopkins & Parker 1984; Sanderson et al. 2000) and second, to maximize the ability to compare between the differently sized marshes in the study area. We randomly selected the first point of the grid, then situated the first row on the edge of the major channel. In September of 2013, we assessed vegetative cover in 2x3-m plots parallel to the major channel. We used the Daubenmire method of determining percent cover for each species (Daubenmire 1968). We re-sampled vegetation in

the fall of 2014 and found no detectable change, so 2013 values were used for analysis. This lack of change in vegetation communities is likely due to elevated salinity levels during California’s historic drought (Chapple and Dronova, 2017). In March of 2016, we sampled the soil at each plot to determine soil salinity in practical salinity units (PSU) at A & L Soil Laboratory in Modesto, CA. At each point, we sampled elevation and GPS position using a Leica Real-Time Kinematic (RTK) system with ± 2 cm vertical accuracy (Callaway et al. 2013).

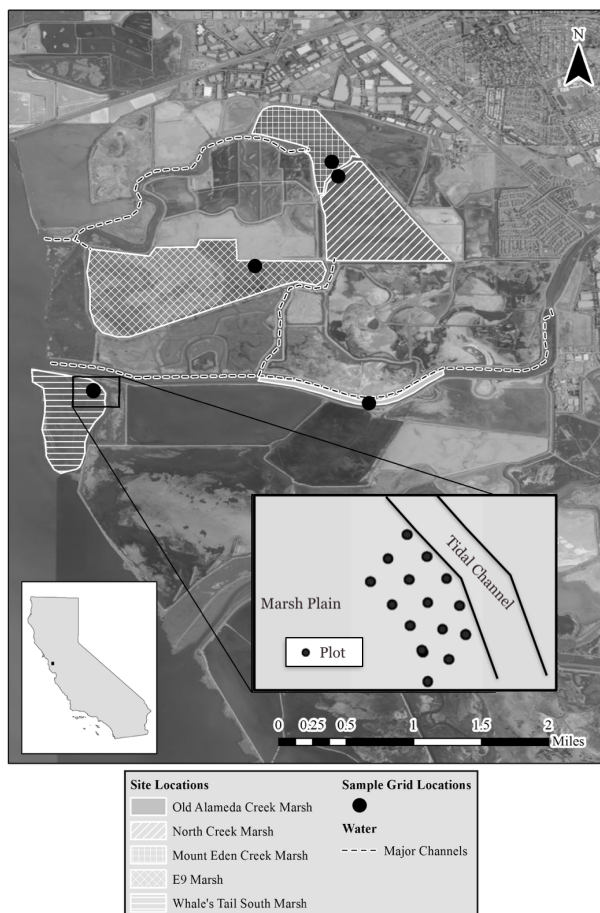


Figure 2: Restoration and Reference Sites at Eden Landing Ecological Reserve, Hayward, CA. Study sites are shown on the aerial image of the study area with the site for each sampling plot noted by a black circle. The inset map shows the layout of the sampling plots at each study site, with each plot separated by 30m.

We examined seed dynamics using two methods of seed sampling at each plot. To measure the number and type of seeds in the soil, we homogenized three circular soil cores 5 cm deep and 6 cm wide (hereafter referred to as “seed bank”). By sampling before seed production in the early fall, we were able to determine the number of seeds retained in each plot from the

previous growing seasons before fall/winter seed production. To measure temporally specific “seed rain” over the winter dispersal window, we attached a 25x25-cm seed collection mat (hereafter referred to as “seed rain”) consisting of two layers of burlap on top of an impermeable layer of landscape fabric at each plot (Diggory & Parker 2011) from mid-September to late January in 2013-2014 and 2014-2015. This window captures the majority of tidal wetland species seed dispersal in California tidal salt marshes (Morzaria-Luna & Zedler 2007). We cleared and maintained a 50cm buffer around each mat to prevent non-tidal seed deposition (Diggory & Parker 2011).

Seed density greenhouse trials

We determined species identities in seed rain and seed bank samples using the seedling emergence method (Gross 1990), which is effective for detecting seeds of halophytes and freshwater-dependent species (Diggory & Parker 2011). This method looks at the viable seeds only, which suits our research questions since restoration efforts are focused on establishing habitat from seed. We cold stratified all samples at 4° C for two months (Diggory & Parker 2011) and spread seed rain and seed bank samples across a mix of potting soil in 30x30cm pots in the Oxford Greenhouses on the UC Berkeley Campus. All samples were watered daily using freshwater, which is appropriate for halophyte species (Diggory & Parker 2011). All samples were grown for a minimum of three months in greenhouse conditions, and seedlings were removed and identified as they emerged. Each sample was left for three weeks after the final seedling removal to ensure that all seeds germinated. Empty trays were placed in the germination area to identify any greenhouse weeds, and greenhouse staff were consulted to determine which species were the result of greenhouse contamination. Seeds detected through these methods were removed from the data prior to analysis.

Data Analysis

To explore the interaction between vegetation, geomorphology and seed distributions across sites, we ran a series of mixed effects models. We employed mixed effects models to prevent pseudo-replication by accounting for variance separately for each set of random effects and ran separate models for restoration and reference sites (Bolker et al., 2009). To explore the factors influencing vegetation cover across sites, we included log-transformed percent vegetation

cover as the response variable, log-transformed distance from major channel, site age and relative elevation as fixed independent effects and site and plot as random independent effects. Since salinity data was collected at a single time point after the other data, we ran a separate model with salinity as the response variable and log-transformed percent vegetation cover, log-transformed distance from major channel, site age and relative elevation as fixed independent effects and site and plot as random independent effects. To analyze seed counts from soil cores and collection mats, we used generalized linear mixed effects models with a Poisson distribution and a log-link function. Poisson models are commonly used for count data and are less sensitive to data that is not normally distributed (Bolker et al. 2009). The generalized linear mixed model approach incorporates random effects (e.g. study site) into the model structure, preventing pseudo-replication by accounting for the variance of each set of random effects separately. We corrected overdispersion in our models by including plot as a random effect (Elston et al. 2001). For seed bank and seed rain, we divided the data into wetland seeds (halophytic species found in California tidal wetlands), and upland species (species unable to survive in saline conditions) and ran models for only tidal wetland species since these are the species that drive the restoration process. To compare seed densities between individual sites, we used a Steel-Dwass non-parametric test in JMP 12 to account for the non-normal distribution of seed density data, comparing both wetland and upland species. To test the difference between seed densities at restoration and reference sites, we used a generalized linear mixed effects model with a Poisson log-link function with site and plot as random effects and class (restoration and reference) as a fixed effect. For all mixed-effects models, we used likelihood ratio testing to determine significance levels for each independent variable (Bolker et al. 2009). In this testing approach, a full model was constructed including all independent variables, then each independent variable was removed and the resulting reduced models are compared to the full model. All generalized linear mixed models and generalized linear models were performed in R using the lme4 package (Bates et al. 2016).

Results

This study reveals distinct patterns in how seeds are distributed across wetland sites of a variety of ages. At restoration sites, vegetation density is driven by physical characteristics at the site (channel proximity and elevation), seed densities are related to vegetation density and soil

salinity is related to channel proximity and vegetation density. Trends are stronger overall in restoration sites, indicating that bio-physical interactions and feedbacks are more important in determining ecosystem structure in early stages of site development. For both seeds and vegetation, density is related to age across the three restoration sites, indicating that directional change occurs in the early stages of site development.

Bio-physical interactions

Across restoration sites, vegetation density was positively related to age ($p=0.001$, $SE=3.072$, $t=3.602$, $df=1$) and relative elevation ($p=0.040$, $SE=3.072$, $t=2.13$, $df=1$), and negatively related to distance from major channel ($p=0.003$, $SE=.009$, $t=-3.127$, $df=1$) (Figure 2). The reference sites both support nearly 100 percent vegetation cover, and cover was negatively related to distance from channel ($p=0.027$, $SE=0.001$, $t=-2.819$, $df=1$) but was not related to relative elevation ($p=0.712$, $SE=0.027$, $t=0.354$, $df=1$) (Figure 3). Species diversity at reference sites was related to relative elevation ($p=0.004$, $SE=0.469$, $t=2.977$, $df=1$) but not distance from channel ($p=0.656$, $SE=0.027$, $t=-0.407$, $df=1$). Diversity was not assessed at restoration sites because we only detected non-*Salicornia* species in one plot out of 45 total.

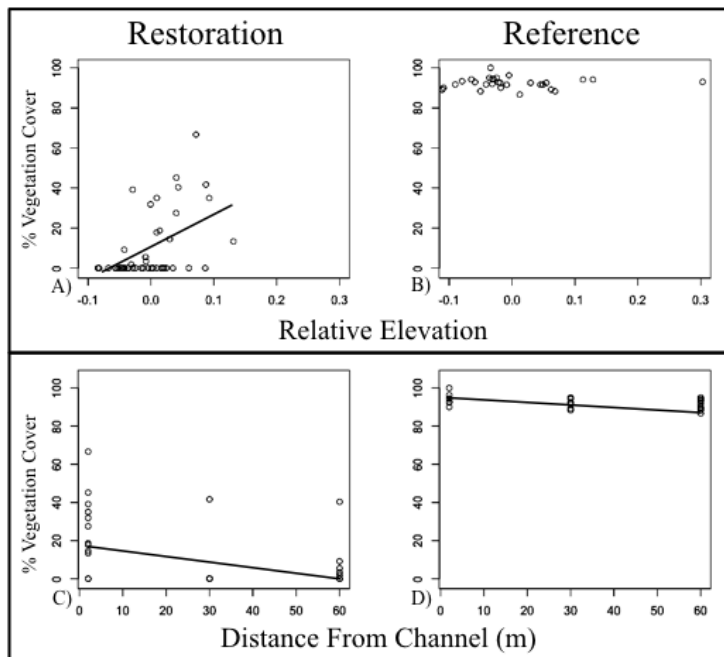


Figure 3: Vegetation density over elevation and distance from channel. A) Vegetation cover over elevation relative to the mean at each restoration site **B)** Vegetation cover over elevation relative to the mean at each reference site **C)** Vegetation cover over distance from major channel at restoration sites **D)** Vegetation cover over distance from major channel at reference sites.

Lines for significant relationships are fit from univariate models, significance levels determined by linear mixed models (see text).

At restoration sites, seeds were preferentially retained in vegetated areas and largely absent from bare areas. In the seed bank, wetland seed density was positively related to vegetation cover ($p=0.018$, $SE=0.408$, $z=2.368$, $df=1$) (Figure 3), but not relative elevation ($p=0.317$, $z=0.999$, $df=1$) channel proximity ($p=0.8347$, $z=-0.209$, $df=1$) or age ($p=0.733$, $z=0.341$). In contrast, seed rain was significantly related to vegetation cover ($p=0.011$, $z=2.536$) (Figure 3), relative elevation ($p=0.001$, $z=3.176$) and age ($p=0.001$, $z=3.278$) but not distance from channel ($p=0.074$, $z=1.789$) (Figure 4). At restoration sites, soil salinity was significantly related to distance from channel ($p=0.001$, $SE=0.012$, $t=3.552$, $df=1$) and vegetation cover ($p=0.040$, $SE=0.016$, $t=-1.957$, $df=1$) but not relative elevation ($p=0.798$, $SE=0.345$, $t=-0.261$, $df=1$).

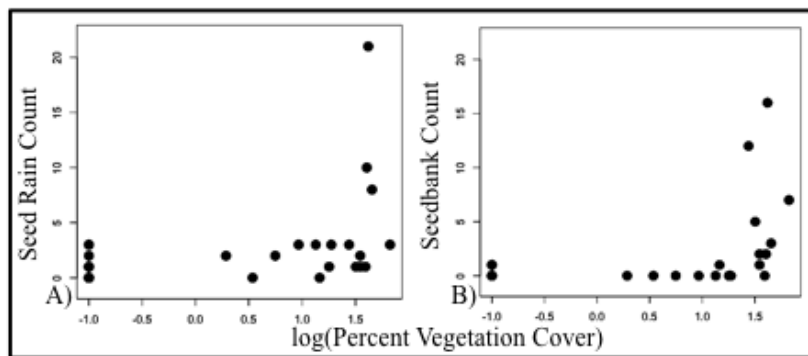


Figure 4: Seed density over log transformed percent vegetative cover at restoration sites. A) Total wetland seed rain collected on burlap mats during winter 2013-14 and 2014-15 **B)** Total wetland seed bank collected in September 2013. P values generated using Poisson generalized linear mixed models.

At reference sites, soil salinity was related to relative elevation ($p=0.020$, $SE=0.703$, $t=-2.285$, $df=1$) but not vegetation cover ($p=0.166$, $SE=4.966$, $t=-1.306$, $df=1$) or distance from channel ($p=0.230$, $SE=0.043$, $t=1.127$, $df=1$). Soil salinity was significantly lower in reference sites compared to restoration sites ($p=0.000$, $SE=0.055$, $t=5.26$, $df=1$). For reference sites, seed rain density was significantly related to vegetation cover ($p=0.047$, $SE=28.581$, $z=2.035$, $df=1$) but not distance to channel ($p=0.549$, $SE=0.243$, $z=0.599$, $df=1$). Seed bank density was not related to vegetation cover ($p=0.104$, $SE=20.301$, $z=1.699$, $df=1$) or distance to channel ($p=0.269$, $SE=0.165$, $z=1.105$, $df=1$).

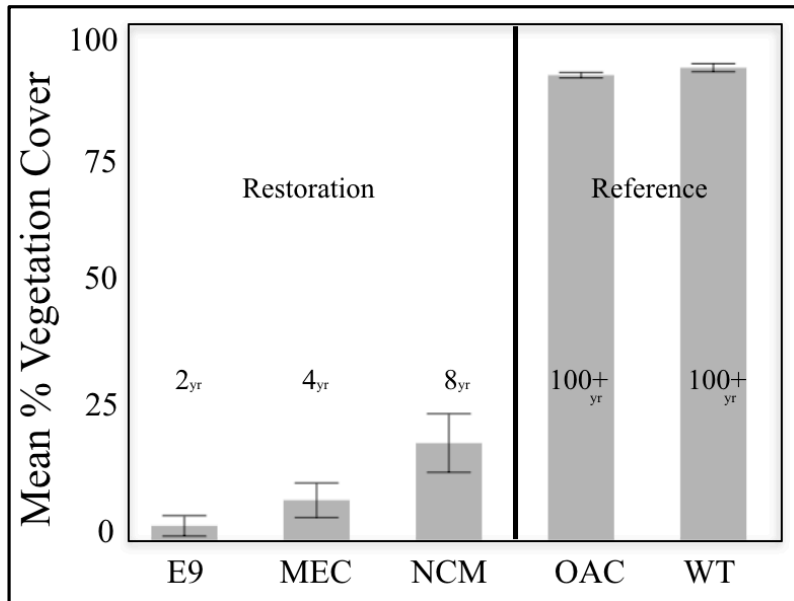


Figure 5: Percent vegetation cover across sites. Percent vegetation cover for restoration sites in order of age: E9, Mount Eden Creek (MEC), North Creek Marsh (NCM). Reference sites: Whale’s Tail (WT), Old Alameda Creek (OAC).

Vegetation Cover and Seed Density Over Site Age

Vegetation cover ($p=0.001$, $SE=0.411$, $t=-5.129$), seed rain ($p=0.048$, $SE=0.711$, $z=-1.974$) and seed bank ($p=0.000$, $SE=0.524$, $z=-4.674$) were all greater in reference sites compared to restoration sites (Figure 5, Table 1). For restoration sites, vegetation, seed rain and seed bank increased significantly with the age of the site (vegetation: $p=0.008$, $SE=0.077$, $t=2.796$; seed rain: $p=0.000$, $SE=0.069$, $z=6.656$; seed bank: $p=0.000$, $SE=0.070$, $z=3.757$) (Table 1). The oldest restoration site (NCM) had significantly more seeds in the seed bank than the younger two sites (E9 and MEC), statistically similar seed bank density to one reference site (WT) and significantly fewer seeds than the other reference site (OAC) (Table 2a). For seed rain, NCM had significantly more seeds than the two younger reference sites, and statistically equivalent numbers of seeds compared to the two reference sites, which also had significantly more seeds than E9 and MEC (Table 2b). There were no statistically significant differences between upland species density across all sites. At the restoration sites, *Salicornia* accounted for 98.9% of total vegetative cover and *Frankenia salina* accounted for 1.1%. In the restoration sites, *Frankenia* was only found at NCM. In the reference sites, *Salicornia* accounted for 91.6% of total cover,

with *Frankenia salina* (6.6%), *Grindelia stricta* (1.0%), and *Jaumea carnosa* (<1%) accounting for the remainder.

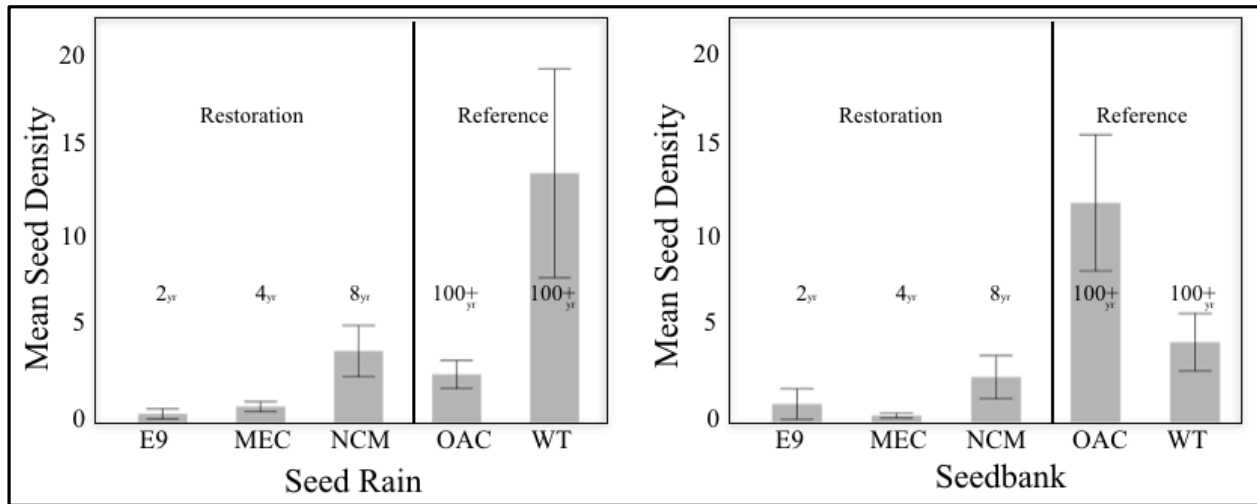


Figure 6: Seed bank and seed rain across restoration and reference sites.

At the restoration sites, *Salicornia pacifica* accounted for 57% of the total seeds in the seed rain and 70% of the wetland seeds with *Salicornia europea* (25%), *Distichlis spicata* (1%), *Scirpus americanus* (1%), and *Typha spp.* (3%) accounting for the remainder of wetland species seeds. In the seed bank, *Salicornia pacifica* accounted for 17% of the total seeds and 82% of the wetland species seeds with *Frankenia salina* (9%), *Salicornia europea* (7%) and *Attriplex triangularis* (2%) making up with remainder. In the seed rain at the reference sites, *Salicornia pacifica* accounted for 67% of the total seeds and 81% of the wetland species with *Frankenia salina* (17%), *Limonium californica* (<1%), *Scirpus americanus* (<1%), and *Distichlis spicata* (<1%) accounting for the remainder. In the seed bank, *Salicornia pacifica* accounted for 51% of the total seeds and 86% of the wetland species seeds with *Frankenia salina* (6%), *Scirpus americanus* (5%) and *Grindelia stricta*, *Jaumea carnosa*, *Salicornia europea* and *Attriplex triangularis* (all <1%) accounting for the remainder. Notably, seeds from upland species unable to establish in salt marshes accounted for 83% of seeds in the restoration sites and 49% of the seeds in the reference sites.

Discussion

These results indicate that a series of bio-physical interactions influence the spatial pattern of seed dispersal. At the restoration sites, vegetation patterns are determined by relative

elevation, channel proximity and age of restoration site. These vegetation patterns significantly influence where the seed bank of wetland species is concentrated, with significantly higher densities found in plots with higher vegetation cover. Seed rain density was related to vegetation as well, but also to relative elevation and site age. The density of seeds in the seed bank was significantly lower for restoration sites compared to reference sites, a trend that is supported by all site-to-site comparisons except the comparison between the oldest restoration site (NCM) and the Whale's Tail reference site. In seasonal seed rain over the winters of 2013-2014 and 2014-2015, reference sites had more seeds than the two youngest restoration sites, (except for OAC and MEC, but the difference is marginally significant). However, the oldest restoration site (NCM) contained more seeds than the two younger restoration sites, and was statistically equivalent to the reference sites. Interactions between vegetation and abiotic factors are not as strong at the reference sites, where physical conditions are more homogenous and vegetation cover is significantly higher. Vegetation cover and seed density significantly increased with age at restoration sites, which indicates that most seeds are likely produced by vegetation at the site rather than arriving from adjacent reference sites. This is supported by the fact that seed rain density at the oldest restoration site was greater than seed rain at one of the reference sites (OAC) (Table 1) and that upland seeds unable to establish in saline areas comprised the majority of the seed bank at both sites. The patterning of seed dispersal in these restoration projects indicates that vegetation development will be heterogeneous depending on bio-physical interactions.

Two mechanisms likely explain the aggregation of wetland species seed banks around vegetated areas. The first is local seed production. Tidal wetland species seeds are likely to disperse close to their parent plant (Leck & Simpson 1994; Rand 2000), and dispersal from surrounding wetlands in similar wetlands in Southern California was low (Morzaria-Luna & Zedler 2007). At the restoration sites, areas with higher vegetative cover also had lower salinity, which likely increased seed production (Janousek & Mayo 2013). At the reference sites, seed rain was positively related to vegetation density, further supporting the presence of this mechanism. The lack of sub-dominant species in the restoration sites indicates that dispersal may not reach from source populations to adjacent sites. This highlights the importance of local production for more rare species that may not arrive passively on the tide (Diggory and Parker 2011).

The second mechanism is likely related to flow modulation by existing vegetation (Bouma et al., 2007). Density in seasonal seed collection mats was significantly related to vegetation density, but also age and relative elevation. Seed rain was spread over a wide range of vegetation densities, and a small number of seeds were found in bare areas. In contrast, seed bank was only related to vegetation density, only one seed was found in bare areas in the seed bank sampled, and seed densities greater than one were only found only in areas with more than 30 percent vegetation cover. This indicates that seeds are spread more widely across the marsh surface during the peak of seasonal dispersal, but only retained over time in highly vegetated areas. Previous work has found that more frequently inundated areas contained fewer seeds (Neff et al. 2009) and that export via tidal flow may limit the amount of seeds retained in tidal areas (Huiskes et al. 1995; Diggory and Parker 2011). Interactions between vegetation and flow processes can increase the aboveground trapping of sediments in vegetated areas and can accelerate flow in bare areas, leading to lower rates of sediment deposition (Bouma et al. 2007; Morris et al. 2002; Temmerman et al. 2012). Our results indicate that similar processes may be influencing seed retention, with vegetation slowing flow and allowing for propagule retention (Gurnell et al. 2004).

At the restoration sites, both vegetation cover and channel proximity were significantly associated with reduced soil salinity. Since lower salinity conditions increase the likelihood of seed germination (Janousek et al. 2014), vegetated areas and areas closer to the channel are likely to be key “safe sites” that allow for the germination of wetland species. Sub-dominant species were present in low densities at the reference sites and in very low densities in soil cores at the oldest restoration site (NCM), where vegetation patches were present but only comprised 1.1% of measured cover. Sub-dominant seeds were only found in areas with *Salicornia* cover of greater than 25%, indicating that denser clumps of *Salicornia* could be aiding retention of subdominant species at restoration sites. Since *Salicornia* is shown to inhibit the growth of sub-dominant species through competition (Armitage et al. 2006), arriving seeds may be unlikely to gain competitive advantage, but lowered salinity in existing patches may allow for initial germination. Notably, our study took place during historic drought conditions, which increased salinity levels in the bay and likely limited primary productivity (Zedler 1983) for all species, but especially for less salt tolerant sub-dominant species (Chapple et al. 2017). During this period, salinity in the Bay significantly increased over time, the mean annual rate of change at the oldest

restoration site was over ten times slower than during the previous period and the importance of channels for vegetation presence increased compared to the previous period at the oldest restoration site (NCM) (Chapple and Dronova 2017). Longer term data collection would be beneficial to capture the sensitivity of these findings to salinity variability.

In a recent study, greater density of transplanted tidal marsh plants reduced erosion, slowed flow and increased oxygen levels in experimentally manipulated restoration treatments, leading to positive feedbacks that increased biomass production (Silliman et al. 2015). Across our sites, we observed that greater vegetation density in passively restored areas was associated with lower soil salinity and seed retention. Harnessing these positive feedbacks to speed the development of restoration sites could help insure that newly established sites are resilient to the impact of sea level rise. In passively restoring areas, the creation of elevated “safe site” mounds in areas away from channels could encourage the development of vegetation by ameliorating salinity to allow for germination and biomass production (O’Brien & Zedler 2006). The addition of mineral sediment has been the primary means of raising marsh surface elevation (Orr et al. 2003), and experimental restoration areas have recently been created in the SF Bay to explore the impacts of increasing geomorphic heterogeneity. Future restoration experiments should also investigate the addition of organic matter as an alternative tool for increasing geomorphic heterogeneity and potentially sequestering carbon (Mcleod et al. 2011). Since our results indicate that sub-dominant species dispersal from source populations to other sites may be rare, future studies should also compare passive restoration, seed addition and seedling transplants across a range of geomorphic settings to assess cost benefit ratios of different restoration approaches. Increasing the rate of vegetation establishment under current sea level conditions is thought to be the best strategy for increasing the resilience of tidal wetland restoration projects to rising sea levels (Goals Update 2015). Manipulating the bio-physical interactions that govern seed dispersal and vegetation development has the potential accelerate the process of recruitment, thus initiating the feedbacks that maintain tidal wetland elevations, allowing these developing ecosystems to keep pace with rising tides (Kirwan and Megonigal 2013; Morris et al. 2002).

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Tables:

Table 1: Bio-physical attributes and seed densities across reference and restoration sites.

The average value for site characteristics and the seed count data including the standard deviation across each sampling plot for each site is listed; with the average for the two references sites “Reference” and the average from the three restoration sites “Restoration.”

| Site | Mean Elevation (m) ± SD | % Vegetation Cover ± SD | Mean wetland seed rain count ± SD | Mean wetland seed bank count ± SD |
|--------------------|-------------------------|-------------------------|-----------------------------------|-----------------------------------|
| Reference | 2.018 ± 0.085 | 92.367 ± 2.714 | 8.379 ± 16.868 | 7.62 ± 10.540 |
| WT | 2.033 ± 0.094 | 93.077 ± 3.144 | 13.733 ± 22.308 | 4.133 ± 5.768 |
| OAC | 2.002 ± 0.074 | 91.607 ± 2.053 | 2.64 ± 2.898 | 11.357 ± 13.206 |
| Restoration | 1.582 ± 0.079 | 9.922 ± 16.756 | 1.756 ± 3.556 | 1.2 ± 3.138 |
| E9 | 1.643 ± 0.039 | 2.8 ± 7.787 | 0.467 ± 1.060 | 0.933 ± 3.081 |
| MEC | 1.498 ± 0.062 | 7.856 ± 13.159 | 0.867 ± 1.060 | 0.333 ± 0.488 |
| NCM | 1.605 ± 0.044 | 19.110 ± 22.344 | 3.933 ± 5.457 | 2.333 ± 4.353 |

Table 2a: Seed bank comparisons. Restoration sites: North Creek Marsh (NCM, initiated 2006), Mount Eden Creek (MEC, initiated 2009), E9 (initiated 2012); Reference sites: Old Alameda Creek (OAC), Whale’s Tail (WT). Reference sites are underlined, significant differences are marked with a *.

| Sites | | Z | p |
|-------------|-------------|--------|---------|
| <u>OACS</u> | MEC | 4.572 | <0.001* |
| <u>OACS</u> | E9 | 4.286 | <0.001* |
| <u>WT</u> | MEC | 3.800 | 0.001* |
| <u>WT</u> | E9 | 3.717 | 0.002* |
| <u>OACS</u> | NCM | 2.982 | 0.024* |
| <u>WT</u> | NCM | 1.828 | 0.357 |
| NCM | E9 | 1.330 | 0.672 |
| NCM | MEC | 1.059 | 0.827 |
| MEC | E9 | 0.646 | 0.967 |
| <u>WT</u> | <u>OACS</u> | -2.209 | 0.176 |

Table 2b: Wetland seed rain comparisons

| Sites | | Z | p |
|-------------|-----|-------|---------|
| NCM | E9 | 3.403 | <0.001* |
| <u>WT</u> | E9 | 3.054 | 0.002* |
| <u>OACS</u> | E9 | 2.931 | 0.003* |
| NCM | MEC | 2.223 | 0.026* |

| | | | |
|-------------|-------------|--------|--------|
| <u>WT</u> | MEC | 2.113 | 0.035* |
| <u>OACS</u> | MEC | 1.867 | 0.062 |
| MEC | E9 | 1.390 | 0.164 |
| <u>WT</u> | <u>OACS</u> | 0.817 | 0.413 |
| <u>WT</u> | NCM | 0.508 | 0.611 |
| <u>OACS</u> | NCM | -0.044 | 0.965 |

Table 2c: Seed bank Upland.

| Sites | | Z | p |
|--------------|-------------|----------|----------|
| <u>WT</u> | MEC | 1.661 | 0.458 |
| NCM | MEC | 1.419 | 0.616 |
| <u>OACS</u> | MEC | 1.249 | 0.722 |
| <u>WT</u> | E9 | 0.878 | 0.905 |
| NCM | E9 | 0.650 | 0.967 |
| <u>WT</u> | <u>OACS</u> | 0.573 | 0.979 |
| <u>WT</u> | NCM | 0.251 | 0.999 |
| <u>OACS</u> | E9 | 0.243 | 0.999 |
| <u>OACS</u> | NCM | -0.377 | 0.996 |
| MEC | E9 | -0.675 | 0.962 |

Dissertation Conclusion

This dissertation demonstrates how ecological filters related to climate, physical conditions, and seed dispersal influence tidal wetland restoration in the SF Bay. Chapter one utilizes vegetation data from the field collected most years between 1990 and 2005 at a restoration site (established in 1975) and a reference site in Marin County, CA to determine how physical and climatic abiotic filters interact to structure plant community trajectories. The results demonstrate that salinity, the most relevant proxy for climate in SF Bay tidal wetlands, influences plant community dynamics at both the restoration and reference sites. At the restoration site, a low salinity period resulting from a series of years that include two major El Nino events notably increases the overall rate of community change away from the initial community and appears to initiate a positive directional trend in the abundance of sub-dominant species characteristic of reference sites. At the reference site, the plant community is variable over time and both community identity and sub-dominant species abundance appear to track low salinity events in a stochastic rather than a directional manner. At both sites, plots containing tidal channels were hotspots for vegetation change. These results highlight the dynamic nature of reference sites and show the impact that climate variability can have on restoration outcomes.

Chapter two uses remote sensing of satellite imagery from 2009, 2011 and 2015 to further explore the influence of physical and climatic abiotic filters at North Creek Marsh, a restoration site in the South Bay Salt Pond Restoration Project (SBSRP) initiated in 2006. The findings show that the mean annual rate of change from mudflat to vegetation during California's historic drought (2012-2015) is more than ten times slower than change between 2009 and 2011, when Bay salinity was significantly lower than during the drought period. Channels were important predictors of vegetation presence in all years, but the magnitude of their effect increased by a factor of roughly two in the 2015 image, showing that channel edges can help buffer the effects of high salinity. These results further highlight the potential for non-linearity in restoration project outcomes related to climate dynamics. Taken together, the results from these two chapters show that climate variability must be taken into account when interpreting restoration project trajectories, and that creating more extensive channel structure may be one way to help buffer the negative effects of elevated salinity.

Chapter three explores seed dispersal patterns across multiple restoration and reference sites at Eden Landing Ecological Reserve, part of the SBSRP. The results demonstrate that tidal wetland seed densities are low and comprised almost entirely of the early colonizing species *Salicornia pacifica* across both reference and restoration sites, but that the most established restoration site has a statistically equivalent number of seeds compared to one of the reference sites. At the restoration sites, vegetation cover is related to both elevation and channel proximity, and seed densities are related to vegetation cover. These results highlight the fact that passive seed dispersal via tidal hydrochory may not be reaching the bare mudflats that managers are hoping to transition to vegetation. The lack of seed density and diversity may pose a problem for reaching vegetation goals, and active planting of marsh species should be pursued as a means of accelerating the restoration process. Further, manipulating elevation and channel structure are both potential means of accelerating restoration project development.

Taken together, these findings highlight some of the less-explored aspects of the tidal wetland restoration process in the San Francisco Bay. The salt-tolerant dominant species *Salicornia pacifica* was the most abundant species identified in all three chapters. *Salicornia* is an important pioneer species driving vegetation colonization of bare mudflats (Brand et al., 2012; Zedler et al., 2003), but also imposes strong priority effects on sub-dominant species' establishment and persistence (Armitage et al., 2006). The long-term data analyzed in chapter one demonstrates that *Salicornia*'s priority effects are contingent on factors related to climate (SF Bay salinity) and channel proximity at both reference and restoration sites. Both stochastic climate factors and abiotic physical factors influence community identity across both site types, but the directional change in sub-dominant abundance at the restoration site indicates that episodic periods of lowered salinity may be crucial for the development of sub-dominant species diversity in developing restoration sites.

Similar patterns emerge looking at the initial colonization of mudflats by *Salicornia* in chapter two. Elevated salinity levels due to California's historic drought were associated with slower rates of mean annual change in vegetation cover compared to a prior time period with lower salinity levels. Channels also became more important predictors on vegetation density in the post-drought 2015 image, further highlighting the interaction between the abiotic physical structure at a site and climate-determined salinity patterns. While previous experimental work has demonstrated the interaction between freshwater availability and physical properties in intact

reference sites (Callaway and Sabraw, 1994; Schile et al., 2011), the findings of chapters one and two demonstrate the influence of the interaction between abiotic and stochastic factors can influence longer-term vegetation change at both reference and restoration sites.

Chapter three demonstrates how seed dispersal interacts with vegetation patterning across a range of reference and restoration sites. Cover of *Salicornia* is significantly related to seed density at the three developing restoration sites. Rather than dispersing widely across the marsh surface, seeds are likely produced and retained in areas with high vegetation cover. Given the importance of abiotic and stochastic factors in determining vegetation patterns discussed in the first two chapters, it is likely that dispersal filters are closely linked to the ecological filters that determine vegetation patterning. This close relationship points to the likelihood of a series of interactive feedbacks, where initial seed establishment occurs during lower salinity years in low salinity zones adjacent to channels and higher elevation areas, these areas increase surface elevation and both produce and retain seeds (Kirwan and Megonigal 2013). This likely leads to hotspots of localized vegetation development that spread over time to fully vegetate the marsh plain. Rather than proceeding in a linear manner, fluctuations in salinity levels appear to influence where, when, and to what extent feedback cycles operate. Taken together, these results highlight the closely intertwined nature of the multiple filters that structure ecological communities, which underscores the need for improved understanding of how these filters interact over time to determine restoration outcomes.

This research highlights a few key directions for future research. While long-term transects similar to those studied in chapter one are exceedingly rare, other methods of understanding how site history determines restoration efforts could help improve contemporary management efforts. For example, historical context plays a critical role in guiding where habitats can be restored based on their past distribution, particularly in areas where extensive alterations have taken place (Jackson and Hobbs 2009; Beller et al. 2016). The field of historical ecology aggregates information from a variety of historical sources to produce spatially explicit data on the historical distribution of ecosystem types (Swetnam et al. 1999; Whipple et al. 2011). These data sources have vastly improved understanding of contemporary landscapes and been used to guide restoration project development, but they have not been integrated into statistical models to help predict restoration outcomes. While some experimental work has explored the influence of recent history (e.g., seeding or active planting) on site development (Grman et al.

2013; Matthews et al. 2009), the interaction of historical land-use with contemporary spatial and environmental factors is an important direction for restoration and conservation research (Brudvig 2011; Suding 2011). Integrating historical and contemporary data could help discern the relative influence of these factors in determining plant community composition and restoration trajectories to guide restoration practice. Across the SF Bay, there is a wealth of restoration projects of varying ages. Restoration interventions are rarely replicated over large areas (Dickens and Suding 2013; Zedler and Callaway 1999) or time periods (Vaughn and Young 2010; Moreno-Mateos et al. 2012), which makes the wide spatial distribution of ecologically similar but variably aged projects in the SF Bay fertile ground for exploring restoration trajectories (Boyer and Thornton, 2012). Moreover, while tidal wetland habitats harbor similar species and physical conditions across the SF Bay, the north and south Bay experience distinct rainfall patterns and levels of freshwater input (Dettinger and Cayan 2003; Callaway et al. 2007), which allows for investigation of how trajectories may differ based on regional climate. By surveying a range of these projects, taking data on plant community identity and abiotic variables, and integrating historical ecology data, variation partitioning methods could be used to understand how different abiotic and historical factors influence restoration.

Understanding how shifting climate regimes may alter system function and change restoration trajectories in the process is another key direction for managing ecosystems in the context of climate change (Suding et al. 2004). Incorporating climate change projections into restoration planning is a promising new to direction for creating habitats that are resilient to global change (Veloz et al. 2013; Zhang and Gorelick 2014). Tidal wetlands worldwide are major targets for restoration efforts due to their extensive history of destruction, high levels of biodiversity and numerous ecosystem services (Barbier et al. 2011). However, sea level rise (SLR) threatens to derail substantial investments in conservation and restoration efforts by drowning vegetation and converting existing and developing tidal wetlands to mudflats (Langley et al. 2013; Kirwan and Megonigal 2013; Mudd et al. 2009; Thorne et al. 2014; Callaway et al. 2007). Efforts to assess the sustainability of existing tidal habitat under SLR scenarios are underway (Schile et al. 2014; Swanson et al. 2014; Stralberg et al. 2011), yet there is still the need to directly explore the interactions between habitat evolution along a restoration trajectory and change due to SLR. Future research could adapt existing model frameworks to explore how

SLR projections interact with projected restoration trajectories to guide where and when to target restoration interventions.

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