Fragmentation Drives Dominant Plant Encroachment on a Horizontal Wastewater Treatment Levee

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Abstract

Urban coastal wetlands protect humans from sea-level rise while providing valuable habitat for wildlife. Degradation and loss of these wetlands threaten urban infrastructure including wastewater treatment facilities. Nature-based adaptive solutions, with the combined purposes of bioremediation, coastal defense, and habitat creation, are being tested to make communities safer and more resilient. The current research examines an experimental horizontal levee installed in 2015 at the Oro Loma Sanitary District in San Lorenzo, California, 5 years after installation. Using quadrat sampling, we compare succession of two plant assemblages – a wet meadow and a riparian scrub community – on an ecotone slope. We use the wet meadow assemblage to document the effects of fragmentation and dominant plant species on plant diversity and abundance. Although most planted species survived from 2015 to 2021, plant diversity decreased over time in both communities. Fragmentation was associated with encroachment by a native dominant willow (*Salix lasiolepis)* and an invasive nonnative jubatagrass (*Cortaderia jubata)* in the wet meadow. Both fragmentation and the presence of the willow or cattails (*Typha*) correlated with reduced native species diversity and cover. In the absence of natural disturbance processes, created wetlands, especially fragmented wetlands with substantial edge, may progress to a successional state dominated by a few species. Future projects might benefit from specifying habitat creation goals in addition to wastewater treatment goals, selecting native plant assemblages that inhibit succession, planting larger patches, and incorporating natural or human disturbance to break dominance cycles.

Introduction

California has lost about 80% of its historical wetlands to alteration, draining, or filling (Zedler 2004). Worldwide, 21% of wetlands have been lost since the 1700s (Fluet-Chouinard et al. 2023). Wetlands provide habitat for flora and fauna, protect coasts from sea-level rise and flooding, improve water quality, and serve as important ecosystems for carbon sequestration (Zedler & Kercher, 2005). In contrast, engineered protections from sea-level rise, such as sea walls, generally harm biodiversity (Duarte et al., 2013). Costanza et al. (2008) calculated that, as of 2008, coastal wetlands provided $23.3 billion (U.S.) per year in storm protection services alone, as well as crucial habitat for sensitive species.

Reestablishing lost wetland biodiversity through restoration can be difficult. Wetlands are particularly susceptible to the formation of vegetative monotypes, because they are landscape sinks (Zedler & Kercher, 2004), often occurring in low-lying areas that accumulate nutrients, propagules, sediments, and other debris from surrounding terrestrial and wetland disturbances. This landscape-level accrual of materials provides invasive and expansive species with the resources they need to form monotypes (Tickner et al., 2001; Stohlgren et al., 1998; Zedler & Kercher, 2004). Invasive and expansive plant species often benefit from increased nutrients, successionally dominating and displacing more sensitive natives (Canavan et al., 2018; Green & Galatowitsch, 2002; Zedler & Kercher, 2005). Zedler and Kercher's (2004) efficient use hypothesis proposes that invasive or expansive species use nutrients and light more efficiently than non-invasive species during succession. Houlahan and Findlay (2004) found that the non-

native species were no more likely to dominate than native species and that dominants of both had similar adverse effects on species richness; indicating that dominants are generally of concern for producing monotypes during succession, regardless of their geographic origins (Houlahan & Findlay, 2004).

Rising sea levels and storm surges due to climate change can lead to increased coastal flooding, especially with lack of natural coastal protection by functioning wetlands. These events can cause a breakdown in crucial services such as wastewater treatment. Coastal cities have historically placed wastewater treatment plants at low elevations near the coasts to reduce cost (Hummel et al., 2018). With the effects of climate change, wastewater treatment plants become more vulnerable to flooding, such that the number of people who would lose wastewater services could be more than five times as high as the number of people at risk of direct flooding due to sea-level rise (Hummel et al., 2018). Higher sea and storm surge levels can reduce the ability of wastewater pollution control plants to discharge sewer overflows and effluent, leading to increased flooding of sewers, streets, and basements (Major et al., 2011; Manuel, 2006).

As sea-level rise caused by climate change threatens urban infrastructure like wastewater treatment facilities (Hummel et al., 2018), ecological engineering and nature-based adaptive solutions are being tested to make urban communities safer and more resilient. The importance of this ecological resilience to extreme weather events is even further highlighted by the continued growth of coastal population centers (U.S. Census Bureau, 2021). Coastal communities are now installing created wetlands for wastewater bioremediation, coastal area defense, and ecological habitat creation (Aydın Temel et al., 2018; Grebenshchykova et al., 2019; Gruber et al., 2008; Markus-Michalczyk et al., 2019). Constructed wetlands are a type of nature-based solution being implemented for bioremediation, as an ecological engineering alternative to traditional wastewater treatment, and can support a wide range of plants and wildlife (De Martis et al., 2016; Zhang et al., 2020). The current research on the ability of created wetlands to retain floristic diversity shows mixed results (De Martis et al., 2016; Saggaï et al., 2017). Some mitigation wetlands have been shown to provide more plant species diversity, richness, and evenness than natural reference wetlands, as well as improved bird habitats (Balcombe et al., 2005; Heaven et al., 2003). However, these authors also identify more species of lower conservation quality, including non-native dominants and pioneer species in mitigation wetlands, indications of disturbed habitat (Balcombe et al. 2005; Heaven et al. 2003). Ongoing study of vegetation dynamics within constructed wetlands is critical for understanding how the unique dynamics of a specific wetland play a role in its ability to retain plant species diversity. The continued ecosystem function of wetlands, including as coastal protection, is especially important in light of sea-level rise and increasing extreme weather events (Costanza et al. 2008; Zedler & Kercher, 2005).

In 2015, the Oro Loma Sanitary District (OLSD) in San Lorenzo, California piloted a wastewater treatment approach, a horizontal levee that uses a low-grade slope (1:30, 1.9°) to allow native planting and protect adjacent land from storm surges. The Oro Loma Horizontal Levee (OLHL) is a multi-disciplinary prototype designed to evaluate how well a horizontal levee treats wastewater, buffers sea-level rise and

flooding, and mitigates wetland habitat loss amid urban density (Okamoto, 2015; Taylor-Burns et al. 2025). Cecchetti et al. (2020) confirmed the levee's ability to produce tertiary-treated effluent from secondary-treated wastewater. No previous researchers have studied successional change in plant assemblages in this created-wetland ecosystem.

The objective of this research was to understand better how wetland plant communities in constructed treatment wetlands may change compositionally over time through succession and resist invasion or expansion of dominant species, despite receiving continuous subsurface nutrient enrichment. We characterize the 2020/2021 composition and species diversity of plants in wet meadow and riparian scrub assemblages on the OLHL ecotone slope and document the changes in composition and diversity over the five years following installation. We specifically explore how successional change in species diversity and relative species abundances differed between these two plant assemblages, and how fragmentation, and the sources and presence of key dominant expansive species affected community succession.

Materials and Methods

The Oro Loma Horizontal Levee ("levee") is located at the Oro Loma Sanitary District (OLSD) treatment facility in in San Lorenzo, Alameda County, California (37.67°N by 122.16°W) on the San Francisco Bay (Fig. 1).

The SF Bay Area has a Mediterranean climate with mean temperatures ranging from 10.3°C to 21.9°C. Average annual rainfall at the site is between 0 and 7.1 cm, occurring mostly in the winter months (NOAA National Centers for Environmental Information, 2021). This site and the surrounding area were tidal marsh and tidal flat habitat (Josselyn, 1983; San Francisco Estuary Institute [SFEI], 1998) until 1911, when the original water treatment facility was built. In 2015 and 2016, working with UC Berkeley researchers, the OLSD added a pilot project to evaluate whether planting native vegetation to form an ecotone slope on a horizontal levee, watered by secondary-treated water through distribution pipes from the adjacent treatment wetland, could serve as nature-based solution to remove further pollutants from the wastewater, protect the facility from flooding, and create native wetland habitat (Fig. 2).

The horizontal levee was planted with a vegetated "ecotone slope", (~ 0.7 ha) divided into 12 vertical cells (12 m x 46 m), separated by 2-m-wide clay berms (Save the Bay, 2017). Dr. Peter Baye worked with staff from Save the Bay, a local nonprofit organization, to model three vegetation suites after local native plant assemblages: swale-depression (swale-depression grade), wet meadow, and riparian scrub (uniform grade) (Jason Warner, General Manager, OLSD, personal communication, December 18, 2019; Save the Bay, 2017). The suites comprised vigorous or "weedy" native species, predicted by organization staff to compete effectively with and prevent establishment of volunteer and non-native invasive species (Donna Ball, personal communication, December 13, 2019; Save the Bay, 2017; Table 1). In wet meadow cells, *Elymus triticoides*, a native rhizomatous grass that can become weedy or invasive in some habitats (Young-Mathews & Winslow, 2010), was planted in the largest proportion, while riparian scrub cells

featured *Salix lasiolepis*, a plant known for vigorous, fast growth, high productivity and efficient nutrient uptake (Kuzovkina & Quigley, 2005).

The three swale-depression cells were planted adjacent to one another with fine topsoil. Three of six wet meadow cells were planted adjacent to one another in fine topsoil, while the other three were planted in coarse topsoil and interspersed with the three riparian scrub cells. The goals of the alternating plantings were to make the site bird-friendly by providing landscape-level vegetative structure (Jason Warner, General Manager, OLSD, personal communication, June 3, 2021). Each cell consisted of 15 horizontal planting grids (12 m x 3 m), repeated down the slope. Save the Bay staff members and volunteers collected, propagated, and planted all vegetation on the ecotone slope during November and December 2015 and January 2016 (Save the Bay, 2017). In 2017, staff members then planted the basin of the adjoining treatment wetland with cattail (*Typha* spp.) and bulrush bulbs (*Schoenoplectus* spp.) to enhance habitat value of the wetland (Fig. 1). Cattail was not planted on the ecotone slope, but the species reportedly encroached onto the slope after the plantings in the treatment wetland. By 2017, the entire site was also invaded by exotic jubatagrass (*Cortaderia jubata*) (Save the Bay, 2017).

Study Design

To contrast successional changes since installation for the wet meadow (WM) versus riparian scrub (R) assemblages on the ecotone slope, we first compare the initial percentage of each species planted in 2015/2016 with its relative percent cover in the field in 2020/2021 using proportions compiled across all 840 wet meadow and 380 riparian scrub quadrat samples (WM = 312 m^2; R = 141 m^2) Fig. 3). We assess potential effects of fragmentation on succession and invasion in the wet meadow assemblage by contrasting changes in percent cover across the 420 quadrats from the three contiguous (“buffered” or “BWM”) wet meadow cells with the 420 quadrats from the three wet meadow cells that are interspersed with riparian scrub (“fragmented” or “FWM”). We then evaluate how the mean per-quadrat diversity of planted wet meadow species changed through time in each of the four cell types.

We describe likely sources of encroaching plant propagules in each assemblage and cell type with a focus on occurrences of a key invasive exotic species, *Cortaderia jubata*, and dominant encroaching species.

Finally, we examine how presence of key dominant or invasive plant species, either individually or cumulatively, affects community diversity and individual percent cover of planted and volunteer species at the single quadrat level.

Data Collection and Sampling

In most cells, JF placed 10 stratified-random 0.3 m x 0.3 m PVC quadrats along each of fourteen 12-m transects distributed across eight of the horizontal planting grids for a total of 140 quadrats per cell (Fig. 4). In general, JF set two transects in six of the grids, but only one transect in the remaining two. In

riparian cell 12, we skipped the transects in the top two grids, as they were impenetrable with dense vegetation, yielding 120 quadrats.

JF positioned each quadrat using a vertical tape measure from the top edge of the cell and a horizontal transect tape measure from the nearest clay dividing berm. To measure percent cover accurately, JF marked each side of the quadrat with ten lines to denote 100 subdivisions. The quadrat was placed above the plants to be measured and below the horizontal transect tape. As needed, JF estimated the percent cover of *S. lasiolepis* canopy above the quadrat using a spherical densiometer (Forestry Suppliers Concave Model-A). Due to multiple canopy layers and bare ground, total percent cover for a quadrat could exceed or be less than 100%. Field data was collected during the fall and summer, as this was the best phenological period for plant identification, and plants were identified using planting lists, iNaturalist, and the Jepson Manual (Baldwin et al., 2012). To generate 2015/16 data values, quadrats were virtually sampled from the original planting plans using Python (version 3).

Data Analysis

To assess overall successional change, we first averaged the percent cover of each species over all quadrats when planted and in 2020/2021 for each of the cell types overall; WM, R, BWM, and FWM with a Texas Instrument-83 (TI-83) calculator. We also used a TI-83 calculator to calculate one-proportion *z*-tests to estimate the likelihood that the proportions of each species in a cell-type differed statistically between the two dates.

We also calculated Simpson's Reciprocal Diversity Index (*RDI*) in Microsoft Excel (version 16), using species richness and percent cover of each plant species (Tomascik & Sander, 1985; Onaindia et al., 2004; Oswalt et al., 2007), for the subset of quadrats in which any planted species survived to the 2020/2021 season, as the metric generates a null outcome for zero values.

To assess changes in all planted species' *RDI* since installation, we used paired *t*-tests (SPSS version 27)

Because the data could not be normalized, we used a Mann-Whitney *U* test in SPSS to compare the change in the *RDI*'s in the buffered and fragmented WM among three different plant community subsets: a) planted wet meadow species; b) any ecotone-slope-planted species (wet meadow, riparian scrub, or swale depression); and c) all plants found on the horizontal levee, including volunteer and exotic species.

To assess the relative sources of propagules, encroaching or invading species were put into three categories: (a) species planted elsewhere on the ecotone slope, (b) species planted in the treatment wetland, and (c) volunteer species not planted in either the treatment wetland or the ecotone slope. We used two-proportion *z*-tests to contrast propagules sources in WM versus R and BWM versus FWM cells. For FWM, we used the more conservative one-sided test to reflect the greater likelihood of encroachment by riparian species.

For the principal invasive exotic species we encountered, *C. jubata*, we used chi-square tests of independence in SPSS to compare presence/absence across quadrats in WM versus R and FWM versus BWM cells.

To assess how the presence of *S. lasiolepis*, *Typha*, or both together affected planted species succession in the wet meadow assemblage, we compared RDI and total percent cover of wet meadow species in each quadrat between installation and the 2020/2021 field season using a Kruskal-Wallis test in SPSS. Since *S. lasiolepis* was already present in the riparian area, we did not assess its effect on the riparian assemblage.

Results

In 2020/2021, the dominant species on the ecotone slope were *S. lasiolepis* and *Typha* spp. These species both deposited thick layers of thatch. A majority of the *Typha* that was recorded was solely thatch material. Leaf litter from *S. lasiolepis* was found in most instances where live *S. lasiolepis* was recorded.

Changes in Plant Community Parameters: Proportional Change in Species' Cover Since Planting

In the wet meadow, all species initially planted in 2015/2016 were still present in 2020/2021 (Table 2a). Proportions of *Juncus balticus articus*, *Baccharis glutinosa*, and *Euthamia occidentalis* increased compared to initial plantings ($z = 4.54$, 5.07, 5.54, respectively, $p < 0.001$). All other wet meadow species decreased measurably through time ($z <- 2.85$, $p < 0.001$), except for *Carex praegracilis*, whose apparent decline was minor enough that it was not statistically detectable ($p = 0.21$). In the riparian scrub cells, proportions of *Salix lasiolepis* and *Carex barbarae* increased substantially by 2020/2021 ($z = 57.11$, $p < 0.001$; $z = 2.72$, $p = 0.006$; Table 2b), and *Rubus ursinus* maintained its original planting proportions. All other species planted in the riparian scrub cells decreased through time ($z < -2.19$, $p < 0.001$), including *Cornus sericea* and *Sambucus nigra*, which were no longer present by 2020/2021 on the ecotone slope.

Every species planted in a wet meadow was found in greater proportion in the buffered (Table 2c) compared to the fragmented cells (Table 2d). Three wet meadow species, *Ambrosia psilostachya*, *Symphyotricum chilense*, and *Lythrum californicum* did not persist in any fragmented wet meadow samples.

Changes in Plant Community Parameters: Changes in Species Diversity

Simpson's reciprocal diversity of planted species decreased substantially, especially in the riparian scrub assemblage, between the original installation and the 2020/2021 field season. For the wet meadow, the mean *RDI* dropped from 0.31 when planted to 0.19 (t (650) = -9.14, $p < 0.001$; Figure 5a), and the riparian

scrub planted species *RDI* dropped from 0.26 to just 0.11 in 2020/2021 (t (378) = -10.08, p < 0.001; Figure 5b).

For the buffered wet meadow cells, the planted *RDI* dropped from an initial mean of 0.30 to 0.21 (t (395) = -5.07, p < 0.001; Figure 5c), and the fragmented wet meadow fell even further, from a mean *RDI* of 0.32 to 0.14 (t (254) = -8.3, p < 0.001; Figure 5d).

Interactions among species in Buffered and Fragmented Wet Meadow Cells

Overall, the buffered WM cells supported higher median diversity of native species installed on the ecotone slope than the fragmented wet meadow cells, both in terms of the WM species diversity (z (standardized U) = 5.31, p < 0.001*;* Figure 6a) and overall diversity (WM, R, and swale-depression species) (z (standardized U) = 2.16 p = 0.031; Figure 6b). When volunteer and invasive species were included, however, the fragmented WM was more diverse than the buffered WM (z (standardized U) = -4.6, p < 0.001; Figure 6c).

Sources of Encroaching and Invasive Species

By 2020/2021, the FWM cells had much greater percent cover of species not planted in those cells than the BWM cells (z < -20.74, p < 0.001; Figure 7a), predominately *S. lasiolepis* from riparian scrub cells and *Typha* from the treatment wetland. The fragmented cells also retained much lower percent cover of original wet meadow species than the buffered cells (z = 32.56, p < 0.001). Although fragmented and buffered WM cells did not differ in overall proportions of volunteer or exotic species (z = -0.58, p = 0.95), the FWM also had more quadrats with *C. jubata* than the BWM ($\chi^2(1) = 21.53$, p < 0.001; Figure 8).

The wet meadow assemblages had a higher proportion of encroaching and invasive species than the riparian scrub assemblage (z > 5.69, p < 0.001; Figure 7b). About 39.8% of the wet meadow area contained species from other cells, mostly comprising *S. lasiolepis* encroaching from riparian scrub cells. The riparian scrub quadrats had no detectable encroachment from wet meadow species, however *C. jubata* occurred more frequently in the riparian scrub assemblage compared to the wet meadow ($\chi^2(1) = 4.51$, p = 0.034; Figure 8).

Effects of Salix lasiolepis, *Typha* on WM Diversity and Total Cover

In the wet meadow assemblage, by 2020/2021, quadrats encroached with either *S. lasiolepis*, *Typha spp.*, or both had lower diversity (H(3) = 45.68, p<0.0001; Figure 9a) and lower total percent cover of the originally planted WM species (H(3) = 316.43, p<0.0001; Figure 9b). The effect of S. *lasiolepis* presence on total WM planted-species cover was significantly greater than Typha alone.

Discussion

This study documents a substantial reduction in plant diversity in the five years post-installation of an ecotone slope on a horizontal levee designed to protect a wastewater treatment facility on the San Francisco Bay. Both wet meadow and riparian scrub assemblages planted on the ecotone slope lost diversity over time, but the riparian scrub assemblage in particular became dominated by the hardy native *Salix lasiolepis*. The wet meadow plant assemblage was encroached by both *S. lasiolepis*, from interspersed riparian scrub assemblage, and *Typha*, from the treatment wetland. Our evidence suggests that fragmentation and dominance by species with invasive tendencies played central roles in native plant succession and led to greater invasion by the dominant exotic *Cortaderia jubata*, although the different soil types across these assemblages may have played a role in their succession. Our results support the idea that designs for nature-based solutions would benefit from incorporating larger habitat patch sizes, but that they may also require ongoing intervention and adaptation to limit effects of fragmentation, species invasion, and succession and achieve habitat creation goals.

Natural wetland ecosystems rely on flooding and drought to maintain their biodiversity and ecological function (Middleton, 1999; Zedler, 2000). This ecotone slope contrasted two native wetland plant assemblages, wet meadow and riparian scrub, which are adapted to distinct natural hydrological disturbance regimes. Shallow water tables and soil saturation are characteristic of wet meadows, with soils remaining moist for much of the year (Barbour et al., 2007; Zentner et al., 2003). Riparian ecosystems tend to have more intense hydrological regimes, with hydrological disturbance and sediment deposition being important for maintaining riparian vegetative composition (Barbour et al., 2007; Tabacchi et al., 1998). Cells on the ecotone slope, in contrast, receive constant subsurface flow, but the topsoil was often dry during our survey period. Lack of a natural hydrologic disturbance regime to break dominance may have contributed to the riparian scrub assemblage's overwhelming growth of *S. lasiolepis*, its loss of two planted trees, *C. sericea* and *S. nigra*, and reduction of most riparian understory species, helping explain why the riparian scrub assemblage lost more native diversity than the wet meadow. Although the ecotone slope's hydrological regime was somewhat more like a wet meadow, historically wet meadows in the San Francisco Bay area are also seasonally flooded (Fox et al., 2015). Early successional ecosystems are susceptible to diversity loss and woody species proliferation in the absence of seasonal disturbance (Keddy & Rezicek, 1986, Greenberg et al., 2011; Williams et al., 1987). In our study, over five years the wet meadow assemblage transitioned from a grassland to a forb and shrubland. In 2012, Ratajczack et al. documented that woody species encroachment in grasslands reduces community species richness, and several authors have shown that *Baccharis pilularis* invasion completely changes the plant community and ecosystem function of grasslands (Williams et al., 1987; Zavaleta & Kettley, 2006).

Many authors have argued that communities composed of species that vary in phenology, reproductive process, and ecological function resist invasion, particularly by functionally similar species (Byun, 2013; Fagúndez & Lema, 2019; Fried et al., 2015; Zedler, 2000). The riparian scrub community may have experienced substantially less *Typha* encroachment compared to the wet meadow due to inclusion of *S. lasiolepis* in the planting palette. Plumb et al., (2013) document considerable reduction of *Typha* biomass under increased shade and moisture of hardwood canopy. By that argument, light conditions in

the wet meadow may have been more conducive to *Typha* establishment, persistence and survival than in the riparian scrub assemblage. Over twice as much *Typha* invaded the fragmented WM, however, despite it having much higher levels of *S. lasiolepis* than the buffered WM. Compared to larger habitat patches, fragments provide a disproportionate amount of edge, which is conducive to the introduction and establishment of species with invasive qualities (Cronk & Fuller, 1995). In this case, encroachment of *S. lasiolepis*, a riparian scrub assemblage species, into the fragmented wet meadow can be explained by the large amount of shared edge facilitating its movement. Greater *Typha* and *C. jubata* encroachment into fragmented versus buffered wet meadow is more puzzling, however, and suggests that encroaching *S. lasiolepis* may even have facilitated invasions of other species at lower densities, possibly by shading out smaller WM and other riparian species.

Created urban wetlands that treat wastewater may be particularly vulnerable to domination by vegetative monotypes, due to the continuous input of nutrient-rich wastewater (Canavan et al., 2018; Green & Galatowitsch, 2002). Consistent with Zedler and Kercher's (2004) efficient use hypothesis, *Salix lasiolepis'* superior growth and productivity, more efficient nutrient uptake than competitors, and drought and salinity tolerance likely permitted it to withstand the conditions on the ecotone slope better and even directly suppress other planted species (Ericsson, 1981; Elowson, 1999; Frieswyk & Zedler, 2006; Kuzovkina & Quigley, 2005; Woo & Zedler, 2002). Unlike other species, *S. lasiolepis* often benefits from partial limb breaks as a means for lateral dispersal through epicormic shoots and adventitious roots. Using growth morphology as a dispersal mechanism allows it to outcompete neighboring plants (Boland 2024). *Typha* is wind pollinated and some species of *Typha* can have up to 420 million pollen grains per inflorescence, which can remain viable for weeks (Grace & Harrison 1986). Once established, *Typha* spp. form dense, nearly monotypic stands; it is often taller than the species it displaces; it uses nutrients efficiently; and it leaves behind an abundant amount of thatch that can suppress other species' germination or growth (Larkin et al., 2012; Newman et al., 1996; Vaccaro et al., 2009).

We find that abundance of the two dominant native wetland plants in our system, *Salix lasiolepis* and *Typha* spp. reduced plant community diversity and altered community structure where they invaded the wet meadow. Weiher & Keddy (1995) suggest that *Typha* litter can even act as a "filter," causing extant plant communities to differ from the communities represented in the seed bank.

The combined presence of *Typha* and *Salix lasiolepis* and layers of thatch in the fragmented wet meadow cells may have created a double encroachment pressure, resulting in the greater declines in diversity than in the buffered, which only faced encroachment from treatment wetland plants. Overall, although Typha proved to be an important expansive species, the native, planted, riparian species S. lasiolepis proved to have the greatest effect on ecosystem succession and diversity in the absence of natural hydrologic disturbance.

The major non-native invasive threat to the wet meadow was *Cordateria jubata*. *C. jubata* has spread throughout the ecotone slope, although it has been actively managed by the OLSD (Personal communication, Jason Warner, General Manager, OLSD and David Sedlak, Environmental Engineering,

U.C. Berkeley). *C. jubata* demonstrates rapid growth and resource use under high water and nitrogen availability conditions (Vourlitis & Kroon, 2013). It also produces copious seeds, allowing its populations to persist by creating strong and continuous propagule pressure that considerably increases the probability of further expansion (Lambrinos, 2008). The greater presence of *C. jubata*, in the riparian scrub and fragmented wet meadow cells may have resulted from the effects of fragmentation, including the loss of three planted species in the fragmented wet meadow, which could have left more niche availability for *C. jubata* to fill and colonize.

In addition to abiotic disturbances, wetland ecosystems in California evolved for millennia with management, such as burning, harvesting, and tending, by indigenous peoples. Natural anthropogenic disturbance shaped the distribution and abundance of managed species (Hankins, 2013; Lightfoot & Lopez, 2013; Stevens, 2020), and the role indigenous management has played for millennia in maintaining biodiversity is well-documented (Berkes et al., 2000; Mistry & Bernardi, 2016; Stevens, 2020; Zedler & Stevens, 2018). Stevens (2020) found that indigenous gathering, tending, and cultivating of *C. barbarae* for basket weaving enhanced its distribution and abundance, and understory species, such as *C. barbarae*, often fail to colonize restored riparian forests without human support.

Typha and *Salix* have also been harvested and used by native peoples worldwide for food, medicine, clothing, shelter, and other tools (Bates & Lee, 1990; Grace & Harrison, 1986; Liptay, 1988; Motivans & Apfelbaum, 1987; Prashith et al., 2017; Tawfeek et al., 2021). Through genocide, slavery, and disease, however, regular indigenous ecosystem management and tending in California abruptly declined with European colonization (Zedler & Stevens, 2018). Loss of harvesting and burning led riparian canopies to close and tule marshes to progress to impenetrable and senescent states. Interestingly, although *C. barbarae* in this system successionally declined in both fragmented and buffered wet meadow cells, the species expanded without intervention in the riparian scrub assemblage, reflecting its tolerance and higher survivability under low-light conditions from a *S. lasiolepis* canopy (Moore et al., 2011). This suggests that more understanding of interspecific interactions and effects of traditional management as a natural disturbance are needed to maintain habitat diversity and quality.

Conclusions and Recommendations

Our findings underscore the importance of nuanced application of nature-based solutions. In the absence of natural disturbance processes, such as seasonal overland water flow or scouring, fragmentation may drive constructed wetlands to progress to a successional state dominated by fewer species. In this horizontal levee system, plant assemblage and patch size both strongly influenced community invasibility, expansion of dominant natives, *Typha* and *S. lasiolepis*, and spread of non-native *C. jubata*. Future projects would benefit from planting larger patches with lower edge ratios to facilitate ecosystem resistance to invasion and diversity loss.

The biological complexity of historic undamaged ecosystems usually informs restoration of natural disturbance regimes (Angelstam, 1998; Middleton, 1999; Odion & Sarr, 2007) or active management

(Hobbs et al., 2007) to achieve a specific desired ecosystem or state. Constructed treatment wetlands designed to fulfill multiple goals (wastewater treatment, flood control, and native habitat creation) tend to be limited in the amount of hydrologic disturbance they can incorporate.

Subsurface flow is important for removing contaminants, some projects' primary goal, but overland flow, or at least thorough soil saturation, is important for maintaining wetland habitats on the ecotone slope. Previous authors find that natural hydrological processes are overlooked in constructed wetlands (Grimm & Köppel, 2019), and temporal and spatial regimes are mostly homogenized (Bockelmann et al., 2002). The final 2018 phase of this project removed most of the overland flow, eliminating the natural hydrological disturbance.

In cases such as this, designing plant assemblages to resist invasion, possibly by installing later successional habitats with fewer, more competitive species, may reduce costs of collecting, propagating, and growing plant species while still meeting habitat goals, and retaining overland flow and incorporating anthropogenic disturbances like mowing may be practical to maintain species diversity (Zedler, 2000).

Given the current loss of biodiversity and wetland habitat worldwide and in California, projects like this one are crucial to restore healthy, diverse urban ecosystems and make cities more livable and resilient for people, plants, and animals, especially in this era of global climate change (Matthies et al., 2017; Norton et al., 2016). Sea-level rise will only increase constraints on wetland habitat. We have shown that plant communities in projects such as this must be monitored and maintained to ensure they maintain the biodiversity needed to sustain critical habitat and ecological resilience, vibrant green spaces, and resilient urban ecosystems.

Declarations

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Competing Interests

The authors have no relevant financial or non-financial interests to disclose.

Authors' contributions

Joia Fishman and Dr. Rachel O'Malley conceived the ideas and designed methodology; JF collected the data; JF and RM analyzed the data; JF wrote the first draft of the manuscript. Both authors contributed critically to the drafts and gave final approval for publication.

The authors declare no competing interests.

Data availability

Upon publication, all data associated with this manuscript will be made publicly available in the Dryad digital repository.

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Tables

Tables 1 and 2 are available in the Supplementary Files section.

Figures

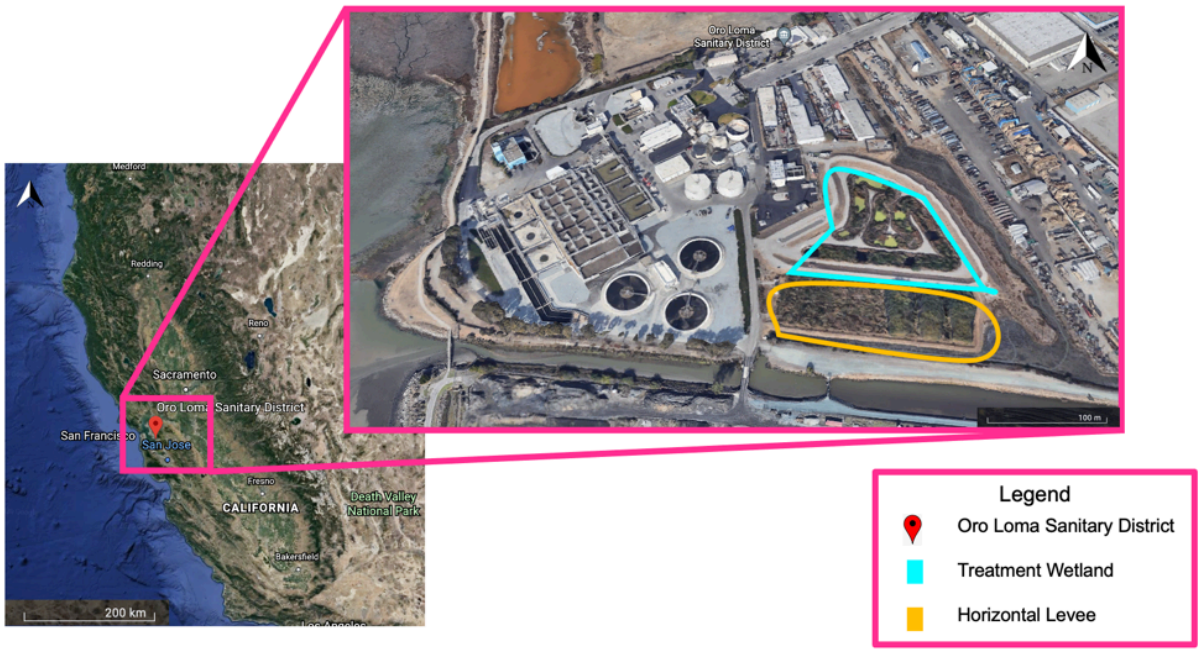

Figure 1

Treatment wetland and ecotone slope at the Oro Loma Sanitary District in San Lorenzo, California (Adapted from Google Earth [2020])

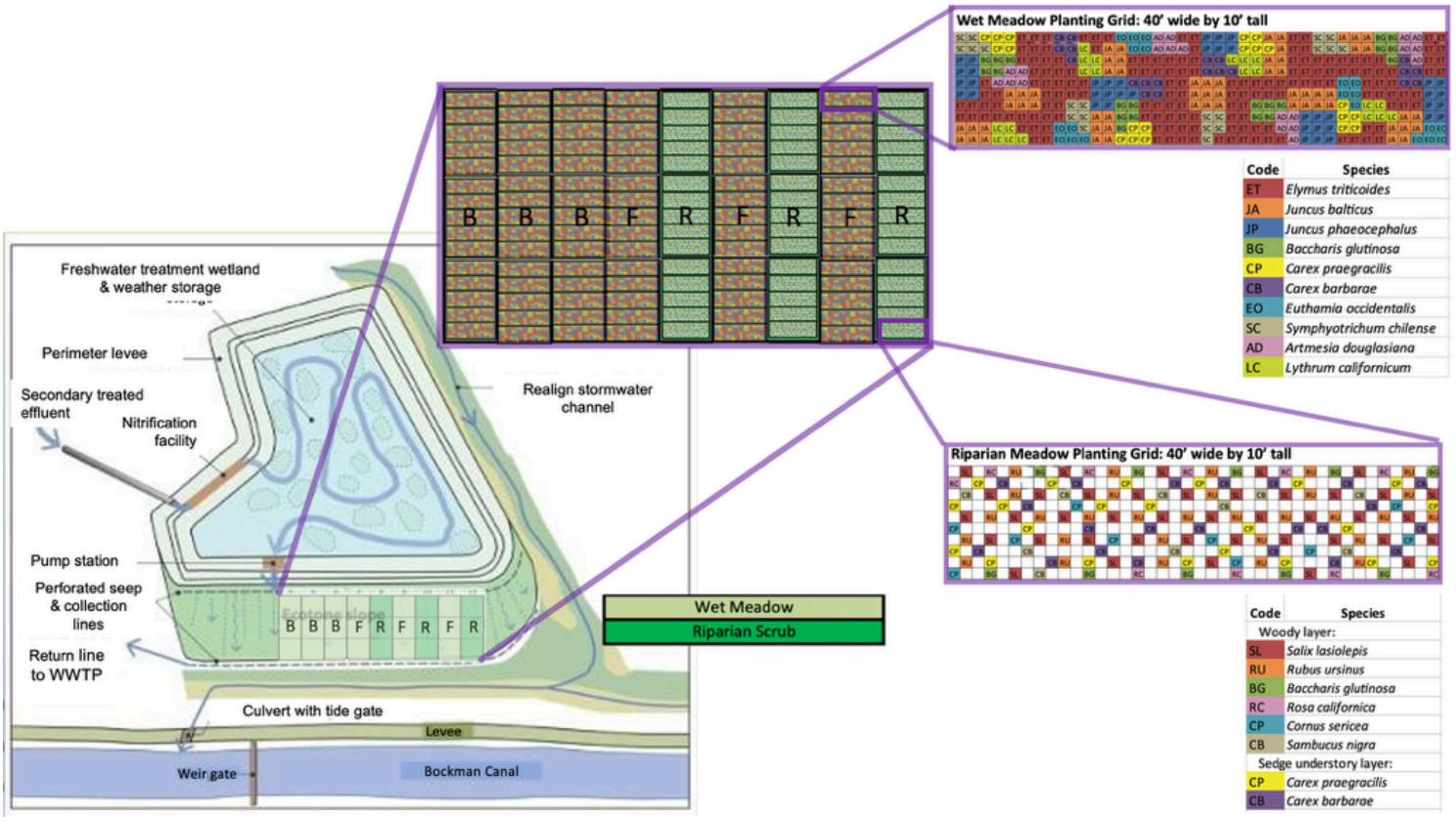

Figure 2

Relationship of the treatment wetland to the ecotone slope showing twelve vertical cells with planting grid design. B = buffered wet meadow cells, F = fragmented wet meadow cells, and R = riparian scrub cells. (Adapted from Save the Bay, 2017; Environmental Science Associates [ESA] planning documents)

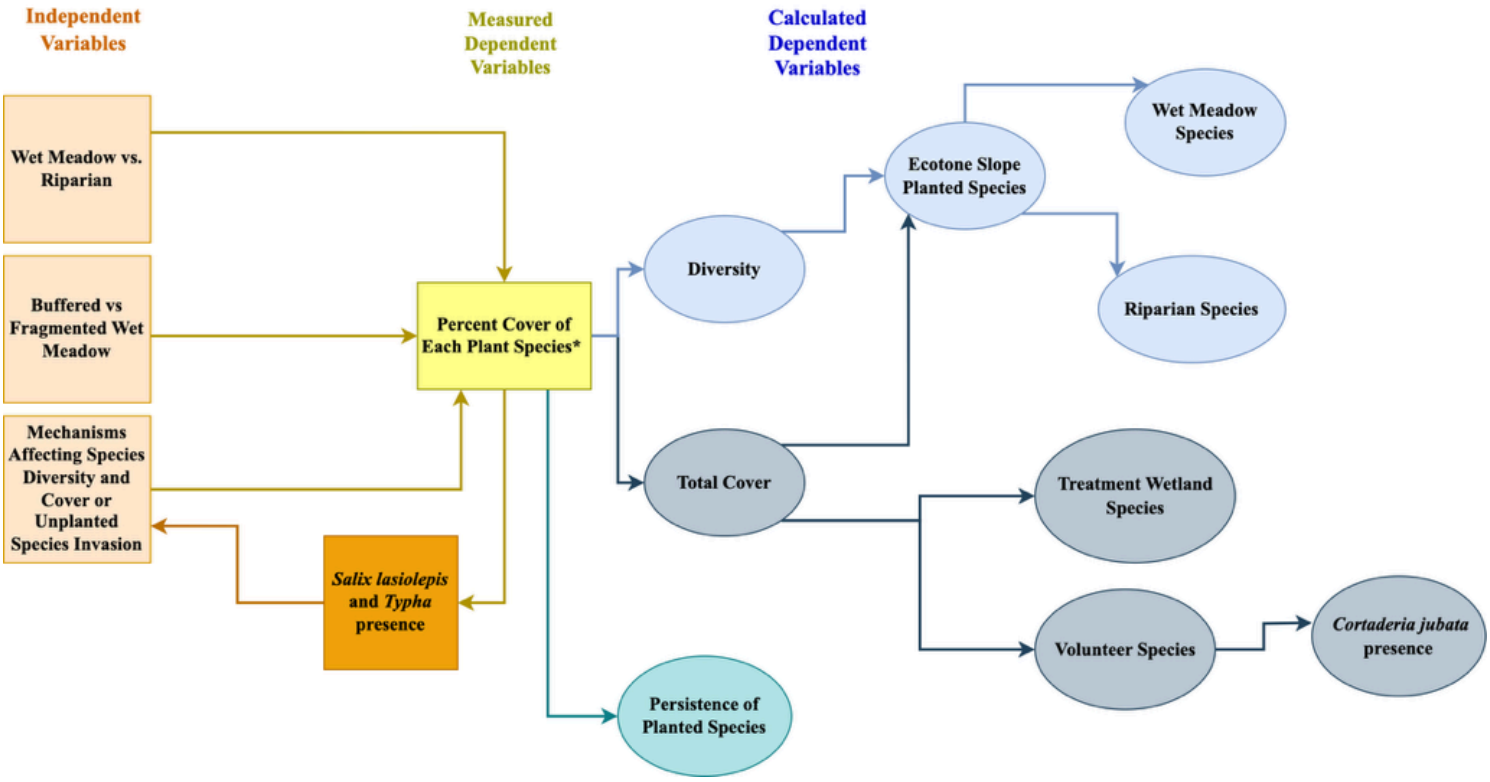

Figure 3

Study Design. To estimate the 2015/16 percent cover, a Python data processing script was used to randomly sample quadrats from original planting documents. In 2020/21 percent cover was measured in the same quadrats in the field

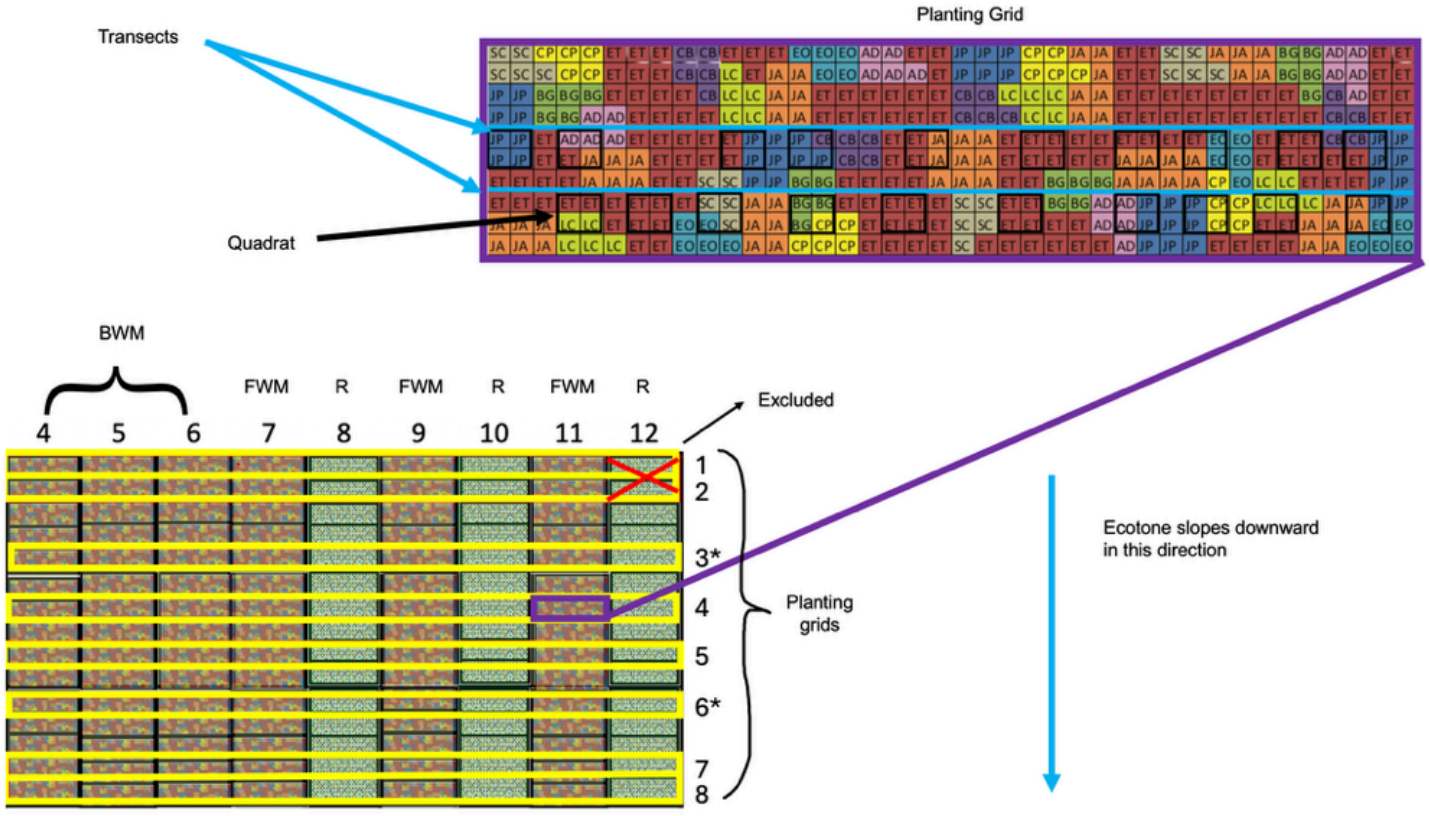

Figure 4

Sampling scheme. Adapted from ESA planning documents. BWM = Buffered Wet Meadow, FWM = Fragmented Wet Meadow, R = Riparian. *Grids 3 and 6 only had 1 transect each. Yellow belts delineate sampled areas

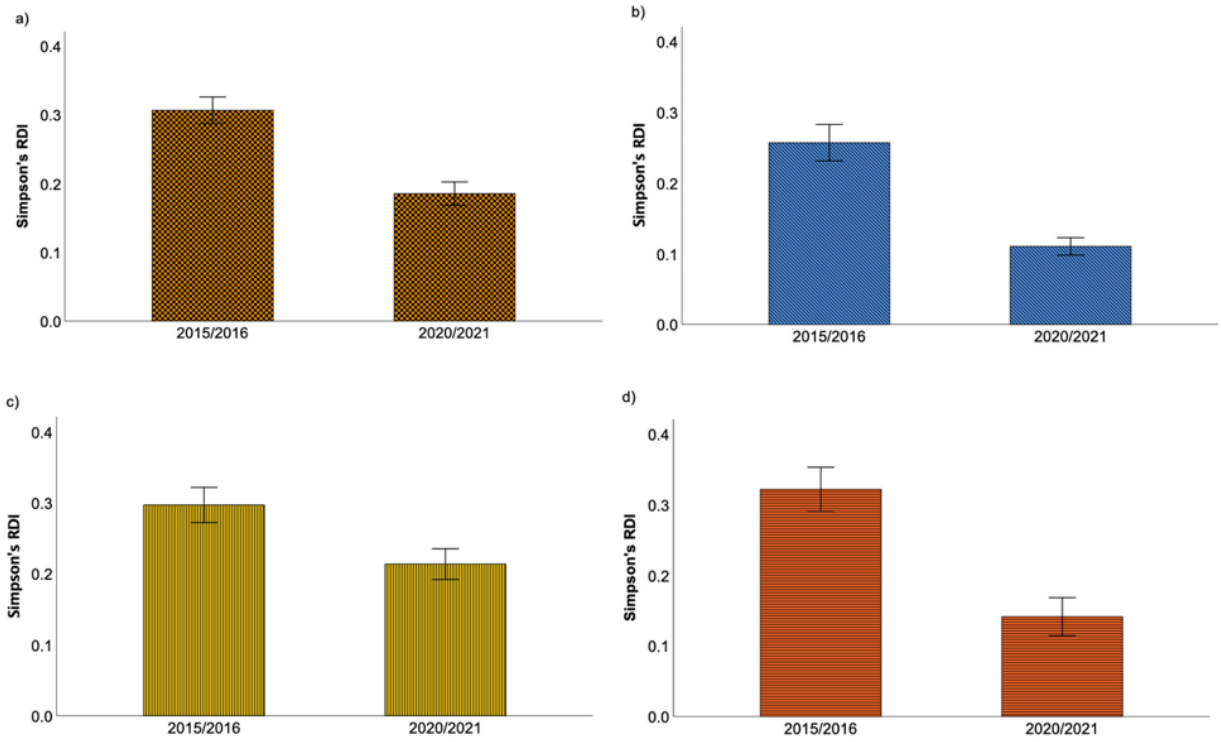

Figure 5

Change in Simpson's Reciprocal Diversity for planted species on the ecotone slope from installation in 2015/2016 to 2020/2021 in a) wet meadow (n = 651), b) riparian scrub habitat (n = 379), c) buffered wet meadow (n = 396), and d) fragmented wet meadow (n = 255) plant assemblages. Error bars represent a 95% confidence interval around the mean.

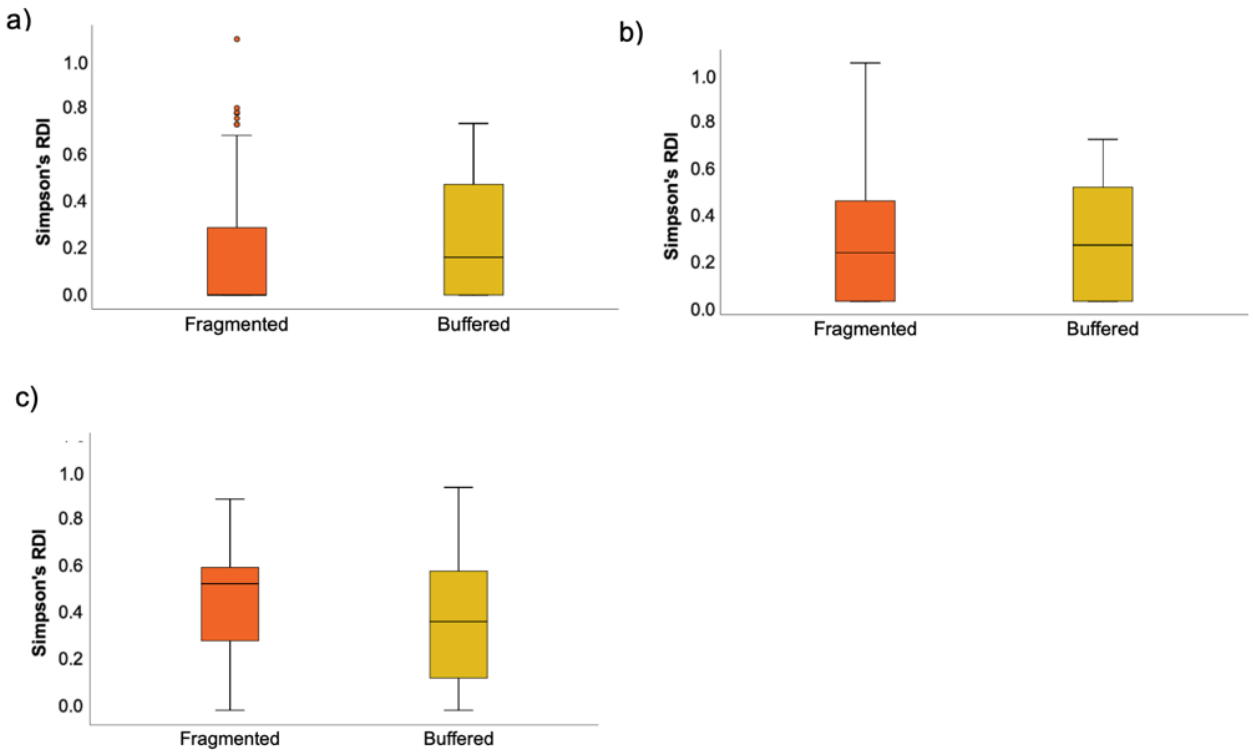

Figure 6

Diversity of the buffered versus fragmented WM a) planted wet meadow species (buffered, n = 396, fragmented, n = 255), b) all species installed on the ecotone slope (buffered, n = 398, fragmented, n = 408), c) all plant species including volunteer and invasive species (buffered, n = 420, fragmented, n = 420). All differences are significant, $p<0.5$

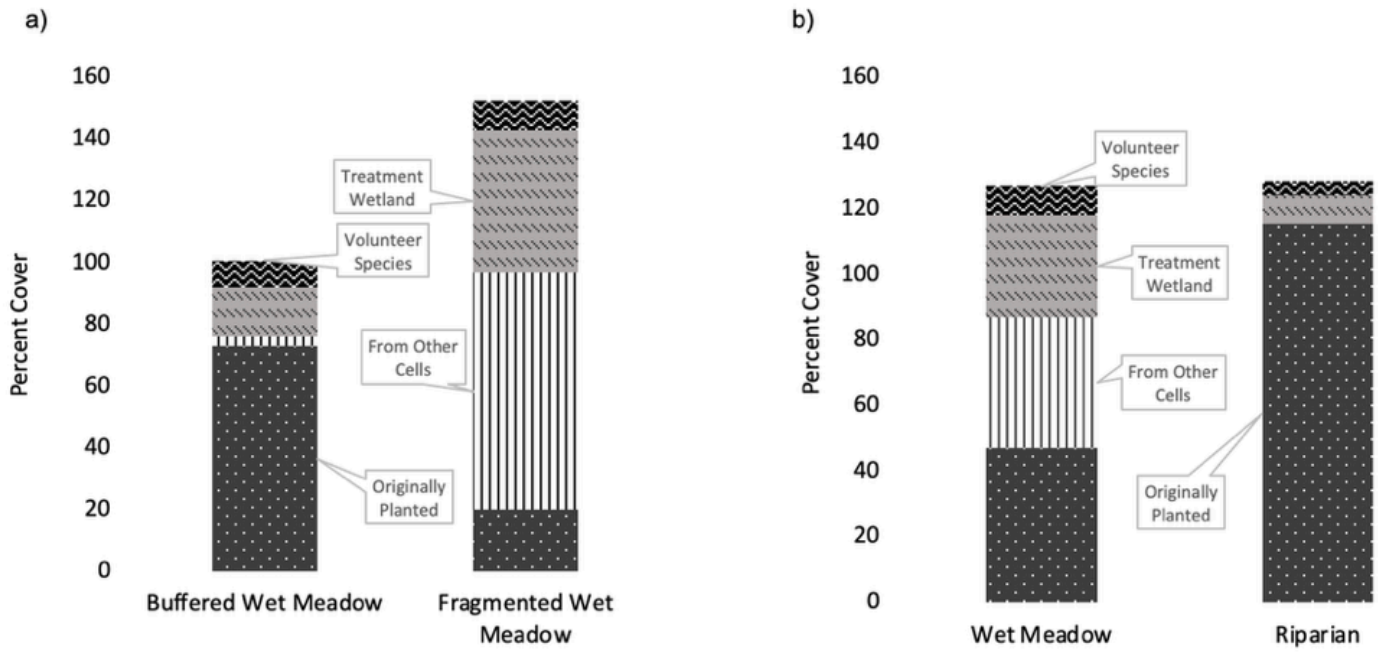

Figure 7

Propagule source for (a) wet meadow and riparian scrub cells and (b) buffered and fragmented wet meadow. The y-axis goes over 100% due to overlapping canopy cover.

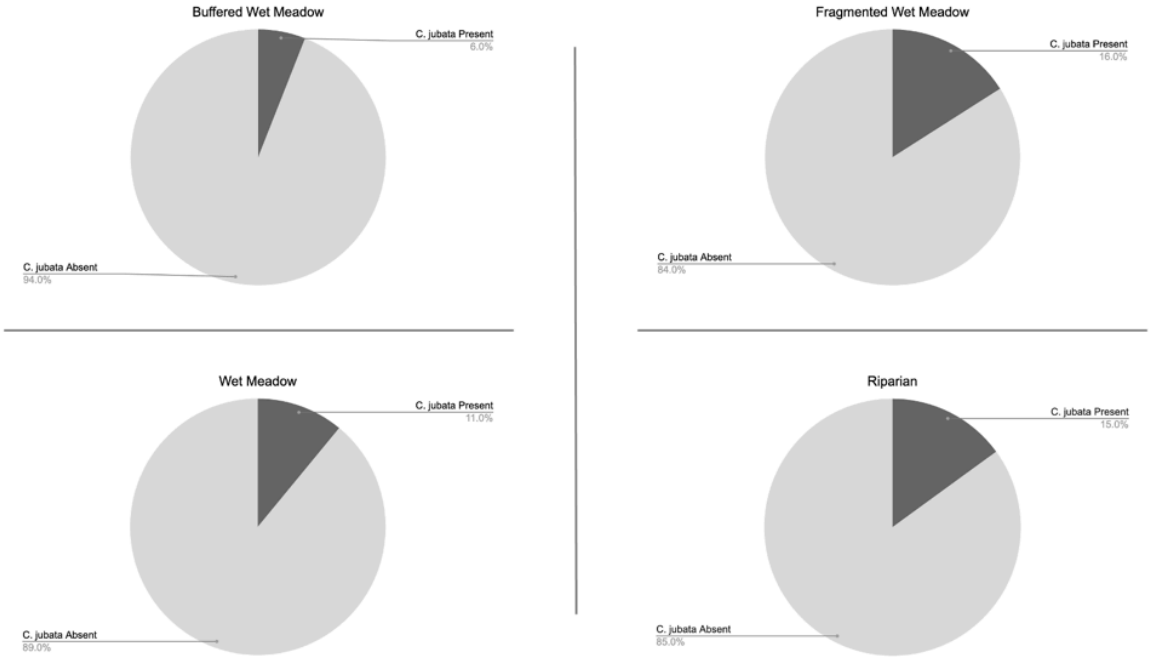

Figure 8

*Cortaderia jubata*occurrence in wet meadow, riparian scrub, buffered wet meadow, and fragmented wet meadow quadrats.

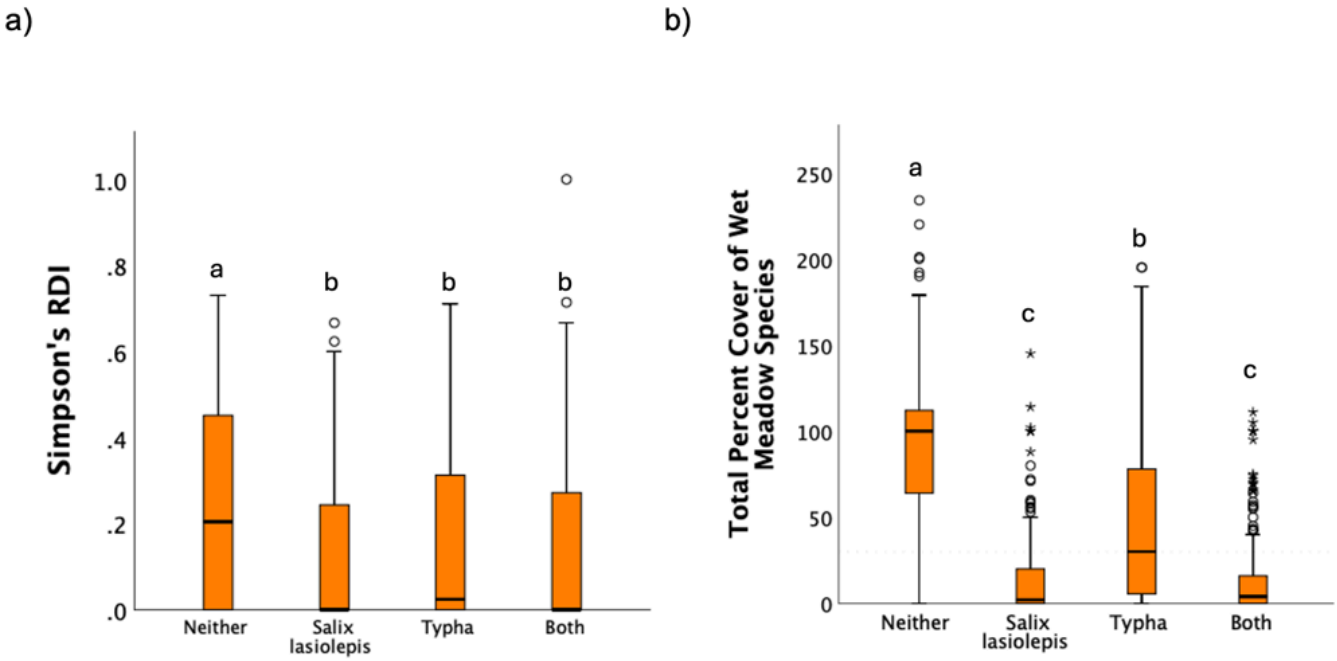

Figure 9

The relationship between the presence of two dominant species on planted wet meadow species' a) diversity (n = 651) and b) cover (n = 840). Bars with different letters differ significantly, $p < 0.001$

Supplementary Files

This is a list of supplementary files associated with this preprint. Click to download.

- Tables.docx