FLORIDA INTERNATIONAL UNIVERSITY

Miami, Florida

THE EFFECT OF WATER LEVEL AND SALINITY ON CARBON DYNAMICS IN AN EVERGLADES SUBTROPICAL BRACKISH ECOTONE WETLAND

A thesis submitted in partial fulfillment of

the requirements for the degree of

MASTER of SCIENCE

in

BIOLOGY

by

Amanda Richey

2023

To:	Dean Michael R. Heithaus
College of Arts, Sciences and Education

This thesis, written by Amanda Richey, and entitled The Effect of Water Level and Salinity on Carbon Dynamics in an Everglades Subtropical Brackish Ecotone Wetland, having been approved in respect to style and intellectual content, is referred to you for judgment.

We have read this thesis and recommend that it be approved.

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Date of Defense: May 16, 2023

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Florida International University, 2023

ACKNOWLEDGMENTS

This work was funded by the National Science Foundation (NSF) Award number 2047687. Dissemination of this work in the form of poster presentations was supported by the Institute of the Environment and the Florida Coastal Everglades LTER at Florida International University. J. Wakefield at SFWMD provided guidance for using DBHydro. D. Rondeau and C. Walker at Everglades National Park provided clarity into data collection methods for the water level stage and specific conductivity data at coastal station ENPHC. S. Oberbauer maintained field campaigns to the ecotone flux tower and provided insights on sensor information and feedback. P. Prajapati processed the raw flux, water level, and specific conductivity data for the ecotone eddy flux tower site used in this analysis. I would also like to thank M. G. McLeod, L. Lamb-Wotton, P. Kliendl, members of the Malone Disturbance Ecology Lab, and my committee for their feedback and steadfast support in the development and completion of this project. Last but not least, I would like to thank S. Malone for her support, patience, and guidance throughout this process.

ABSTRACT OF THE THESIS

THE EFFECT OF WATER LEVEL AND SALINITY ON CARBON DYNAMICS IN AN EVERGLADES SUBTROPICAL BRACKISH ECOTONE WETLAND

by

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Florida International University, 2023

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Changes in water level and salinity cause dynamic shifts in plant community composition and ecotone development in coastal ecosystems. Given varying carbon (C) sequestration capacities of coastal wetlands, it is important to understand how hydrology and saltwater intrusion affect CO_2 fluxes. This study's objective was to understand the impact of hydrology in an ecotone transitioning from a freshwater marl prairie to a mangrove scrub in the Everglades. I explored long-term trends in water level and salinity and identified the relationship between these two variables. Next, I compared rates of net ecosystem exchange of CO_2 (NEE) under different hydrologic conditions by fitting light and temperature response curves. Ecosystem CO_2 uptake rates were less sensitive to changes in water level than respiration rates. Although sawgrass (*Cladium jamaicense*) declined over the study period, the proliferation of mangroves (*Rhizophora mangle*) maintained CO_2 uptake, making the ecotone's C sequestration capacity resilient to variable hydrology.

Key words: coastal ecotones, hydrology, mangrove, sawgrass, eddy covariance

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I. INTRODUCTION

Coastal wetlands play a major role in the global carbon (C) cycle through the development of large C pools (Alongi 2020). Primary productivity captures atmospheric carbon dioxide (CO_2) and incorporates it into both terrestrial and aquatic vegetation as organic C (Schlesinger & Bernhardt 2013). In wetland ecosystems, inundation limits aerobic respiration due to anoxic conditions. Limited aerobic respiration contributes to slower decomposition, steady organic C accumulation in soils, and long-term sequestration (McLeod et al. 2011). Although wetlands have a great capacity for C sequestration, these ecosystems can also be a significant source of CO_2 to the atmosphere when soils are exposed to air and aerobic respiration is possible (Hopkinson et al. 2019; Anselmann & Crutzen 1989; Whiting & Chanton 1993). Coastal wetlands face changing hydrology that influence their ability to incorporate CO_2 from the atmosphere and retain C over longer time periods.

Coastal wetlands exist along salinity gradients dictated by tidal influence and freshwater flow. Ecotones develop parallel to coastlines between freshwater and saltwater ecosystems and are composed of species that can withstand high variability in salinity due to variable water sources (Wasson et al. 2013; Ross et al. 2000). The position of ecotones can fluctuate with competition in the plant communities and directional changes in abiotic conditions (Lloyd et al. 2000; Smith & Goetz 2021). While plant communities may experience more stress within ecotones compared to adjacent ecosystems, they can also be more responsive and resilient to changing conditions (Wasson et al. 2013; Jiang et al. 2012) making them useful indicators of broader changes to coastal landscapes.

Globally, land and water management and accelerating sea-level rise are changing coastal wetlands' structure by altering salinity gradients. Decreases in freshwater flow and sea-level rise contribute to saltwater intrusion in freshwater and brackish systems (Herbert et al. 2015; Meeder et al. 2017; Ross et al. 2000). Additionally, infrastructure barriers can inhibit landward migration of coastal ecosystems, resulting in "coastal squeeze" where ecosystem expansion is constrained on both the seaward and landward sides (Schuerch et al. 2018). Noted ecosystem-scale responses to climate and anthropogenic drivers include mangroves encroaching into brackish and freshwater marshes (Saintilan et al. 2014), wetland species migrating into uplands (Osland et al. 2022), and declines in ecosystem productivity (Ross et al. 2000).

In coastal wetlands, the capacity to capture CO_2 and store it in the ecosystem can be enhanced or reduced with climate and saltwater intrusion (Coldren et al. 2016; Doughty et al. 2016; Lu et al. 2017; Zhang et al. 2019). Mangrove encroachment in brackish and freshwater marshes can increase ecosystem productivity and organic C accumulation (Doughty et al. 2016; Vaughn et al. 2020). On the other hand, coastal wetland productivity is reduced when species are physiologically stressed by prolonged inundation (Zhao et al. 2019), intense drought (Malone et al. 2013), or large increases in salinity in freshwater or brackish systems (Weston et al. 2014; Wilson et al. 2018). Enhancing C sequestration in coastal wetlands, by protecting productive areas and alleviating stressful conditions, could be a tool to mitigate future climate change (McLeod et al. 2011), but these ecosystems could exacerbate climate change if they become net CO_2 sources to the atmosphere (Holmquist et al. 2018).

In the Florida Everglades saltwater intrusion has caused significant changes in the structure and function of subtropical coastal wetlands (Chambers et al. 2019; Meeder et al. 2017). Changes in salinity have co-occurred with mangrove encroachment into fresh and brackish marshes (Krauss et al. 2011; Meeder et al. 2021), peat collapse in long hydroperiod marshes (Chambers et al. 2019), and the development of a low productivity zone in the southeastern saline Everglades ecotone (Egler 1952; Ross et al. 2000). While mangrove encroachment can increase CO_2 uptake rates (Troxler et al. 2013), peat collapse and low productivity zone development can lead to C loss from the ecosystem and declines in CO_2 uptake (Charles et al. 2019; Sklar et al. 2019). Everglades wetland ecosystems have variable CO_2 uptake rates and functional responses to inundation, leading to differences in productivity and C sequestration (Jimenez et al. 2012; Malone et al. 2021; Troxler et al. 2013; Zhao et al. 2019). However, little is known about the effect of hydrology on CO_2 fluxes in the saline ecotone, where water level and salinity are variable. In this study, changes in net ecosystem exchange of CO_2 rates (NEE) are evaluated in response to variable environmental conditions.

The primary objective of this project is to understand how hydrology influences CO_2 fluxes in coastal ecotones. To meet this objective, I will evaluate the following questions: How has surface water level and salinity changed over time along the southeast coastline

(Q1)? What is the relationship between surface water level and salinity at the ecotone compared to a freshwater and a saline ecosystem (Q2)? How do CO_2 dynamics change under different water levels at the ecotone (Q3)? How do CO_2 dynamics compare between the ecotone and freshwater marl prairie (Q4)?

I hypothesize that water level would increase over time in a shallow estuary along the southeast Everglades coastline, reflecting sea level rise (Meeder et al. 2017; Parkinson & Wdowinski 2022) (H1). Additionally, water level and surface salinities have different relationships depending on relative freshwater and marine influence in ecotonal wetlands. For example, a positive relationship between water levels and salinity could indicate marine-driven change at coastal sites, whereas a negative relationship could indicate increased freshwater availability (Price et al. 2006; Troxler et al. 2014). Evaporation can further increase salinity as the wetland approaches drier conditions (Herbert et al. 2015; Wilson et al. 2018), and salt tolerant plant communities can increase relative soil salinity compared to freshwater communities when exposed to more saline groundwater (Wendelberger and Richards 2017). However, additions of water (regardless of freshwater or marine source) can dilute surface salinity through increased volume. I hypothesize that the ecotone would have both marine and freshwater influence, reflected as a positive relationship between water level and salinity under low water levels and a negative relationship under high water levels (H2).

Inundation can limit NEE in Everglades freshwater wetlands, which are co-dominated by sawgrass (*Cladium jamaicense*) and muhly grass (*Muhlenbergia filipes*), through decreased CO_2 uptake and limited aerobic respiration (Malone et al. 2021; Schedlbauer et al. 2010; Zhao et al. 2019). Alternatively, in Everglades mangrove scrub ecosystems, red mangrove (*Rhizophora mangle*) CO_2 assimilation rates increase with increasing water level across dry and wet habitats (Hogan et al. 2022). Elevated salinity can stress both sawgrass and mangroves, reducing CO_2 uptake (Barr et al. 2009, 2010; Wilson et al. 2018). Within short hydroperiod brackish ecotones higher water levels are essential for reducing salt stress through dilution (Ewe et al. 2007; Wilson et al. 2018; Meeder et al. 2017). Therefore, I predicted greater CO_2 uptake rates and less ecosystem respiration under higher water level and lower salinity conditions compared to lower water level and higher salinity conditions (H3). Last, I expect the ecotone to differ from the freshwater marl prairie in its CO_2 dynamics because of different community composition with different uptake rates and responses to inundation (H4) (Barr et al. 2009; Hogan et al. 2022; Zhao et al. 2021). This research will advance our understanding of changing hydrologic conditions' effects on coastal wetland ecosystems' CO_2 dynamics.

II. METHODS

II. A. Study Sites

The Florida Everglades has a year-round growing season marked by wet and dry seasons with distinct precipitation and overland surface freshwater flow (Davis & Ogden 1994). Average annual precipitation is approximately 1380 mm (Davis & Ogden 1994; Obeysekera et al. 1999). Roughly 70% of precipitation arrives during the wet season

(May - October) in thunderstorms while dry season (November - April) precipitation comes from continental fronts (Davis & Ogden 1994; Obeysekera et al. 1999). Surface freshwater flow in the Everglades is managed by the South Florida Water Management District (SFWMD) through a network of levees, canals, and pumps (Davis & Ogden 1994; Loveless 1959). Surface water levels lag wet season precipitation by one to three months, such that water levels are lowest at the end of the dry season and increase throughout the wet season (Light & Dineen 1994). The seasonal difference in freshwater surface flow across the greater Everglades landscape impacts pore water salinity in coastal ecosystems. During the dry season in the Taylor Slough ecotone, pore water can reach hypersaline conditions (>40 PSU) (Troxler 2021), stressing vegetation (Ewe et al. 2007; Troxler et al. 2014).

In the southeastern Everglades, the landscape is bisected by canals and roads that redirect overland flow and constrict the landward movement of plant communities (Davis et al. 2005; Ross et al. 2000). Within this portion of the landscape, different plant communities and land cover types exist, including fresh and brackish marl prairies, a low productivity zone where plant species are sparse, and mangrove scrub on the coast. Mixed salinity tolerance communities (containing sawgrass and spikerush, *Eleocharis cellulosa*) and the low productivity zone have migrated inland (Fuller & Wang 2014; Ross et al. 2000) and mangrove encroachment into marl prairies are evident in this region (Meeder et al. 2021). Studies by Meeder et al. (2017) and Ross et al. (2000) suggest that the locations and expansion of mixed salinity tolerance communities and the low productivity zone are driven by volume of freshwater discharge.

I quantified how water levels and salinity have changed at one long-term site in a shallow estuary, the relationship between water level and salinity at a coastal site and an ecotone site, and the effect of variable hydrologic conditions on NEE rates at an ecotone site and a freshwater marl prairie site. To understand how conditions along the Everglades coastline are changing, I utilized water level and salinity data from a SFWMD long-term monitoring station (ENPHC; 25.25416, -80.44427) (Figure 1). To understand how hydrology impacts CO_2 dynamics, I quantified how NEE responds to low and high water levels at an ecotone site, located between freshwater marl prairie and coastal mangrove scrub (SE-1; 25.3539, -80.3810) (Figure 1). To evaluate ecotone CO_2 dynamics under variable water levels relative to other ecosystems in the landscape, I compared CO_2 parameters at the ecotone to previously reported parameters at an AmeriFlux freshwater marl prairie ecosystem site (TS/Ph-1; 25.4379, -80.5946) (Figure 1).

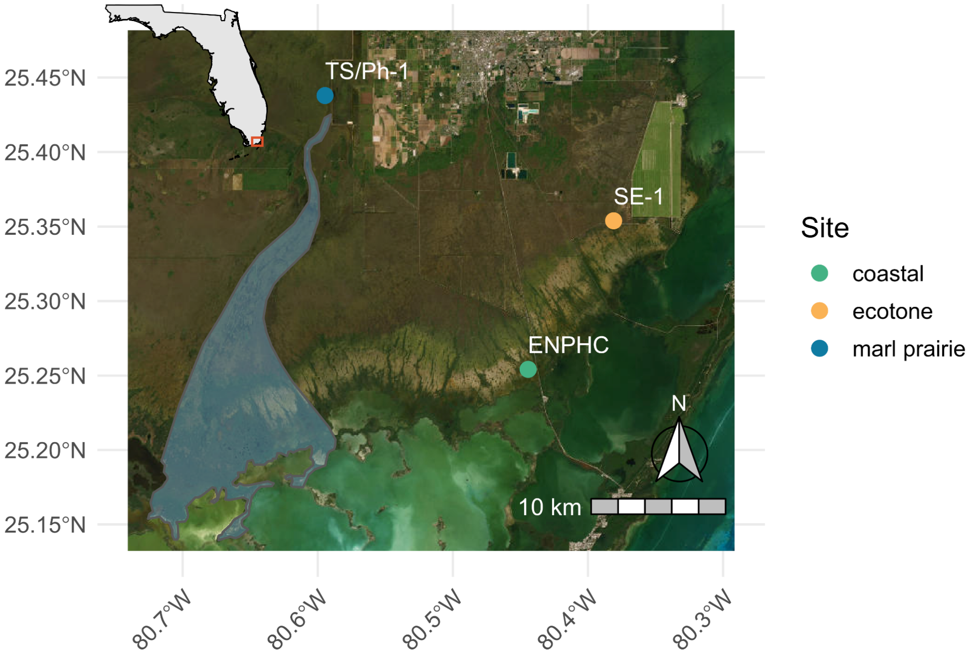

Figure 1. Long-term water level and salinity monitoring site (ENPHC), the AmeriFlux research site at the ecotone between freshwater marl prairies and mangrove scrub (SE-1) and AmeriFlux research site in freshwater ecosystem (TS/Ph-1).

II. B. Data Acquisition

I obtained hydrologic data from the SFWMD's public data repository, DBHYDRO, using the *gethydro* function in the 'dbhydroR' package (Stachelek 2017). Daily mean water level and specific conductivity data were obtained for the coastal site (ENPHC) from July 29th, 1993 to May 5th, 2022. This site was chosen because it had greater than 10 years of data available. The SFWMD measured daily water level using shaft encoders and specific conductivity data was measured using an OTT-PLS-C (OTT HydroMet, Kempten, Germany). Water level values were recorded on the NAVD88 vertical datum. Specific conductivity values were converted to salinity (PSU) using an equation detailed in (Lewis 1980).

Continuous half-hourly water level was measured at the ecotone site flux tower for salinity (ES-2 sensor; METER group, Pullman, Washington) and at the tower pond for water level (HOBOware U20-001-01; Onset, Bourne, Mass.) (Figure 2). Water level (m) was logged every half hour as the change in relation to the soil surface. Electrical conductivity (dS m^{-1}) and water temperature (°C) were also logged every half-hour. Both the water level and electrical conductivity loggers were positioned to maintain constant inundation. Pre-processing of high frequency electrical conductivity data included filtering values above 7999 dS m^{-1} from the time series. Electrical conductivity values at the ecotone site were converted to salinity (PSU) using the equation detailed in (Hill et al. 1986). Additionally, spatial variability of water level and salinity was recorded using a meter stick and handheld salinity sensor (TDS meter or a refractometer) at random locations within the eddy covariance tower footprint approximately once per month during tower maintenance. This was done to understand landscape heterogeneity in water level and surface salinity at the towersite.

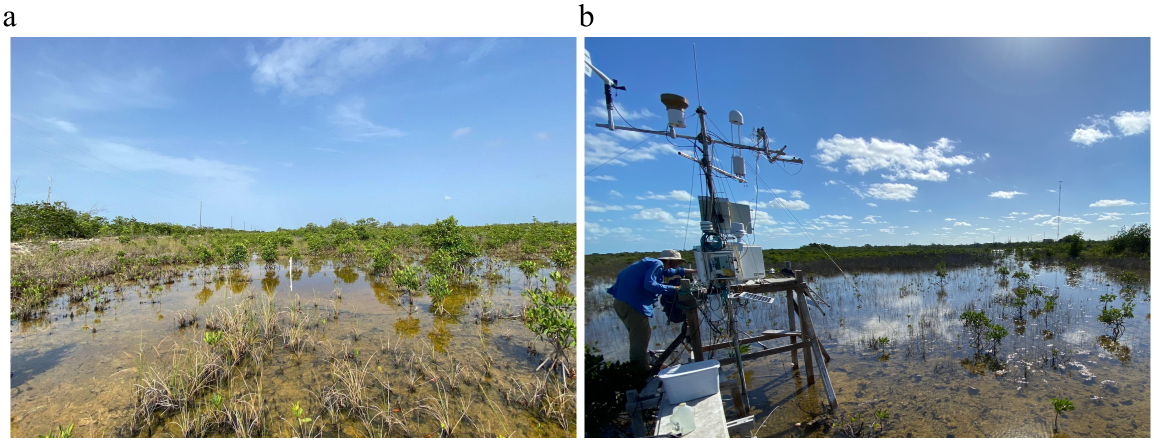

Figure 2. Locations for continuous monitoring instrumentation at ecotone site SE-1. The continuous water level logger is located in the tower pond (a) while the electrical conductivity logger is located beneath the gas flux and meteorology tower (b). Photographs courtesy of L. Wood.

Net ecosystem exchange rates were obtained from an AmeriFlux tower in the Everglades ecotone between the freshwater marl prairie and a mangrove scrub (US-EvM; 25.3539, -80.3810). Using the eddy covariance method (Aubinet et al. 2012), CO_2 and H_2O concentration were captured using a Li-COR open path infrared gas analyzer (LI-7500; Li-COR Biosciences, Lincoln, Nebraska). A sonic anemometer (CSAT3; Campbell Scientific Inc, Logan, Utah.) was used to measure sonic temperature and three dimensional wind velocity. Together the gas analyzer and anemometer were used to calculate the movement of gas between the ecosystem and the atmosphere. Data was collected at 10 Hz on a CR1000 datalogger (Campbell Scientific Inc., Logan, Utah), averaged every half-hour and stored on flash cards. Photosynthetically active radiation (PAR), the proportion of incoming solar radiation that plants use to photosynthesize (400

- 700 nm), was measured using a PAR Lite (Kipp and Zonen Inc., Delft, Netherlands) sensor. Air temperature (ºC) and relative humidity were measured using a HMP60 (Vaisala, Vantaa, Finland). Meteorological data were collected every 15 seconds on a CR1000x data logger, averaged every half-hour (Campbell Scientific Inc., Logan, Utah), and stored on flash cards. Raw flux data were processed using EddyPro software (Li-COR Biosciences, Lincoln, Nebraska). With atmospheric convention, negative NEE indicates net ecosystem CO_2 uptake, while positive NEE indicates net ecosystem CO_2 loss to the atmosphere.

Fluxes were filtered to remove erroneous data (NEE > - 5, NEE < 5 μmol CO_2 m^{-2} s^{-1}). Values were filtered further during conditions insufficient for flux measurements, such as: a) insufficient turbulence between the atmosphere and surface, b) incomplete half-hourly averages arising from routine instrument maintenance and calibration, and c) environmental conditions interfering with gas analyzer signal strength, such as rain events or bird fouling in the sensor path (Jimenez et al. 2012; Malone et al. 2014, 2021; Zhao et al. 2019). Thirty-seven percent of daytime data and 62% of nighttime data were filtered. The NEE data were split into low water level and high water level conditions corresponding with the ecotone water level and salinity relationship breakpoint. In the daytime data, 34% of the low water level data were removed and 41% of high water level data were removed. In the nighttime data, 59% of the low water level data were removed.

II. C. Data Analysis

Generalized additive mixed models (GAMMs) were used to evaluate changes in conditions over time using the *gamm* function in the ‘mgcv’ package in R (Wood & Wood 2015). Generalized additive mixed models are a nonparametric method for assessing relationships between variables (Wood 2017). Nonlinear relationships were explored through the use of smooth functions of predictor variables. Smooth predictor variables can also be grouped by factors using a ‘by’ argument within the smooth term to evaluate factor-smooth effects (Wood 2017). Basis functions for the smooth terms were kept as the default thin plate regression splines and restricted maximum likelihood (REML) was used (Wood 2017). For multivariate GAMMs, multicollinearity was assessed before developing a model using the *ggpairs* function in the ‘GGally’ package (Schloerke et al. 2021) and concurvity was evaluated using the *concurvity* function in the ‘mgcv’ package (Wood & Wood 2015). The assumptions of this approach are normality and homogeneity of variance of the residuals. These were evaluated with diagnostic plots using the *gam.check* function in the ‘mgcv’ package (Wood & Wood 2015). Following model fit, I used the *gam.check* function to ensure that k was optimized (Wood & Wood 2015).

Temporal autocorrelation was evaluated using the Durbin Watson test statistic in the ‘car’ package (Fox et al. 2007) and by plotting the autocorrelation function (*acf)* and the partial autocorrelation function (*pacf*) on the residuals (R Core Team 2021). The models’ correlation structures were accounted for by using the corARMA argument and fitting parameters suggested by the acf and pacf plots. The explanatory power of the final models were considered using the deviance explained of the gam portion of the final model (Wood 2017). Predictor smooth terms were considered significant if p values were less than 0.1.

II. C. 1. Q1: How has surface water level and salinity changed over time along the southeast coastline?

I measured changes in the mean seasonal water level over time. Using data from the coastal site ENPHC (Figure 1), I evaluated changes in mean seasonal water level over time by including year grouped by season (wet or dry) as the predictor variable. Although the dry season in this region extends from November to April and the wet season from May to October, water levels lag behind the seasonal definitions (Light & Dineen 1994). I accounted for this by shifting the onset of the wet season back two months, based on the lag that explained the most deviance in mean water levels averaged over the entire study period at the coastal site. I repeated this analysis for mean seasonal surface salinity.

II. C. 2. Q2: What is the relationship between surface water level and salinity at the ecotone compared to a freshwater and a saline ecosystem?

I measured the relationship between water level and salinity over time and in space at the ecotone site. I used univariate GAMMs to evaluate the relationship between water level and salinity. This analysis was limited to moderate salinity conditions (< 18 PSU) observed in 2021 for the high frequency continuous logger data at the tower and values observed in 2021 and 2022 for the spatially variable field measurement data. Next, I compared patterns observed at the coastal site to infer if the ecotone site had marine water source influence. Daily mean water level and salinity relationships were compared across sites for 2021.

II. C. 3. Q3: How do CO_2 dynamics change under different water levels at the ecotone?

I measured differences in ecosystem productivity and respiration by comparing light (Falge et al. 2001; Reichstein et al. 2012) and temperature response curves (Falge et al. 2001; Reichstein et al. 2012) for low water level and high water level conditions. Nonlinear response curves of NEE to variable environmental conditions were evaluated using the *nls* function in the 'nlstools' package (Baty et al. 2015). Light and temperature response curves were fit using different models, following (Jimenez et al. 2012; Malone et al. 2014). Light response curves were fit using a modified Michaelis-Menten saturation model (Falge et al. 2001; Jimenez et al. 2012; Johnson & Goody 2011) (Eq. 1):

$$NEE_{day} = R_{eco} - \frac{\alpha\phi P_{max}}{\alpha\phi + P_{max}} \qquad \text{Eq. 1}$$

Where R_{eco} is ecosystem respiration (μmol CO_2 m^{-2} s^{-1}), α is the apparent quantum efficiency of CO_2 uptake ($\frac{CO_2}{\delta\phi}$), ϕ is PAR (μmol m^{-2} s^{-1}), and P_{max} is the maximum CO_2 uptake rate on the ecosystem scale (μmol CO_2 m^{-2} s^{-1}). R_{eco} is the sum of all the respiratory fluxes in the tower footprint during the time sampled, including autotrophic respiration from primary producers and heterotrophic respiration from microbial communities (Chapin et al. 2006). Apparent quantum efficiency of CO_2 uptake is a measure of how efficiently light is captured and used to photosynthesize (Reichstein et al. 2012). Photosynthetically active radiation (PAR) is the proportion of incoming solar radiation that is used by plants to photosynthesize (400 to 700 nm) (Reichstein et al. 2012). Maximum CO_2 uptake rate (P_{max}) is the ecosystem limit on the capacity to fix CO_2 when PAR is not limiting (Reichstein et al. 2012).

To understand how respiration differs under different water level conditions, I fit temperature response curves using a modified Arrhenius equation (Falge et al. 2001; Jimenez et al. 2012; Logan 1982) (Eq. 2):

$$NEE_{night} = R_{eco} = R_0{}^{b*T_{air}} \qquad \text{Eq. 2}$$

Where R_{eco} is ecosystem respiration (μmol CO_2 m^{-2} s^{-1}), R_0 is the base respiration rate at 0 ºC (μmol CO_2 m^{-2} s^{-1}), *b* is an empirical coefficient that reveals the sensitivity of NEE to air temperature, and T_{air} is air temperature (ºCelsius). Standard error confidence intervals for parameters derived from response curve models were estimated using the *nlsBoot* function in the ‘nlstools’ package (Baty et al. 2015). Data was randomly sub-sampled 100 times with replacement.

I split the dataset into day (PAR > 0) and night (PAR = 0) components to fit light and temperature response curves. Response curves were fit under two water level conditions for the day and night components. This analysis used daily average water level to categorize high and low water level and all other variables (NEE, PAR, air temperature) used half-hourly data.

II. C. 4. Q4: How do CO_2 dynamics compare between the ecotone and freshwater marl prairie?

Comparisons between the ecotone flux tower and short hydroperiod freshwater marl prairie were conducted using parameters of Equation 1 and Equation 2. Previously published values for AmeriFlux tower (US-Esm; 25.4379, -80.5946) were used for the short hydroperiod freshwater marl prairie. The data collection and processing were conducted as described above for the ecotone tower site.

I compared the light and temperature response curves reported in this study to previously reported response curves for the short hydroperiod freshwater marl prairie ecosystem to determine how similar the ecotone is to freshwater ecosystems containing the same graminoid species. The comparison for marl prairie used information reported in (Jimenez et al. 2012) for a wet month with the highest water level above the surface (September, water level was 0.4 m above surface) and a dry month (January, water level was at the surface) in 2009.

III. RESULTS

III. A. Q1: How has surface water level and salinity changed over time along the southeast coastline?

Water levels showed increasing trends from 1993 - 2022 (Figure 3a). Water levels increased at the coastal site during both the dry and wet seasons. From 1994 to 2022, mean dry season water level increased by 0.18 m. From 1993 to 2021, mean wet season water level increased by 0.13 m. Water levels were higher in the wet season by 0.13 m on average compared to the dry season (Figure 3b).

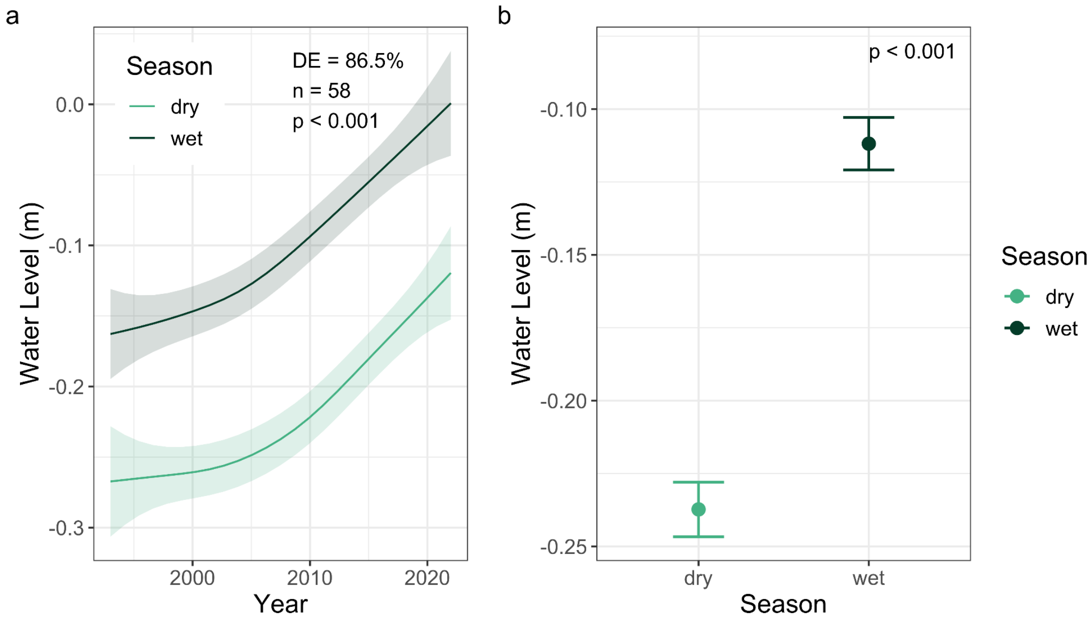

Figure 3. Mean seasonal water level by season from 1993 - 2022. The smoothed effect of year is grouped by season (a). The parametric effect of season on the mean water level is included (b).

Surface salinity increased over time at the coastal site (Figure 4a). The average dry season salinity increased to approximately 22 PSU before leveling off in 2005, while wet season salinity increased linearly over time (Figure 4a). On average, surface salinity was 13.38 PSU lower in the wet season compared to the dry season (Figure 4b).

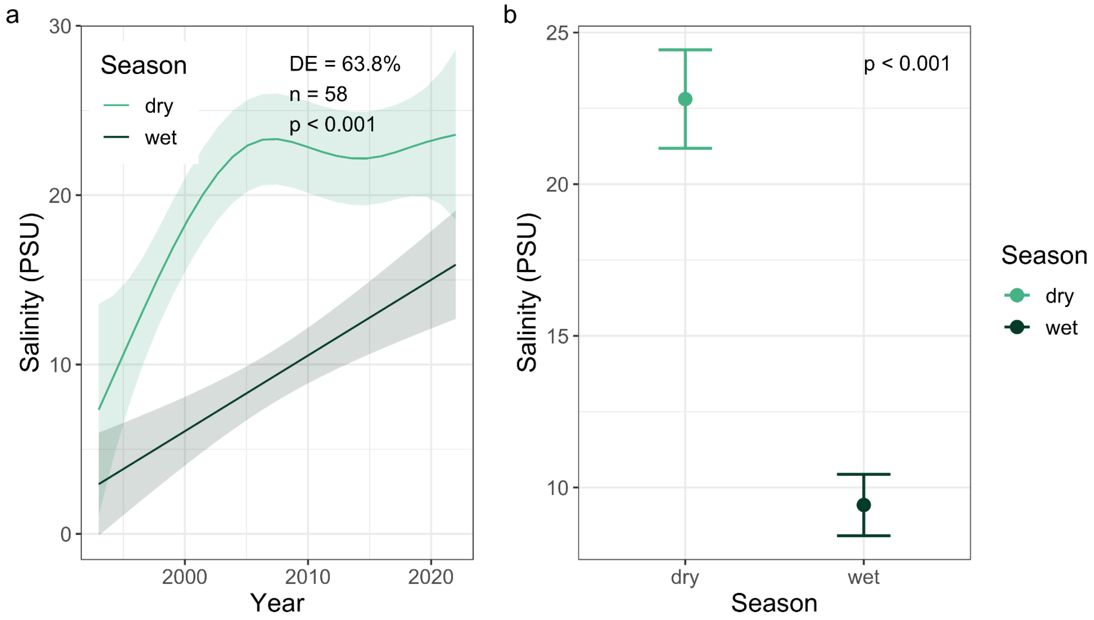

Figure 4. Mean seasonal surface water salinity from 1993 to 2022. The smoothed effect of year is grouped by season (a). The parametric effect of season on the mean salinity is included (b).

III. B. Q2: What is the relationship between surface water level and salinity at the ecotone compared to a freshwater and a saline ecosystem?

At low water levels the relationship between water level and salinity at the ecotone site matched the relationship observed at the coastal site (Figure 5b). Water level was a significant predictor of salinity at both sites. The coastal site had the larger range of salinity values (1.06 to 34.17 PSU) and mean salinity for the year was 17.21 PSU. The mean salinity at the coastal site was 14.54 PSU in the wet season (July to December) and 19.92 PSU in the dry season (January to June). The ecotone site salinity values ranged from 0 to 4.43 PSU with mean salinity of 0.48 PSU. Water level and salinity increase together at the coastal site (Figure 5a). At the ecotone site, water level and salinity increased together at water levels below 0.614 m, then salinity decreased with increasing water levels above 0.614 m (Figure 5b). At low water levels, the ecotone site shared the positive relationship observed at the coastal site.

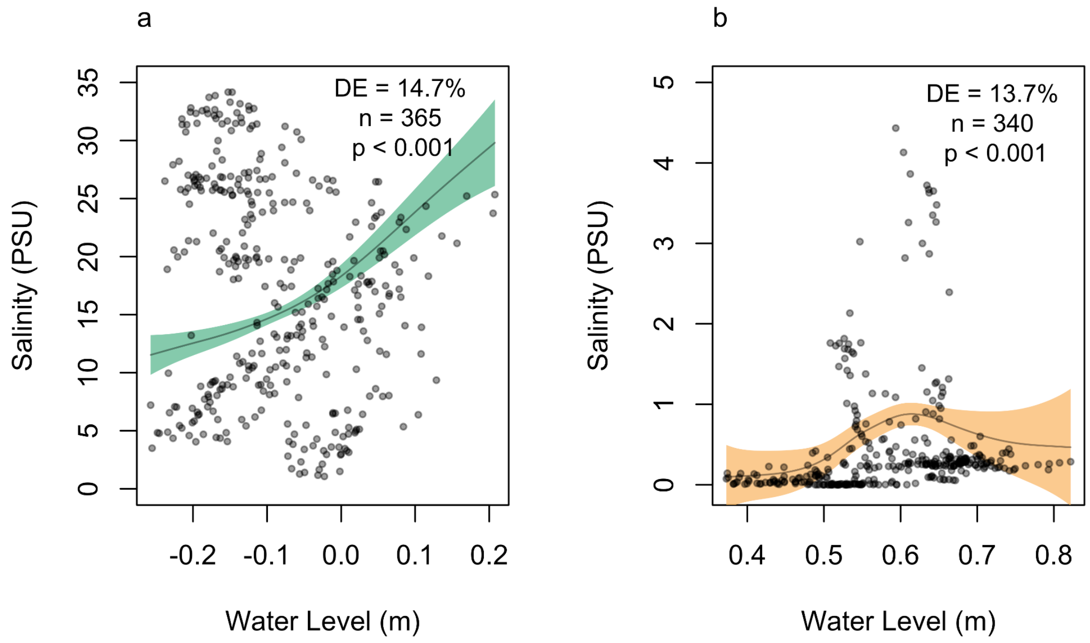

Figure 5. Daily mean water level against daily mean salinity for a coastal site (a) and ecotone site (b) for the most recent complete year of data available for each site (2021). Model deviance explained and significance of the water level predictor variable is noted in the top right corner of each panel.

Water level and salinity had distinct relationships at different spatial and temporal scales in the ecotone (Figure 6). The spatially variable landscape water level (0 to 0.58 m) and salinity (0.04 to 16.1 PSU) were positively correlated, with the highest salinity (16.1

PSU) co-occurring at higher water level (0.5 m) in 2022 (Figure 6a). Interestingly, the high frequency tower water level and salinity were positively correlated below 0.614 m and negatively correlated above 0.614 m, with the majority of salinity values greater than 1 PSU falling between water levels of 0.5 and 0.65 m (Figure 6b). When landscape salinity was compared against high frequency water level from the tower, there was a negative correlation below 0.676 m and positive correlation above this water level (Figure 6c). Landscape water level and tower water level were negatively correlated, suggesting topographic heterogeneity on the landscape (Figure 6d). Despite the different spatial scales of measurement, a water level of 0.614 to 0.676 m contained an inflection point in the water level and salinity relationship (Figure 6b and 6c). Water level was a significant predictor of salinity across spatial and temporal scales (Figure 6a - 6c).

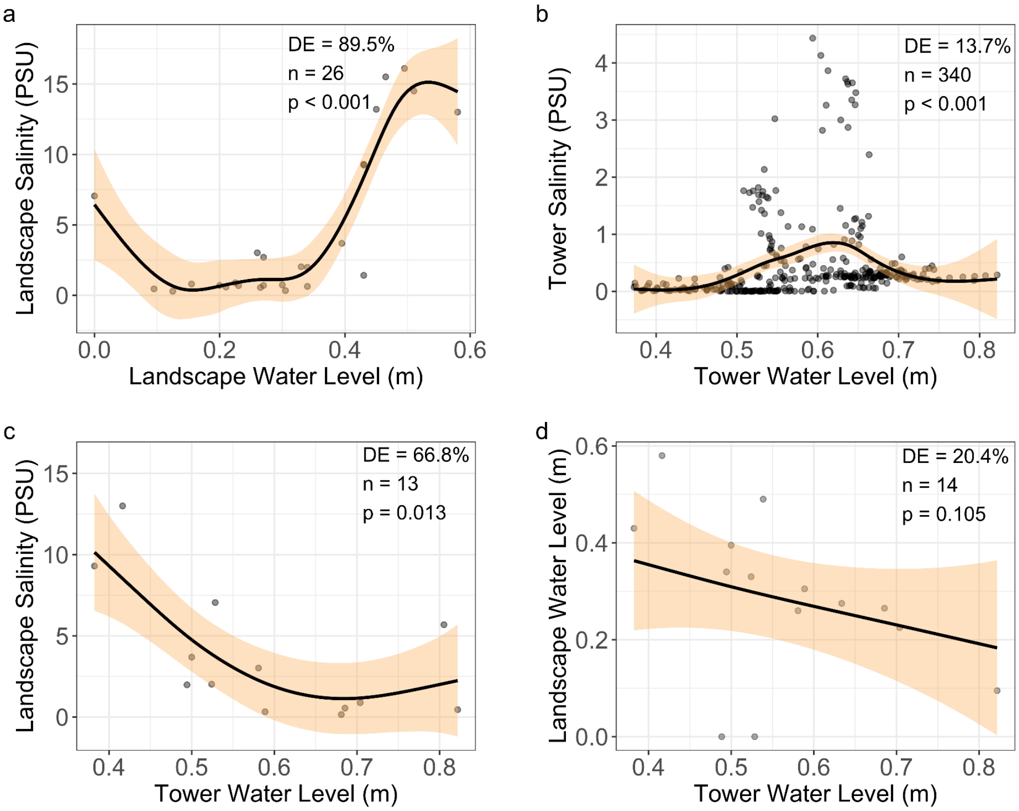

Figure 6. Daily mean water level against daily mean salinity at the ecotone site across spatial and temporal scales. Top row compares water level and salinity using the same measurement approach for spatial variability in the landscape (a) and high resolution temporal variability at the tower (b). Bottom row shows variables collected on the landscape compared to high resolution water level for salinity (c) and water level (d). Model deviance explained and significance of the water level predictor variable is noted in the top right corner of each panel.

III. C. Q3: How do CO_2 dynamics change under different water levels at the ecotone?

Environmental conditions were variable throughout 2021 (Figure 7). Continuous water levels ranged between 0.373 and 0.822 m above the surface, while landscape grab samples ranged between 0.0 and 0.58 m (Figure 7a). Continuous salinity and landscape grab samples also varied, with continuous salinity ranging from 0 to 4.43 PSU and landscape salinity ranging from 0.04 to 13 PSU. Landscape salinity values were also lower later in the year (Figure 7b).

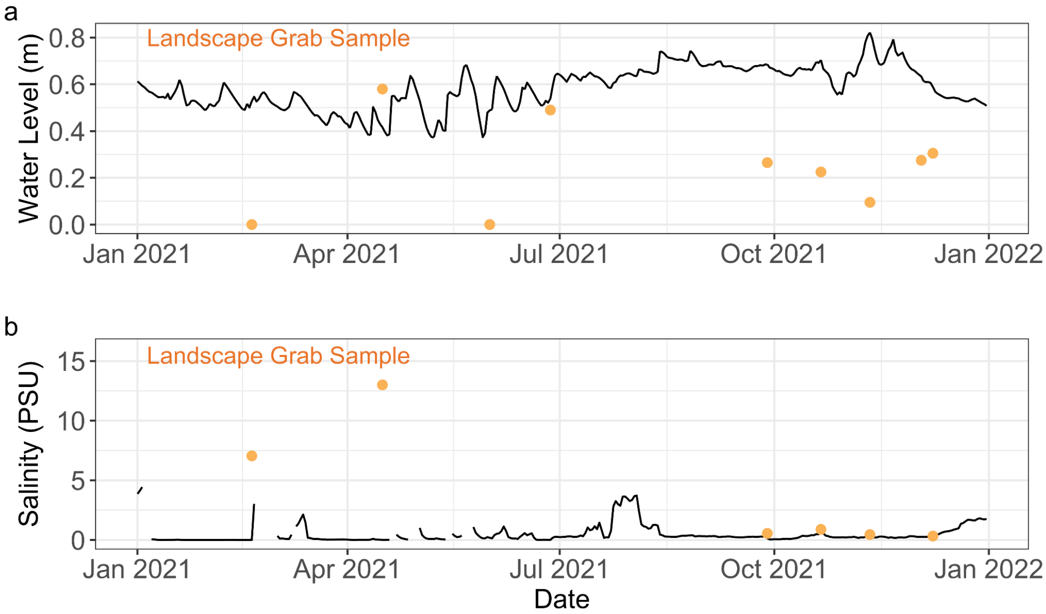

Figure 7. Mean daily environmental conditions and instantaneous measurements of landscape water level (a) and salinity (b) 2021-2022 at the Everglades ecotone.

The half hourly NEE ranged from -4.99 to 4.99 at the ecotone site. During the day, NEE ranged from -4.99 to 4.93 μmol CO_2 m^{-2} s^{-1} with a mean value of -0.98 μmol CO_2 m^{-2} s^{-1}. At night, NEE ranged from 0.002 to 4.99 μmol CO_2 m^{-2} s^{-1} with a mean value of 0.92 μmol CO_2 m^{-2} s^{-1}. Average hourly NEE followed a diurnal pattern with lower values (more uptake) in the day and higher values at night (Figure 8). The range of NEE values was larger under low water level conditions (Figure 8).

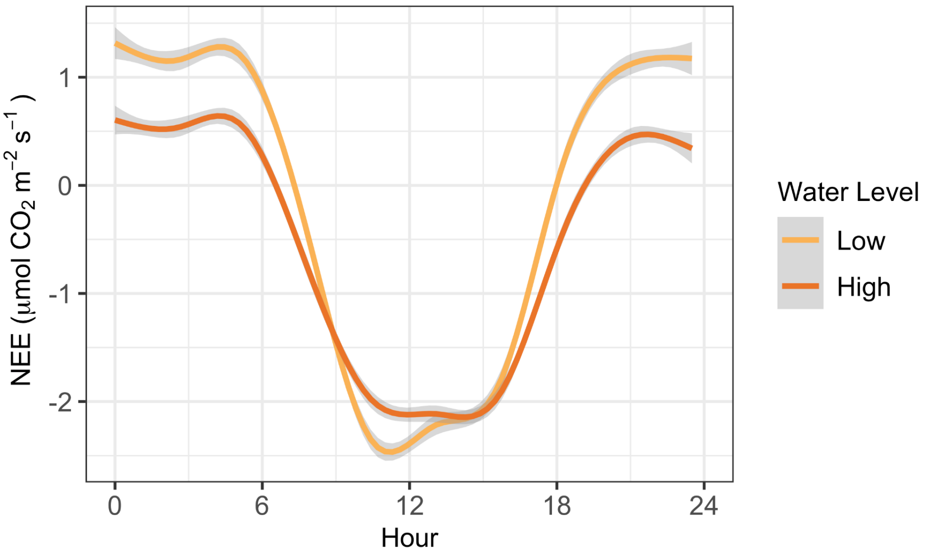

Figure 8. Hourly mean NEE under low (<0.614 m, light orange) and high (> 0.614 m, dark orange) water level conditions over a 24 hour period. Only days that had at least 32 observations of NEE (n = 127) were included.

Small differences in NEE occurred under low and high water levels, controlling for PAR. Low water level conditions had higher uptake rates (P_{max} = -3.693 ± 0.073) under low PAR conditions compared to high water level conditions (P_{max} = -2.812 ± 0.073) (Figure 9). This may suggest that higher water levels inhibit short statured vegetation photosynthetic capacity at dawn and dusk. Maximum ecosystem CO_2 uptake rates (P_{max}), and ecosystem respiration were lower under higher water levels, while apparent quantum efficiency (α) was higher under high water levels (Table 1).

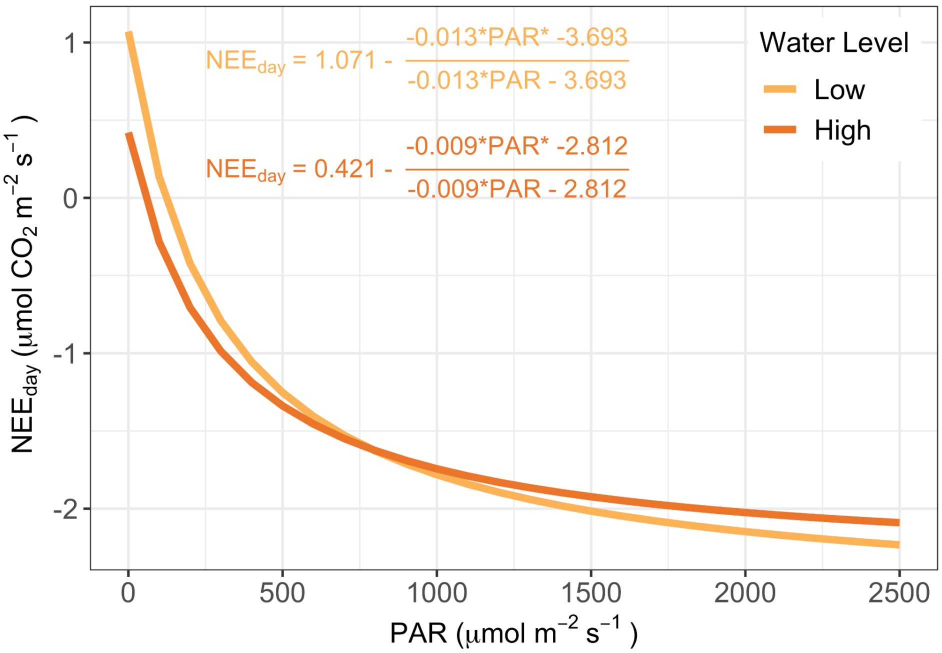

Figure 9. Light response curves for low (<0.614 m, light orange) and high (> 0.614 m, dark orange) water level conditions at the ecotone.

Table 1. Parameter estimates and standard errors (S.E.) from light response curves under low and high water level conditions at the ecotone.

Water Level Condition (n)	α (S.E.)	p-value	P_{max} (S.E.)	p-value	ER (S.E.)	p-value
Low Water Level (5154)	-0.013 (0.001)	<0.001	-3.693 (0.073)	<0.001	1.071 (0.037)	<0.001
High Water Level (3196)	-0.009 (0.001)	<0.001	-2.812 (0.073)	<0.001	0.421 (0.040)	<0.001

Temperature response curves differed by water level condition (Figure 10). Under low water levels, NEE increased exponentially with increasing temperature, indicating that low water levels did not dampen respiration (Figure 10). Under high water levels, NEE did not increase as quickly as at low water levels and stopped at 0.65 μmol CO_2 m^{-2} s^{-1} at 40ºC. Higher water levels buffered the effects of air temperature and limited metabolic activity by decreasing the oxic layer in the soil, though this relationship was not significant (Figure 10, Table 2). The base respiration rate at 0ºC (R_0) was higher under high water level conditions (Table 2).

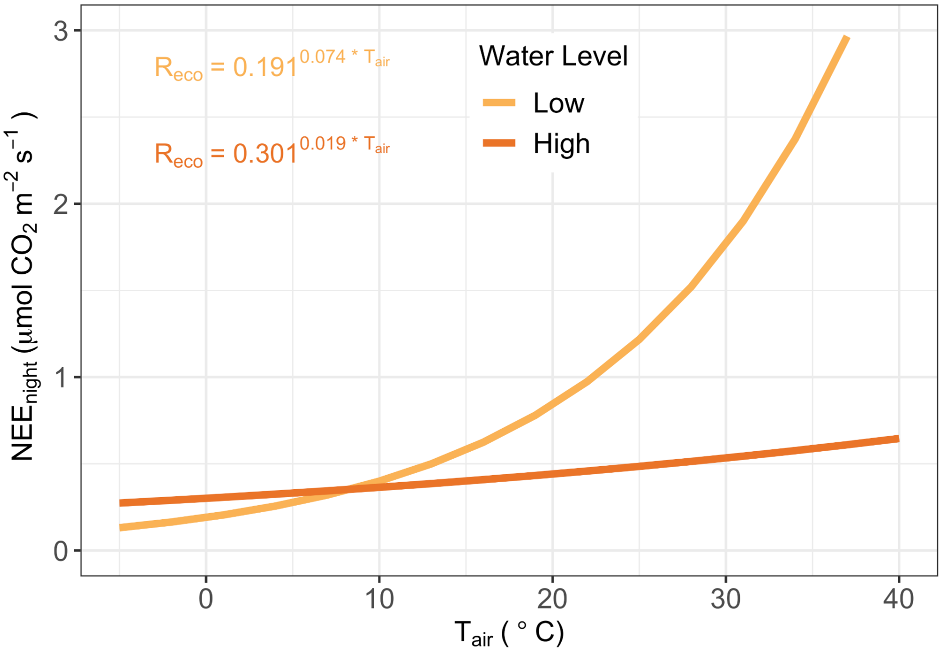

Figure 10. Temperature response curves for low (<0.614 m, light orange) and high (> 0.614 m, dark orange) water level conditions at the ecotone.

Table 2. Parameter estimates and standard errors (S.E.) from temperature response curves under low and high water level conditions at the ecotone.

Water Level Condition (n)	R_0 (S.E.)	p-value	b (S.E.)	p-value
Low Water Level (940)	0.191 (0.058)	<0.001	0.074 (0.011)	<0.001
High Water Level (669)	0.301 (0.244)	0.009	0.019 (0.023)	0.160

III. D. Q4: How do CO_2 dynamics compare between the ecotone and freshwater marl prairie?

The ecotone had larger uptake rates and less variability under different water level conditions compared to the marl prairie (Figure 11). Maximum uptake rates increased from P_{max} = -1.744 (lower confidence level = -2.054, upper confidence level = -1.511) to P_{max} = -3.406 (lower confidence level = -3.752, upper confidence level = -3.160) (Table 3). Water levels above the surface in the marl prairie had the lowest uptake.

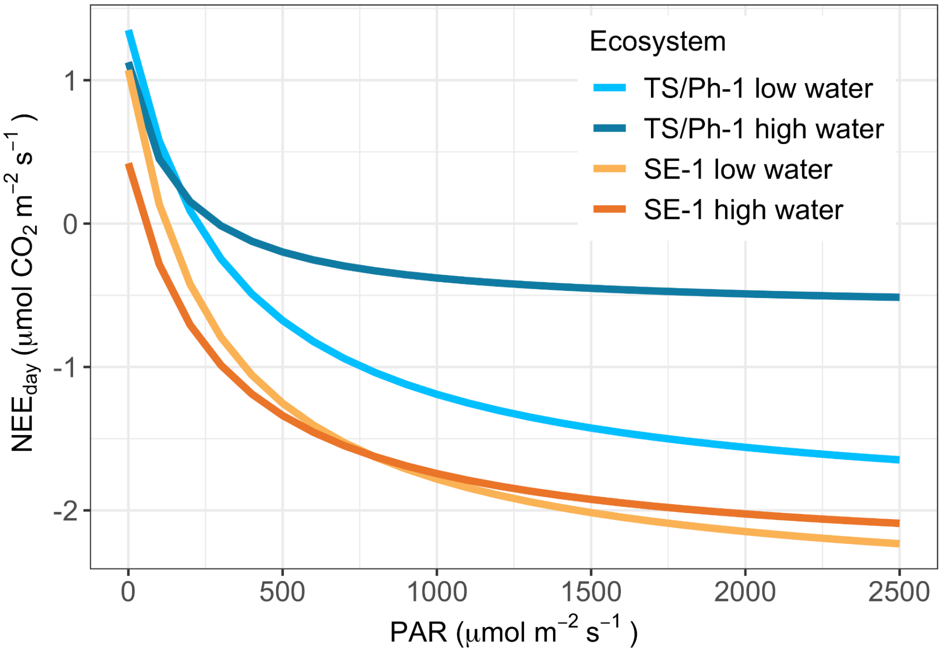

Figure 11. Comparison of light response curves between the ecotone (orange) and the marl prairie (blue) under low (light color) and high (dark color) water level conditions.

Table 3. Parameter estimates and confidence intervals (lower confidence level LCL, upper confidence level, UCL) from light response curves under low and high water level conditions at the marl prairie.

Water Level Condition	α	LCL	UCL	P_{max}	LCL	UCL	ER	LCL	UCL
Dry	-0.010	-0.015	-0.007	-3.406	-3.752	-3.160	1.350	1.097	1.700
Wet	-0.011	-0.022	-0.006	-1.744	-2.054	-1.511	1.126	0.886	1.444

Ecosystem respiration trends differed in the ecotone and the marl prairie (Figure 12). In the ecotone, higher water levels dampened respiration, but in the marl prairie respiration in the dry condition was higher than the wet condition until 30 ^{o}C (Figure 12). Base respiration (R_0) was highest for the dry marl prairie at 0.689 μmol CO_2 m^{-2} s^{-1} (lower confidence level = 0.529, upper confidence level = 0.863) (Table 4). This could be because the lower water level (water level 0 m above the surface) allows both plants and microbial communities to respire more efficiently. The respiration was highest at high temperature (> 30 ^{o}C) in the ecotone under low water level conditions and the marl prairie under wet conditions. The similar trend between the low water level condition in the ecotone and wet month condition in the marl prairie could be because these conditions represent similar water levels above the surface (0.373 to 0.614 m for the ecotone; 0.4 m for the marl prairie) in each respective ecosystem. Respiration was lowest at median and high temperatures (15 to 40 ^{o}C) in the ecotone under high water level conditions.

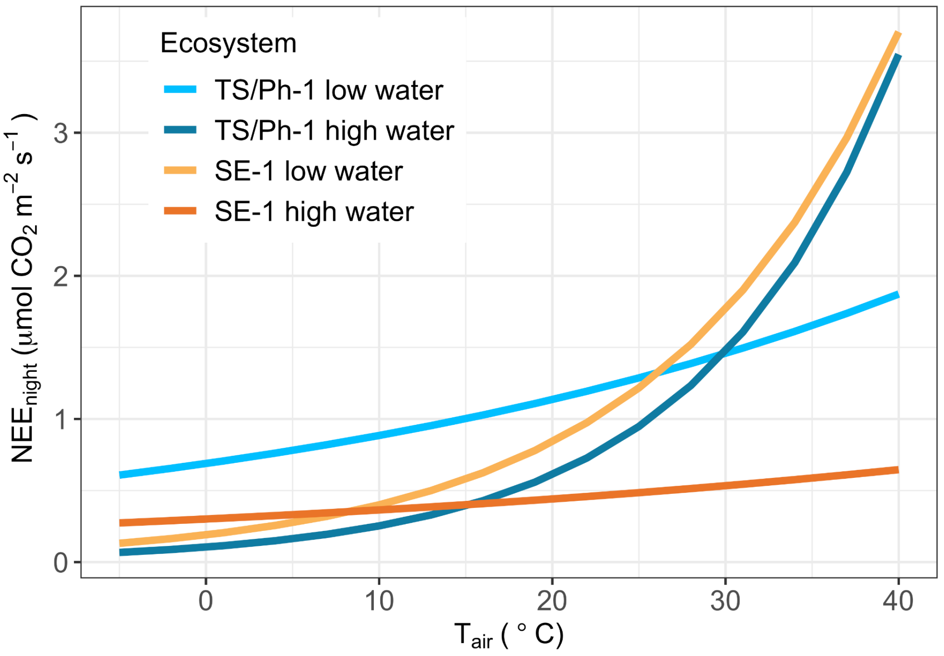

Figure 12. Comparison of temperature response curves between the ecotone (orange) and the marl prairie (blue) under low (light color) and high (dark color) water level conditions.

Table 4. Parameter estimates and confidence levels from temperature response curves under low and high water level conditions at the marl prairie.

Water Level Condition	R_0	LCL	UCL	b	LCL	UCL
Dry	0.689	0.529	0.863	0.025	0.008	0.043
Wet	0.105	0.009	1.072	0.088	0.000	0.178

IV. DISCUSSION

The primary objective of this research was to understand how hydrology influences CO_2 dynamics in a subtropical coastal ecotone. Water level and salinity have increased along the southeast Everglades coastline, which may be an indication of sea level rise and/or alterations in seasonal freshwater flow. In the brackish ecotone, the relationship between water level and salinity resembled a coastal ecosystem with a positive relationship at low water levels (<0.614 m) and a freshwater ecosystem with a negative relationship at high water levels (>0.614 m). Patterns in CO_2 dynamics differed between the freshwater marl prairie and the ecotone, suggesting that ecotones can be resilient to changes in hydrology.

Comparisons between CO_2 dynamics in the ecotone and the freshwater marl prairie show differences in the sensitivity to hydrologic changes. The ecotone's CO_2 uptake rates were less sensitive to water level compared to the marl prairie, where high water levels decrease photosynthetic uptake (Jimenez et al. 2012; Malone et al. 2021). When water levels increase in the short statured marl prairies, water covers vegetation, which limits ecosystem uptake by decreasing the ability of plants to photosynthesize (Schedlbauer et al. 2010). Inundation also leads to the development of anoxic conditions in the soil and limits aerobic respiration from plant roots and soil microbial communities (Mitsch & Gosselink 2015). Under dry conditions in the marl prairie both CO_2 uptake rates and ecosystem respiration increase, with uptake rates increasing more than respiration (Jimenez et al. 2012; Malone et al. 2014; Schedlbauer et al. 2010; Zhao et al. 2019). Average dry season CO_2 uptake rates in the marl prairie exceeded uptake in the ecotone (Jimenez et al. 2012; Schedlbauer et al. 2010). In one study in the marl prairie, base respiration at 0ºC did not decrease substantially at water levels greater than 0.30 m, suggesting that water level effects on soil oxygen availability are limited above this threshold (Zhao et al. 2019). This is contrary to the results in the ecotone where base respiration was higher under high water levels.

The different CO_2 uptake sensitivity to water levels in each ecosystem is explained by different community composition and species responses to inundation. The ecotone contains sawgrass, spikerush, red mangroves, and aquatic periphyton communities, while the short hydroperiod marl prairie is co-dominated by sawgrass and muhly grass, and contains periphyton. All of the emergent aquatic plant species have different photosynthetic capacities and tolerances to inundation and salinity stress (Barr et al. 2009; Hogan et al. 2022; Zhao et al. 2021). Scrub red mangroves have higher average photosynthetic capacity (8 - 10 μmol CO_2 m^{-2} s^{-1} and 2 - 14 μmol CO_2 m^{-2} s^{-1} ; Barr et al. 2009; Hogan et al. 2022) than sawgrass (7 μmol CO_2 m^{-2} s^{-1}; Zhao et al. 2021). All species' photosynthetic capacities decrease under inundation and salinity stress, though at different rates. Hogan et al. (2022) found CO_2 assimilation rates for scrub red mangroves were higher in drier tree island center habitats in the dry season (~10 μmol CO_2 m^{-2} s^{-1}) compared to wetter tree island edge habitats in the wet season (~5 μmol CO_2 m^{-2} s^{-1}), but that CO_2 assimilation rates increased with increasing water level, regardless of habitat or season. (Barr et al. 2009) measured the lowest photosynthetic capacity of scrub red mangroves (> 4 μmol CO_2 m^{-2} s^{-1}) when surface water salinity was hypersaline (37 ppt), though there were limited observations of these conditions. In a mesocosm inundation experiment, (Zhao et al. 2021) found sawgrass photosynthetic capacity decreased to ~ 4 μmol CO_2 m^{-2} s^{-1} over time when exposed to elevated water levels (10 and 35 cm above the surface) for prolonged periods. Additionally, the marl prairie has higher CO_2 uptake than the ecotone when the marl prairie is dry because the site is co-dominated by muhly grass, which has increased photosynthetic capacity (6 - 10 μmol CO_2 m^{-2} s^{-1}) in dry conditions (Zhao et al. 2021). In the ecotone, mangroves and periphyton could maintain productivity at higher water levels when sawgrass is stressed or submerged. This might explain why CO_2 uptake was not responsive to higher water levels in the ecotone. The composition of the ecotone is also likely to continue to shift to mangrove dominance in the future with shifting hydrology.

Hydrology will change in the ecotone, driven both by saltwater intrusion from sea-level rise and increased freshwater flow. Sea-level rise is accelerating in south Florida, outpacing accretion rates for coastal scrub mangrove ecosystems (Parkinson & Wdowinski 2022). Marine influence from sea-level rise in this karstic landscape results in groundwater-based saltwater intrusion that is spatially variable across the landscape and can reach further inland than ecosystems with direct tidal connection (Price et al. 2006). Increasing marine influence from saltwater intrusion will change the water level and salinity relationship by bringing more saline water into the ecotone and increasing the threshold value for water level to dilute salinity. Freshwater flow will also increase in the ecotone with the planned Biscayne Bay Southern Everglades Ecosystem Restoration (BBSEER) project under the Comprehensive Everglades Restoration Plan (CERP) (National Academies of Sciences, Engineering, and Medicine 2022). The BBSEER project will increase dry season freshwater flow, which will decrease the range of water levels observed in the ecotone (National Academies of Sciences, Engineering, and Medicine 2022). In the study year, water levels in the ecotone did not drop below the surface, so the C dynamics in dry conditions are unknown. Proposed freshwater delivery plans could lead to consistently wetter and less variable conditions in the ecotone.

Changing hydrology may influence the location of and community composition within the ecotone. Studies in the Everglades indicate that the locations of estuarine ecotones (Dessu et al. 2018), and the mixed salinity tolerance communities (Meeder et al. 2017) and low productivity zone on the southeast coast (Ross et al. 2000) are driven by volume and timing of freshwater delivery. On the southeast coast, mixed salinity tolerance communities and the low productivity zone are further inland where there is less water delivered in the dry season (Meeder et al. 2017; Ross et al. 2000). The low productivity zone is likely to continue to migrate landward because of saltwater intrusion, though the rate of expansion may decrease with increased freshwater delivery during the dry season (Sklar et al. 2019). Red mangroves will continue to establish in marl prairie where there are already mangroves to produce propagules, as has been previously documented in this area in vegetation surveys (Ross et al. 2000) and using sediment cores (Meeder et al. 2017). Alternatively, increased freshwater volume and decreased water level variability could limit mangrove expansion if water levels are so high that they limit seedling growth or prevent propagules from establishing.

Changing hydrology will also influence CO_2 dynamics in the ecotone. As the ecotone shifts toward a taller and more inundation and salinity tolerant assemblage, ecosystem CO_2 uptake will likely remain insensitive to high water level. Higher water level will also limit respiration by acting as a physical buffer that increases anoxia in the soil, regardless of the dilution effect on salinity. Under anoxic conditions, aerobic respiration in roots and soil microbial communities is reduced. With CO_2 uptake rates maintained and respiration dampened at high water level, the ecotone could act as a net CO_2 sink as water levels increase.

V. CONCLUSION

Low elevation coastal wetlands are undergoing rapid structural and functional transformation due to climate change and land and water management. Inundation and salinization beyond plant species' tolerances stress communities, while shifting disturbance regimes can rapidly kill stressed vegetation (Lagomasino et al. 2021; Stagg et al. 2021). Increases in salinity lead to ecosystem transitions, with halophytic species replacing freshwater species (Fuller & Wang 2014; Saintilan et al. 2014). Seawater nutrient subsidies also influence the inland expansion of ecotones (Koch & Snedaker 1997; Smith & Goetz 2021) and can contribute to ecosystem degradation (Deegan et al. 2012; Mahoney & Bishop 2017). Coastal ecotones will continue to develop and shift inland because of accelerating sea-level rise (Smith & Goetz 2021), so it is important to study how they maintain function under changing conditions (Herbert et al. 2015; Osland et al. 2022) and how they compare to adjacent ecosystems (Coldren et al. 2016; Guo et al. 2017; Jiang et al. 2012).

This study indicates that coastal ecotones can persist and maintain function where there is sufficient hydrologic and landscape connectivity. In the ecotone, water levels got high enough to first connect saline portions of the landscape and then dilute surface salinity. Hydrologic connectivity and variability contributes to ecosystem function by alleviating stressful conditions such as prolonged inundation and salt stress. Additionally, mangroves maintained CO_2 dynamics in the ecotone by making ecosystem uptake rates insensitive to high water levels while respiration was dampened. Mangroves first migrated from the coast through tidal connection and then had optimal hydrologic conditions that allowed them to establish in the ecotone. Landscape connectivity contributes to coastal ecosystem persistence by allowing coastward communities to migrate inland as abiotic conditions become less favorable on the coast.

Studying CO_2 fluxes in ecotones allows one to understand how ecosystems maintain CO_2 dynamics along abiotic gradients (Poyatos et al. 2014). As coastal wetlands are transformed by sea-level rise and coastal squeeze globally, it is necessary to evaluate how these ecosystems persist (Schuerch et al. 2018). Because coastal wetland sediments store disproportionately large pools of C (Mitsch & Gosselink 2015), these ecosystems could contribute positive feedbacks to climate change if they are net sources of CO_2 to the atmosphere. This study indicates that coastal ecotones can maintain CO_2 uptake and continue to store C, even under variable conditions.

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