

ECOSYSTEM METABOLISM OF COASTAL TEXAS STREAMS ACROSS
PRECIPITATION REGIMES AND LAND USE GRADIENTS

A Thesis

Presented to

The Faculty of the Department of Biological Sciences
at Sam Houston State University

In Partial Fulfillment

of the Requirements for the Degree of
Master of Science

by

Connor L. Brown

May, 2022

ECOSYSTEM METABOLISM OF COASTAL TEXAS STREAMS ACROSS
PRECIPITATION REGIMES AND LAND USE GRADIENTS

by

Connor L. Brown

APPROVED:

Amber J. Ulseth, PhD
Committee Director

Jerry L. Cook, PhD
Committee Member

Ross J. Guida, PhD
Committee Member

Jeffrey R. Wozniak, PhD
Committee Member

John B. Pascarella, PhD
Dean, College of Science and Engineering
Technology

ABSTRACT

Brown, Connor L. *Ecosystem metabolism of coastal Texas streams across precipitation regimes and land use gradients.* Master of Science (Biology), May, 2022, Sam Houston State University, Huntsville, Texas.

Anthropogenic pressures of land use and climate change have the potential to impact chemical and biological factors that can affect stream ecosystem function. Ecosystem metabolism (i.e., gross primary production [GPP] and ecosystem respiration [ER]), is a metric of stream ecosystem function as it integrates nutrient and carbon cycling. We estimated daily GPP and ER using high temporal frequency oxygen data from nine Texas coastal streams falling along a precipitation and land use gradient. The most arid stream watershed land use consisted of predominantly shrubs and grasses (55%), whereas the most mesic stream watershed consisted of predominantly agricultural land cover (90%). These coastal streams did not show strong seasonal variations of GPP or ER, as often found in more temperate regions. GPP ranged from $0.3 \text{ g } O_2 m^{-2} d^{-1}$ to $0.9 \text{ g } O_2 m^{-2} d^{-1}$, slightly peaking in the middle of the precipitation and land use gradients. ER ranged from $-1.0 \text{ g } O_2 m^{-2} d^{-1}$ to $-4.9 \text{ g } O_2 m^{-2} d^{-1}$ with no apparent trend along the precipitation or land use gradient. These results suggest local factors, such as light and nutrients, may be driving ecosystem metabolism, rather than broad scale processes.

KEY WORDS: Ecosystem metabolism, Primary production, Ecosystem respiration, Net ecosystem production, Land use.

ACKNOWLEDGEMENTS

I would like to thank Dr. Amber Ulseth for everything she's done for me during my time at SHSU. Without her mentorship and endless support, I would not be the ecologist I am today and I am eternally grateful. I also want to thank my friend and mentor, Dr. Kelbi Delaune, for instilling her love of streams into me, her constant support, and encouragement to continue pursuing my education. I would also like to thank all the undergraduates who helped me in the field during my research. Finally, I would like to thank my friends, Chelsea Thorn, Brittany Cornell, and Dani Gray for constant encouragement and countless hours in the field. This material is based upon work supported by the National Science Foundation under Grant No. 1927639.

TABLE OF CONTENTS

	Page
ABSTRACT	iii
ACKNOWLEDGEMENTS	iv
TABLE OF CONTENTS	v
LIST OF TABLES	vii
LIST OF FIGURES	viii
CHAPTER	
I INTRODUCTION	1
Background	1
Ecosystem Metabolism	1
Ecosystem Metabolism Drivers	3
Research Questions	8
II METHODS	10
Study Areas	10
Site Descriptions	10
Ecosystem Metabolism	16
DOC and Nutrients	17
Discharge	18
Statistical Analysis	18
III RESULTS	19
Ecosystem Metabolism	19
DOC and Nutrients	26
Discharge	30

Principal Component Analysis and Structural Equation Model	32
IV DISCUSSION	36
Ecosystem Metabolism	36
DOC and Nutrients	38
Discharge.	40
Precipitation and Land use Gradients	40
Conclusion	41
REFERENCES	42
APPENDIX A	53
Metabolism Data.	53
VITA	62

LIST OF TABLES

Table	Page
1 Site Summary	14
2 Metabolism Summary	25
3 DOC and Nutrient Concentrations	26
4 Summary of Site Discharge	30

LIST OF FIGURES

Figure		Page
1	Conceptual Diagram	8
2	Texas Precipitation Gradient	12
3	Watershed Land Use	13
4	WMC	15
5	TRC	15
6	Gross Primary Production and Ecosystem Respiration	20
7	Gross Primary Production	21
8	Ecosystem Respiration	22
9	Net Ecosystem Production	23
10	Ecosystem Metabolism for Three Sites	24
11	Dissolved Organic Carbon	27
12	Nitrate	28
13	Soluble Reactive Phosphorous	29
14	Site Discharge	31
15	Principal Component Analysis	33
16	SEM 1	34
17	SEM 2	35
18	Tranquitas Creek.	53
19	San Fernando Creek	54
20	Aransas River	55
21	Perdido Creek	56
22	Mission River	57

23	Placedo Creek	58
24	Garcitas Creek	59
25	West Mustang Creek	60
26	East Mustang Creek	61

CHAPTER I

Introduction

Background

Although inland fresh waters cover 1% of the Earth's surface, they disproportionately provide valuable services such as water purification, irrigation, flood control, support biodiversity, nutrient cycling, and carbon storage [54, 72]. Many of these ecosystem services are linked to stream flow regime. Global climate models predict many regions will become more arid. Annual precipitation will decrease, while timing and intensity of precipitation events will increase [23]. With increases in human populations, more land is expected to be urbanized or converted for agricultural use. This can lead to more impervious surfaces, increased nutrient loads, and increased turbidity. Ecosystem functions such as nutrient cycling, and carbon storage respond to changes in a stream's watershed, such as native vegetation being developed for urban, or agriculture uses; or changes in precipitation regime. Changes in climate and land use affects ecosystem functions of streams [30].

Ecosystem Metabolism

Ecosystem metabolism is a measure of ecosystem function and modulates nutrient and organic matter cycling [39, 72]. Ecosystem metabolism encompasses gross primary production (GPP), the fixation of inorganic carbon to organic carbon via photosynthesis, and ecosystem respiration (ER), the mineralization of carbon by autotrophs and heterotrophs. A majority of our knowledge on ecosystem metabolism in rivers comes from small rivers with discharge less than $0.1 \text{ m}^3 \text{ s}^{-1}$, with active benthic zones, rather than large rivers with planktonic zones [9, 33]. Both proximal and distal drivers control GPP and ER. Proximal drivers include light, temperature, nutrients, hydrology, and organic matter, whereas distal drivers include land use, climate, soil, vegetation, and disturbance [11, 39].

GPP and ER can be estimated from diel changes in dissolved oxygen concentrations [51]. GPP is a positive flux because oxygen is released via photosynthesis, and ER, a negative flux because oxygen is consumed during respiration. Net ecosystem production (NEP) is the sum of GPP and ER fluxes. Ecosystems with a positive NEP are autotrophic, because GPP exceeds ER, whereas ecosystems with negative NEP are heterotrophic, because GPP is less than ER [42].

With advances in technology, methods of measuring ecosystem metabolism in streams have changed since the first introduction of open-channel ecosystem metabolism by Odum (1956). Historically, due to measurement constraints, ecosystem metabolism was most often measured on clear weather days for short time periods [9, 51]. Using Odum's original open-channel metabolism method involved collecting samples every 2-4 hours and estimating the dissolved oxygen with titration [51]. Following Odum's method, the first generation of stream sensors to continuously measure dissolved oxygen were developed. Because these sensors were expensive and drifted, they were deployed for short time periods (e.g., 2-3 days) during stable stream flow conditions [9]. However, with advanced sensor technology and computational power, in the last decade we have been able to obtain high-frequency time series of stream water dissolved oxygen and temperature data, ranging from months to years, to calculate ecosystem metabolism. These high frequency estimates of ecosystem metabolism have led to insight into the controls of GPP and ER in streams [5, 8].

Ecosystem Metabolism Drivers

With the insight into controls of GPP and ER, we are beginning to parse out direct and indirect drivers of ecosystem metabolism [11, 27]. Proximal drivers of ecosystem metabolism, such as light and nutrient concentrations, directly drive changes in rates of ecosystem metabolism, while distal drivers, such as precipitation regimes and watershed land use, indirectly drive changes in ecosystem metabolism by driving changes in proximal drivers (Figure 1).

Proximal Drivers

Light controls GPP from daily to seasonal time-scales, as GPP is positively correlated with light availability [8, 48, 60]. For example, streams with little to no riparian vegetation, such as those flowing through urban and agricultural areas, have more light reaching stream primary producers, which drives greater fluxes of GPP when compared to their forested counterparts [2, 8, 11]. Across 72 streams in the United States and Puerto Rico, urban and agricultural streams had a 2-fold increase in GPP vs reference (i.e., non-agriculture and non-urban) streams with riparian vegetation, that was attributed to increased nutrients and light [11]. In an intermittent suburban stream, light was found to be the primary driver of increased GPP despite increased nutrient concentrations [8]. In a semi-arid stream in Nevada, with little riparian vegetation and high light, light was also attributed to high levels of GPP [20]. Even in forested streams, seasonality of leaf cover drives the temporal pattern of GPP. In Walker Branch, a low-order, forested stream located in Tennessee, rates of GPP peaked in spring prior to leaf out but then declined as the canopy closed in summer and fall seasons [2, 60].

Besides canopy cover, factors such as turbidity and slope control light availability to

stream ecosystems [14, 35]. Increasing turbidity within a stream results in less light reaching the primary producers, thus decreasing GPP. Turbidity may have a seasonal component, increasing during rainy seasons and resulting in depressed GPP during those time periods [35]. High riparian slopes, incised stream channels, or canyon walls limit light reaching the primary producers due to shading, resulting in reduced GPP [14, 35].

Temperature also drives both GPP and ER in streams. GPP is expected to increase with increasing temperatures at approximately half the rate as ER [55]. For instance, in geothermal streams, negative NEP increased exponentially with increasing temperature due to the imbalance of increasing GPP and ER [22]. Increasing biomass with increasing temperatures also explained increases in GPP and ER in 12 streams near Reykjavik, Iceland [53]. The recovery rate of primary producer biomass following disturbance, such as scouring, may be in part dictated by temperature. For example, increased temperature was linked to quick recovery rates of GPP and ER following scouring events in a Swiss sub-alpine stream [66].

Nutrient concentrations and ecosystem metabolism can modulate each other, with low nutrient concentrations suppressing ecosystem metabolism and high nutrient concentrations leading to daily decreases in nutrient concentrations coinciding with higher production. For instance, based on a 20-year ecosystem metabolism record in a Spanish River, ER was reduced 2.5-fold and GPP 1.8-fold after the implementation of a waste water treatment plant and subsequent reduction of nutrient concentrations [5]. If nutrients are limited, GPP and ER will be suppressed. With an excess of nutrients beyond demand, nutrients will be transported downstream [18]. Streams with high nutrient loads may have increased ER, which may lead to large fluctuations in oxygen concentrations and may drive streams to

become hypoxic [5]. However, in 72 streams across the United States and Puerto Rico using short-term ecosystem metabolism estimates (e.g. 24-48hr), multiple regression models revealed weak relationships between nutrient concentrations and GPP and ER [11]. As you move from a forested stream to one with increasing urban or agricultural land use, you can expect to see an increase in nutrients from anthropogenic runoff [12, 27]. These increased nutrients could increase rates of ecosystem metabolism.

Dissolved organic matter (DOM) can be a strong driver of ER. DOM in aquatic ecosystems can originate from autochthonous sources such as benthic biofilms, phytoplankton, and macrophytes or allochthonous sources, such as soils and leaf litter [13, 27, 73]. DOM can also vary seasonally. In areas with deciduous vegetation, allochthonous sources dominate in fall and winter, with increasing leaf litter entering the streams. In comparison, autochthonous sources dominate in the summer [1]. In 33 Austrian streams, autochthonous DOM was found in urban and agricultural streams, while allochthonous DOM was found in forested streams [27]. DOM from autochthonous and allochthonous sources vary in their composition and bioavailability. DOM from autochthonous sources has a smaller molecular weight and less aromaticity than DOM from allochthonous sources, and is also more bioavailable (i.e. easily consumed by microbes) [73]. DOM that is more bioavailable is able to fuel microbes resulting in higher fluxes of ER [27]. DOM quantity and quality are also affected by land use of the watershed. For instance, watersheds with agriculture in the watershed will have more DOM from agricultural soils, which tend to be rich in organic matter, and could increase ER [27]. Readily labile DOM is able to be quickly mineralized and provides an energy source for microbes resulting in increased ER fluxes, while intermediate labile DOM is able to provide a downstream subsidy potentially fueling downstream

ecosystem metabolism [71].

Hydrology is another controlling factor of ecosystem metabolism in streams, exerting both direct and indirect forces. At lower flows, streams are more efficient at transforming nutrients and DOM, however, at higher flows streams transport nutrients and DOM downstream [26, 32]. If nutrients and DOM have shorter residence times, that is at higher stream flows, they are more likely to be transported downstream [17, 19]. Frequent high flow events may also alter the geomorphology of streams by incising stream banks, and this will indirectly alter flow and light regimes of the stream [14]. Streams with highly incised banks will receive less light than in streams without incised banks. Frequent high flow events can also increase turbidity, which will further limit the light available to primary producers [14, 35]. Streams with seasonal increases in discharge may have primary producers that are adapted to increases in discharge [43]. For instance, in 10 sub-alpine streams with seasonal high flows, an increase in GPP coincided with snowmelt, but decreased with other scouring events [69]. Hydrology also controls DOM input, with high flows pulsing in large quantities of terrestrial DOM [24, 58]. The increased flow rapidly shunts DOM downstream, decreases residence time and therefore is exported downstream; with decreased flow, residence time of DOM is increased, and is more likely to increase ER [7, 58].

Distal Drivers

Light, nutrient concentrations, and DOM are dependent on precipitation regimes. Arid streams tend to have less riparian cover than mesic forested streams, thus more light compared to forested streams, which will lead to an increase in GPP [20, 35]. Arid streams will

also have less nutrient runoff caused by precipitation events than forested streams. Precipitation transports nutrients through the watershed resulting in high nutrient concentrations within streams with increasing stream discharge [38, 70]. With less nutrients transported to arid streams, GPP and ER will be suppressed. Forested streams will have an increase in DOM from precipitation events bringing in more terrestrial DOM from leaf litter or flushing DOM from soils, which is then transported downstream, where it can fuel microbes resulting in higher fluxes of ER [58, 63]. However, it is unknown how these drivers, dictated by precipitation, will respond to changes along a precipitation gradient and influence ecosystem metabolism.

These distal drivers are also dependent on watershed land use. Urban and agricultural streams tend to have less riparian vegetation than forested streams [11]. Urban and agricultural streams also tend to have higher nutrient loads than unimpacted streams [2, 11, 27]. In six mid-western streams draining row-crop agriculture fields, high rates of GPP and ER were attributed to excess nutrient runoff from fertilizer and increased light availability caused by grass buffer zones [29]. Within 33 Austrian streams, there was no change in the concentration of DOM between urban/agricultural and forested streams, however, the composition of DOM differed with land use [27]. Changes in land cover from forested to urban and agricultural also affects hydrology. Urban streams have more frequent high flows that can cause scouring of the substrate, which may suppress GPP [14, 16, 66, 68].

Light availability, temperature, nutrient concentrations, and DOM are able to directly drive changes in ecosystem metabolism, while precipitation regimes, watershed land use, and hydrology indirectly drive changes in ecosystem metabolism. However, the combined

effects of these proximal and distal drivers on rates of ecosystem metabolism, is less understood (Figure 1).

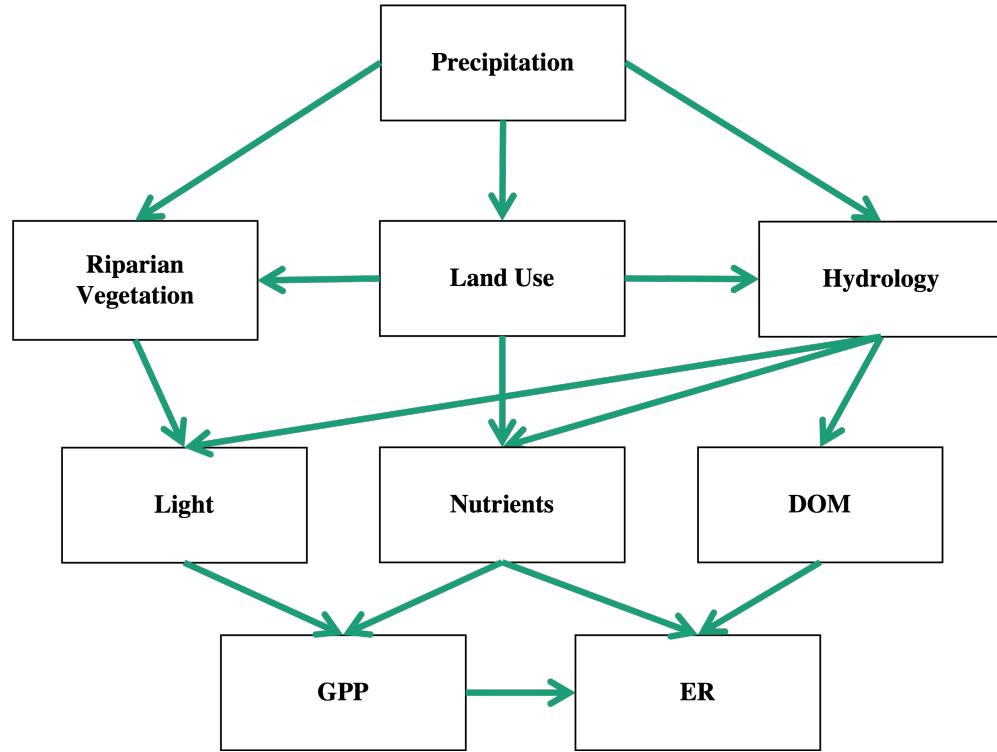


Figure 1: *Conceptual Diagram*. Conceptual diagram of hypothesized interactions between proximal and distal drivers on ecosystem metabolism.

Research Questions

1. How do changes in light, nutrients, DOC, and hydrology that are driven by precipitation regimes drive patterns of ecosystem metabolism?
 - Predictions:
 - Increasing precipitation will cause high discharge, which will increase turbidity, attenuate light reaching the benthos, and suppress GPP.
 - High discharge events will increase scouring or burying events and suppress GPP.

- High discharge events will dilute nutrient concentrations and suppress GPP and ER.
 - As you move from arid to mesic, I expect DOC quantity to increase due to increased precipitation pulsing DOC from the watershed into the streams. Increased DOC will provide more fuel for microbes which will result in increased ER.
2. How do changes in light, nutrients, DOC, and hydrology that are driven by changes in watershed land use drive patterns of ecosystem metabolism?
- Predictions:
 - Forested land that has been converted into agricultural land will have increased light availability from the removal of non-agricultural vegetation. This will drive an increase in both GPP and ER.
 - Forested land that has been converted into agricultural land will have increased nutrients from agricultural runoff, leading to an increase in GPP and ER.
 - Non-agricultural vegetation will decrease light availability, resulting in suppressed GPP.

CHAPTER II

Methods

Study Areas

To address my research questions, I analyzed nine Texas coastal plain streams falling along a precipitation, and subsequently, a land use gradient (Figure 2 and 3). I estimated ecosystem metabolism in these streams from continuous measurements of dissolved oxygen and temperature for the time periods of 2017-2018 and 2020-2021.

Watershed areas for each of the nine sites were delineated from 1/3 arc-second digital elevation models (DEM) from the United States Geological Survey (USGS). I then calculated watershed land usage percentages using the National Land Cover Data-set (NLCD, 2019). All GIS analysis took place in ArcMap (Version 10.8, ESRI, USA) and QGIS (Version 3.22, QGIS Development Team, Switzerland).

Site Descriptions

The annual average precipitation along the coastal plain ranged from 55 cm yr^{-1} in the semi-arid to 135 cm yr^{-1} at the most mesic watershed along the 300 km precipitation gradient [31]. The catchment areas of the streams ranged from 73 to 1787 km^2 (Table 1). Sites are characterized with high turbidity and intact riparian zones, ranging from dense forested canopy areas at the most mesic site to tall grasses at the most arid site (Figure 4 and 5). While these sites had intact riparian zones, watershed land use varied across sites following the precipitation gradient, from semi-arid to mesic, agriculture land use increased from 33% to 82%, while non-agricultural vegetation decreased from 55% to 1% (Figure 3). The precipitation gradient likely drove land use. A majority of sites had sandy substrate that

mobilized during precipitation events. Substrate at other sites was composed of small pebbles and gravel.

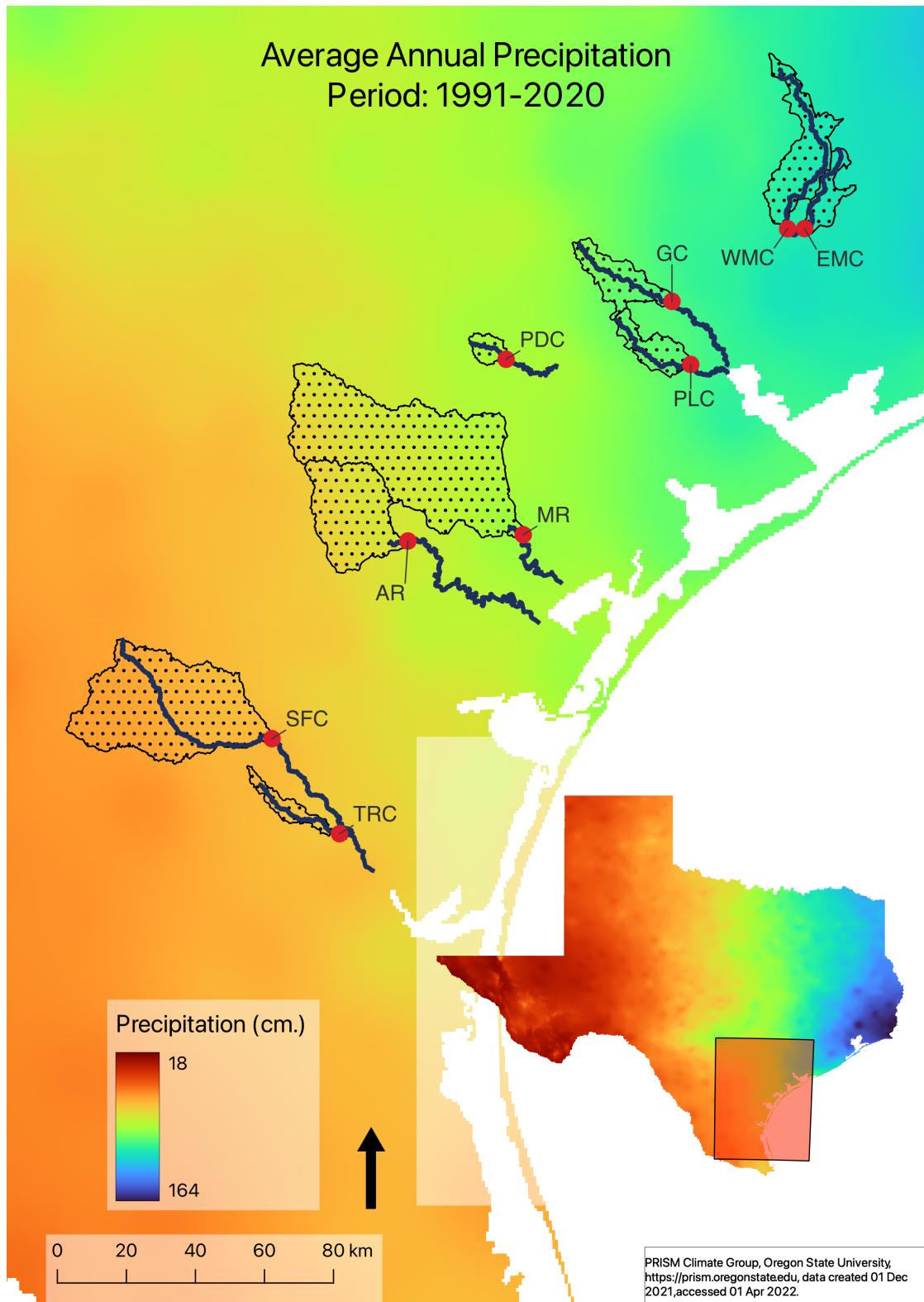


Figure 2: *Texas Precipitation Gradient*. The nine study sites and their watersheds across the 300 km coastal precipitation gradient.

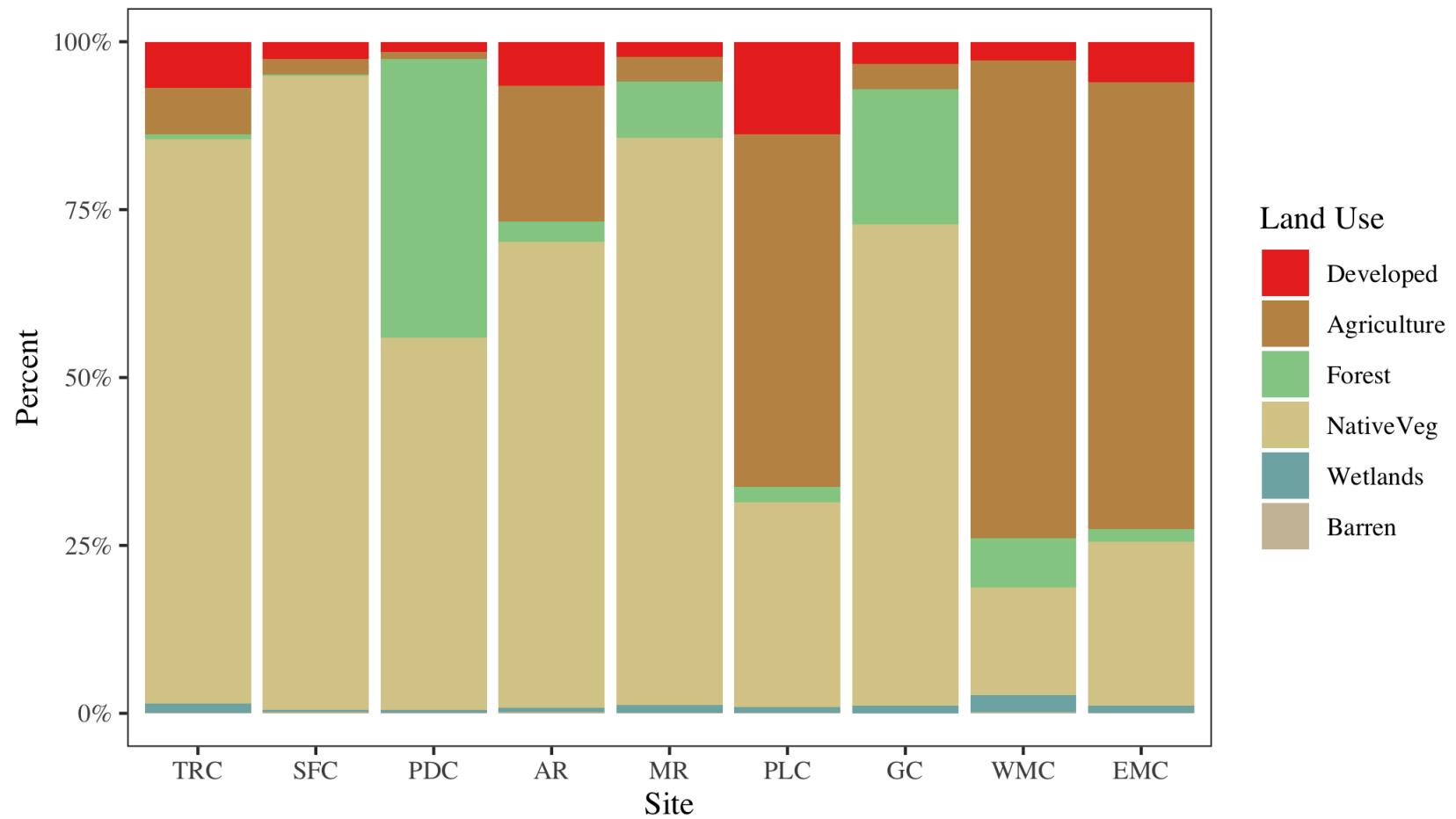


Figure 3: *Watershed Land Use*. Land cover types (%) the nine study sites (Table 1). Sites are arranged from arid (left) to mesic (right).

Table 1: *Site Summary*

Site	Site Code	Watershed Area (km ²)
Tranquitas Creek	TRC	126
San Fernando Creek	SFC	1313
Aransas River	AR	640
Perdido Creek	PDC	73
Mission River	MR	1787
Placedo Creek	PLC	177
Garcitas Creek	GC	273
West Mustang Creek	WMC	461
East Mustang Creek	EMC	140

Note: Sites are arranged top to bottom, arid to mesic, with the site code. The largest watershed was 1787 km², while the smallest watershed was 73 km².



Figure 4: *WMC*. This site is one of the most mesic sites and is characterized with high turbidity, high canopy cover, that likely decreases light availability, and sandy substrate.



Figure 5: *TRC*. This site is the most arid site and is characterized with high turbidity and dense riparian vegetation, likely decreasing light availability.

Ecosystem Metabolism

I estimated daily GPP and ER from continuously measured dissolved oxygen concentrations using a one-station approach [51]. In one-station models, dissolved oxygen (DO) concentrations are used to estimate GPP, ER, and K_O (gas exchange rate [d^{-1}] for oxygen at stream water temperature). DO and temperature were measured every 10 minutes with miniDOT (PME) DO loggers in the stream thalweg, to ensure the water was well mixed. I used the R package StreamLight [62], this package uses NLDAS, LAI, and field measurements to estimate light for each site. GPP, ER, and K_O were modeled using the R package streamMetabolizer [3]. I used high frequency DO, temperature, and PAR to estimate GPP, ER, and K_O using the following equation [34, 35, 37, 69]:

$$O_i = O_{i-\Delta t} + \left(\left(\frac{GPP_d}{\bar{Z}} \times \frac{PAR_i}{\sum PAR_d} \right) + \frac{ER_d}{\bar{Z}} + K_o (O_{sat(i-\Delta t)} - O_{i-\Delta t}) \right) \Delta t$$

Where O_i is the DO (mg L^{-1}) concentration at time i and $O_{(i-\Delta t)}$ is the DO concentration at the time step prior to O_i and Δt is the time-step of the analysis (10 minutes). GPP_d and ER_d are areal fluxes of GPP and ER for day d ($\text{g O}_2 \text{ m}^{-2} \text{ d}^{-1}$). \bar{Z} is daily average stream reach depth (m). The gas exchange rate, K_O is at stream water temperature. DO at saturation, O_{sat} refers to oxygen concentration (mg L^{-1}) at 100% saturation at stream water temperature and barometric pressure [28], which was measured at the Texas A&M University—Corpus Christi Meteorological station ($27^\circ 42' 54'' \text{ N}, 97^\circ 19' 43'' \text{ W}$). PAR_i ($\mu\text{mol m}^{-2} \text{ s}^{-1}$) is photosynthetic active radiation at time i calculated using a function in streamMetabolizer [3] and $\sum PAR_d$, is the light intensity for day d .

The Bayesian model from streamMetabolizer was used to estimate GPP, ER, and K_{600} , the gas exchange coefficient, normalized to normalized to a Schmidt number of 600. I used

partial pooling of K_{600} across all days from each site. The model was run for 2000 warm up steps and then 2000 saved steps, to ensure the Bayesian chains converge [4, 5]. The Bayesian model was run with 4 chains, on 4 cores in parallel.

I used several criteria to evaluate model fit. First, I used the relationship between ER and K_{600} , if ER and K_{600} are strongly related the model did not fit, then days where K_{600} exceeded 100 were thrown out, these are very high values and likely not plausible given the low slope and low turbulence of these coastal plain streams. Days with high stream flow (+ 2 SD) were also removed from the model, high stream flow results in a dilution of the diel oxygen signal, which becomes problematic when trying to estimate GPP, ER, and K_{600} . Additionally, when DO was equal to or less than 0.01 mg L^{-1} , these days were thrown out as this is when sensors were believed to be buried under sediment after large rain events.

DOC and Nutrients

I collected water samples monthly to quantify nutrient ($\text{NO}_3\text{-N}$, $\text{NH}_4\text{-N}$, and $\text{PO}_4\text{-P}$) and DOC concentrations. I filtered water from each site with a $0.7 \mu\text{m}$ pre-combusted glass fiber filter (GFF) into acid-washed 60 mL nalgene bottles for nutrients and acid-washed pre-combusted 40 mL glass vials for DOC for a total of 4 replicates for both nutrients and DOC. All samples were kept cold and in the dark until transported to the laboratory. Nutrient samples were frozen until analysis at Oklahoma State University Soil, Water and Forage Analytical Laboratory. DOC concentrations were measured using a Shimadzu TOC/TN analyzer at Sam Houston State University.

Discharge

To characterize discharge and calculate average reach depth, field measurements of width, velocity, and gage measurements of discharge were retrieved from the United States Geological Survey. Using relationships of depth and discharge from each site, I calculated daily average stream depth, these measurements were then used as \bar{Z} , daily average stream reach depth (m), in the equation above [21, 59, 65]

Statistical Analysis

To quantify the effect of land use and the precipitation gradient on ecosystem metabolism, I used structural equation modeling (SEM) to test my hypotheses (Figure 1) [11, 27]. SEMs are used when there is an underlying mechanism that is causing co-variance between random variables, it also take into account correlated independent variables, measurement error, and provides a more robust analysis compared to multivariate approaches [11, 44]. To group land use categories for the structural equation model, I used a principal components analysis (PCA) [56]. The two land use PCs were used in the structural equation model as a proxy for land use. I included log-transformed monthly estimates of GPP, ER, DOC concentration, and turbidity, monthly averages of NO₃-N, PO₄-P, precipitation, and discharge. I used Standardized Root Mean Square Residual (SRMR) to compare model fit. Statistical analysis was preformed with R version 4.1.0 and lavaan [56, 61].

CHAPTER III

Results

Ecosystem Metabolism

Across all sites, median GPP ranged from 0.12 to 0.77 g O₂ m⁻² d⁻¹, while median ER ranged -0.84 to -10.85 g O₂ m⁻² d⁻¹. ER exceeded GPP across all sites, resulting in median NEP ranging from -0.35 to -10.41 g O₂ m⁻² d⁻¹ (Table 2). All sites were heterotrophic, i.e, where ER exceeds GPP, with very few (1-4) autotrophic days. Across all sites, day to day variability in GPP (CV 1.16 %) was low whereas ER (CV -1.18 %) exhibited slightly more daily variation than GPP (Figure 6). There was a subtle increase in GPP across the precipitation gradient, with the exception of GC where median GPP was low (0.25 g O₂ m⁻² d⁻¹), falling in line with the most arid sites (Figure 7).

Unlike GPP, there was no discernible pattern in ER (Figure 8) nor in NEP (Figure 9) from semi-arid to mesic study sites. ER varies across the precipitation gradient, but ER at WMC was 3-13 fold greater than the other sites (Table 2). At PDC, I was only able to estimate metabolism for 279 days out of the nearly 2 years of data because the stream was completely dry or was disconnected pools during 2020-2021 (Table 2).

Between SFC, AR, and PLC there appeared to be slight spring and summer increases in GPP and ER across the precipitation gradient in 2020, there is not the same pattern in 2017. GPP increased later into the summer as precipitation increased along the gradient (Figure 10).

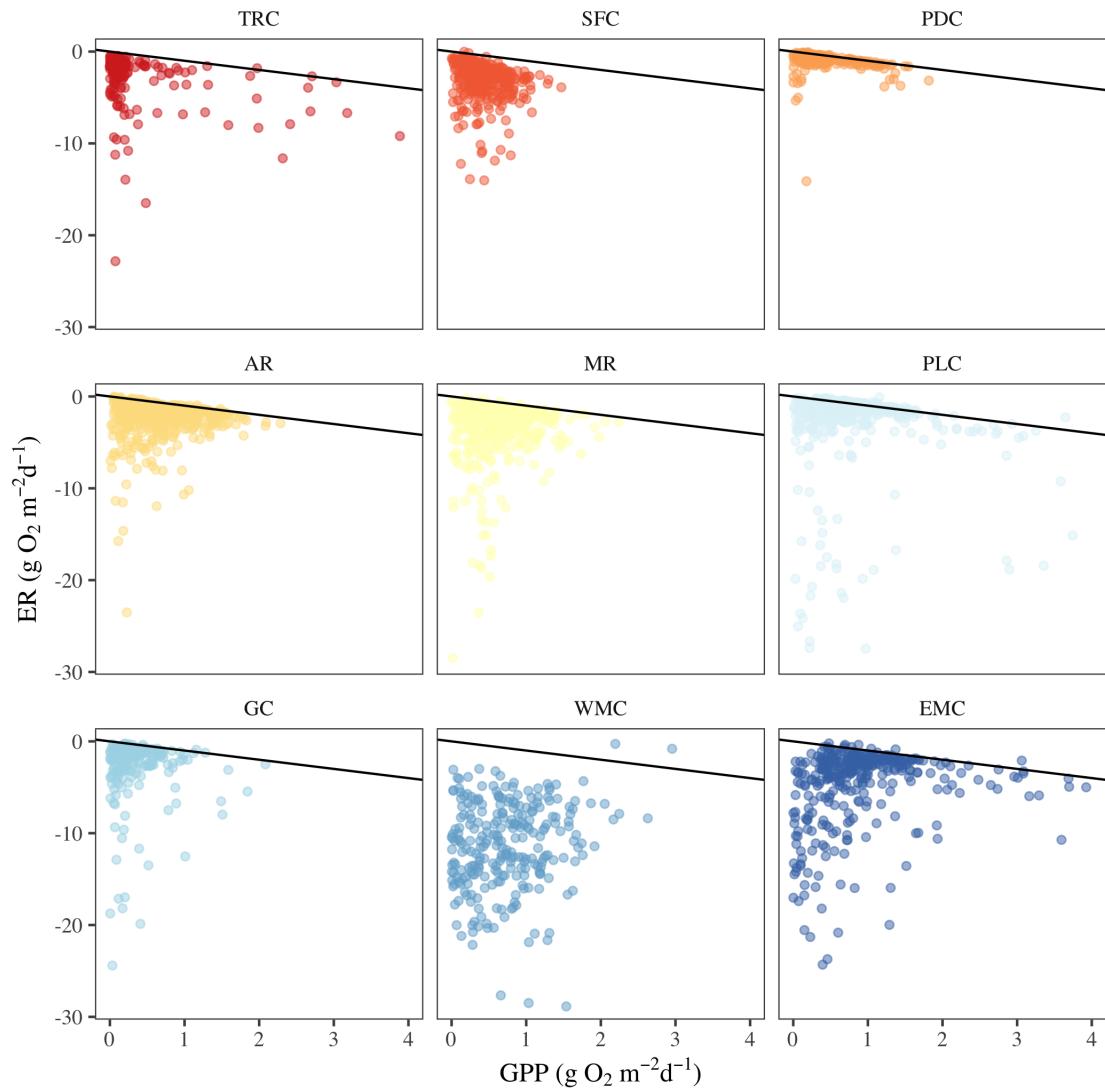


Figure 6: *Gross Primary Production and Ecosystem Respiration.* Sites are arranged from arid to mesic left to right and top to bottom (red to blue). Points above the 1:1 line indicate days of autotrophy where gross primary production (GPP) exceeds ecosystem respiration (ER), and points below are heterotrophic days where ER exceeds GPP. Across all sites, ER was more variable than GPP with very few autotrophic days (e.g. 2 days at WMC and 1 day at PLC and EMC).

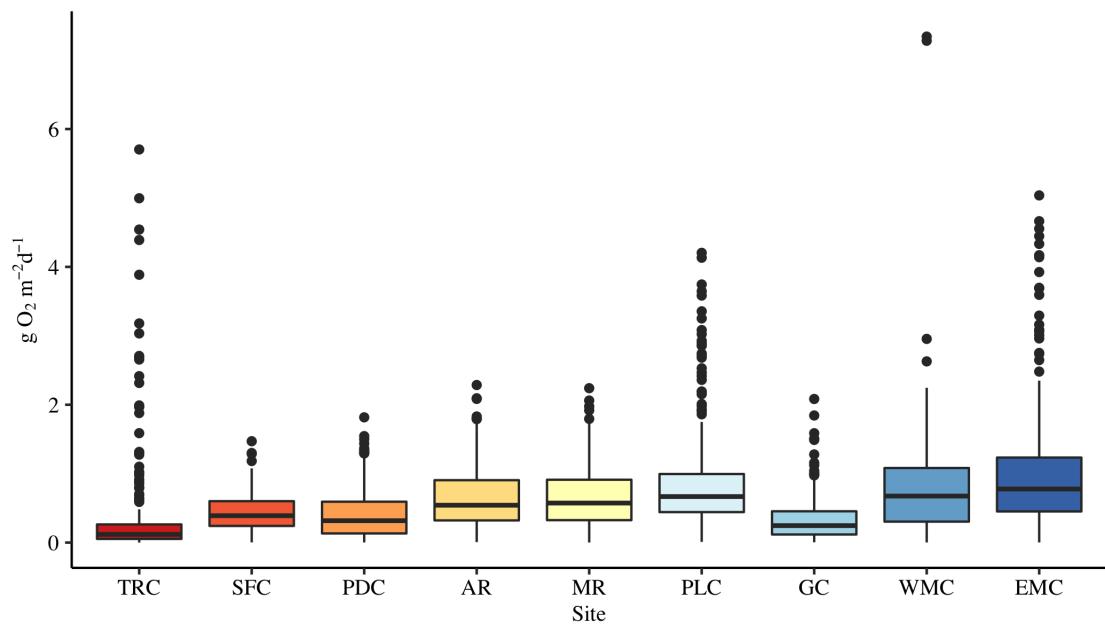


Figure 7: *Gross Primary Production*. There was a subtle increase in GPP across the precipitation gradient (sites are arranged arid to mesic, left to right), with the exception of GC, falling in line with the most arid sites. The boxes are the middle 50 quartile (25 to 75), the line is the median, the tails are 1.5X interquartile range, and any points falling outside of the line are considered outliers.

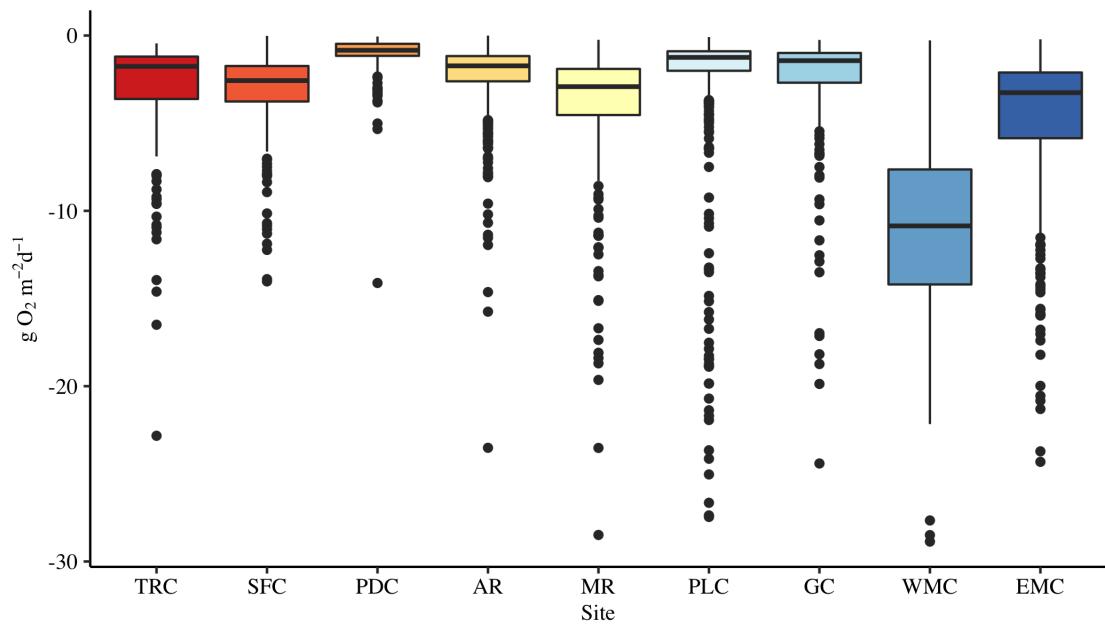


Figure 8: *Ecosystem Respiration*. There appears to be no discernible pattern in ecosystem respiration (ER) along the precipitation gradient (sites are arranged arid to mesic, left to right). The boxes are the middle 50 quartile (25 to 75), the line is the median, the tails are 1.5X interquartile range, and any points falling outside of the line are considered outliers.

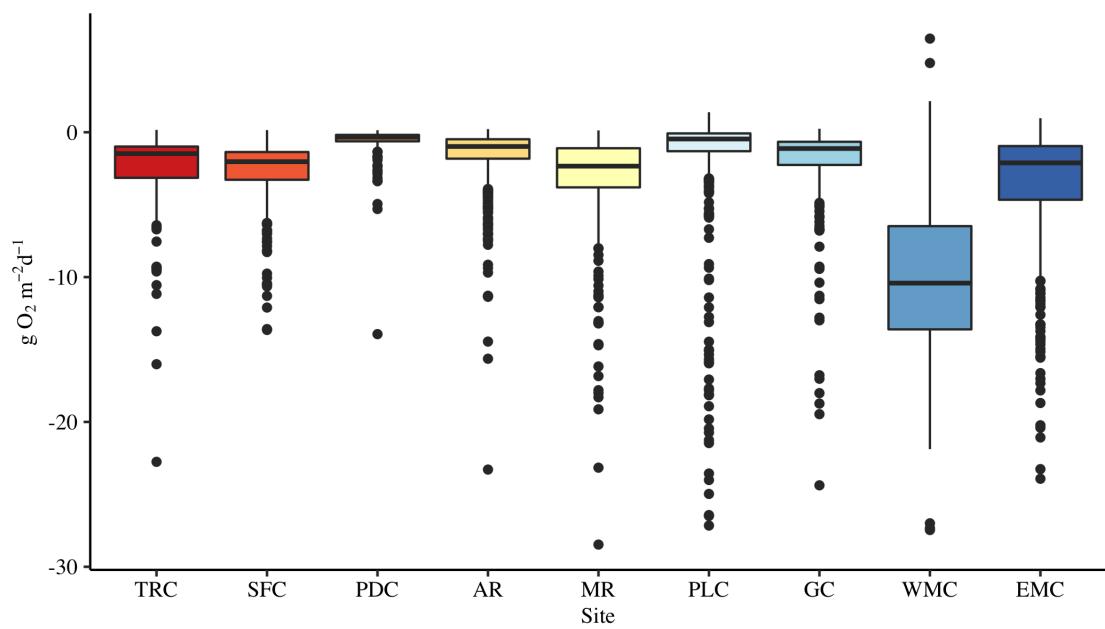


Figure 9: *Net Ecosystem Production*. There appears to be no discernible pattern in net ecosystem production (NEP) along the precipitation gradient (sites are arranged arid to mesic, left to right). The boxes are the middle 50 quartile (25 to 75), the line is the median, the tails are 1.5X interquartile range, and any points falling outside of the line are considered outliers.

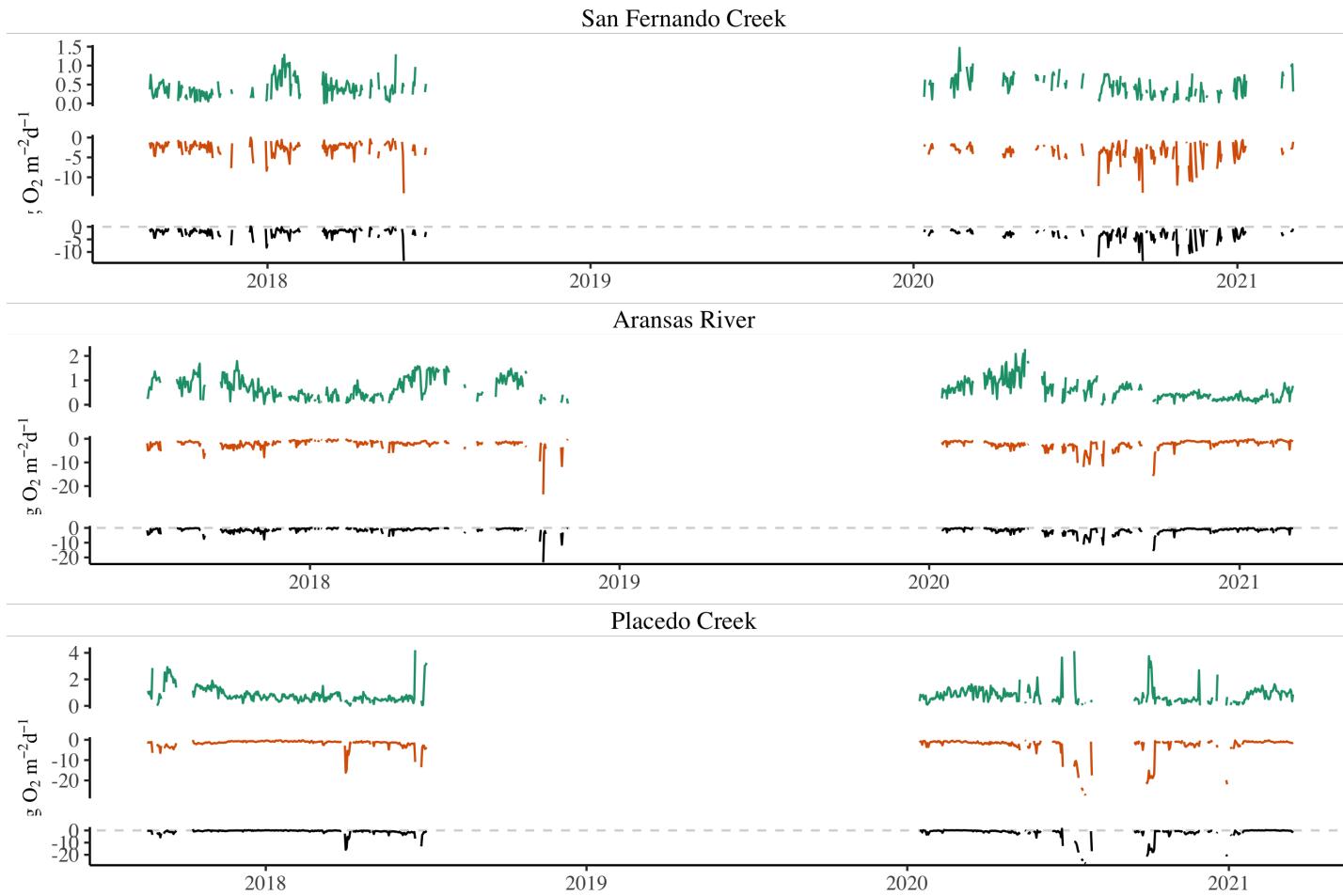


Figure 10: *Ecosystem Metabolism for Three Sites*. Sites are arranged arid to mesic top down. Daily gross primary production (GPP, green lines) does not appear to have a distinct seasonal pattern from 2017-2018. In comparison, during 2020, GPP appeared to vary seasonally across the sites shown here. GPP appears to increase later into the summer along the precipitation gradient, from arid to mesic. Ecosystem respiration (ER, orange lines) has the same pattern but appears to lag behind GPP. Daily net ecosystem production (NEP, black line) mirrors ER.

Table 2: *Metabolism Summary*

Site	Usable Days	Median GPP (g O ₂ m ⁻² d ⁻¹)	GPP 95% CI	Median ER (g O ₂ m ⁻² d ⁻¹)	ER 95% CI	Median NEP (g O ₂ m ⁻² d ⁻¹)	NEP 95% CI
TRC	185	0.12	0.09-0.14	-1.80	-1.16 - -2.10	-1.50	-1.30- -1.70
SFC	365	0.39	0.37-0.43	-2.60	-2.40- -2.80	-2.00	-1.90- -2.20
AR	686	0.54	0.49-0.58	-1.70	-1.60- -1.80	-0.98	-0.89- -1.10
PDC	279	0.32	0.27-0.37	-0.84	-0.73- -0.93	-0.35	-0.30- -0.42
MR	382	0.57	0.53-0.63	-2.90	-2.70- -3.10	-2.30	-2.00- -2.60
PLC	609	0.67	0.63-0.71	-1.20	-1.20 - -1.30	-0.46	-0.39- -0.53
GC	233	0.25	0.21-0.28	-1.40	-1.30 - -1.60	-1.10	-0.97- -1.30
WMC	263	0.67	0.62-0.79	-11.00	-10.00 - -12.00	-10.00	-9.40- -11.00
EMC	352	0.78	0.72-0.83	-3.30	-3.00 - -3.60	-2.10	-1.80- -2.50

Note: Number of days where I was able to estimate ecosystem metabolism, median gross primary production estimates, median ecosystem respiration estimates, and median net ecosystem production of the nine sites. CI, confidence intervals. Sites are arranged from arid to mesic top down.

DOC and Nutrients

Across all sites, average DOC ranged from 5.3 to 12.5 mg L⁻¹ (Figure 11). Along the precipitation gradient from semi-arid SFC to semi-mesic GC, average DOC increased (from 6.4 to 9.3 mg L⁻¹); however, average DOC concentrations at EMC, where land use is predominantly agriculture, were 5.5 mg L⁻¹, and did not follow the pattern of increasing DOC concentrations along the precipitation gradient (Figure 11). Similarly, DOC concentrations at TRC, the driest site with the most non-agricultural vegetation, was the highest along the gradient (12.5 mg L⁻¹) (Table 3).

Unlike DOC concentrations, there were no discernible patterns in nutrients across the precipitation gradient. Two of the sites (SFC and AR) had high levels of NO₃-N and PO₄-P, 20-185x higher for NO₃-N and 10-35x higher for PO₄-P (Figure 12 and 13). Both of these sites receive waste water treatment plant effluent.

Table 3: *DOC and Nutrient Concentrations*

Site	DOC ± SD (mg L ⁻¹)	NH ₄ -N ± SD (mg L ⁻¹)	NO ₃ -N ± SD (mg L ⁻¹)	PO ₄ -P ± SD (mg L ⁻¹)
TRC	12.5 ± 4.8	0.22 ± 0.16	0.39 ± 0.61	0.27 ± 0.28
SFC	6.4 ± 1.16	0.18 ± 0.01	9.25 ± 6.0	4.60 ± 4.40
AR	7.2 ± 1.80	0.16 ± 0.14	5.1 ± 4.50	2.22 ± 1.70
PDC	5.8 ± 5.40	0.14 ± 0.01	0.11 ± 0.20	0.23 ± 0.42
MR	6.9 ± 4.70	0.13 ± 0.10	0.05 ± 0.05	0.13 ± 0.30
PLC	5.3 ± 2.40	0.13 ± 0.05	1.06 ± 1.21	0.23 ± 0.44
GC	9.3 ± 3.15	0.18 ± 0.22	0.16 ± 0.16	0.39 ± 0.56
WMC	9.1 ± 3.20	0.13 ± 0.063	0.26 ± 0.45	0.14 ± 0.08
EMC	5.5 ± 3.55	0.13 ± 0.07	0.45 ± 0.54	0.42 ± 0.83

Note: Average concentrations of dissolved organic carbon (DOC), ammonium (NH₄-N), nitrate (NO₃-N), and phosphate (PO₄-P) across the precipitation gradient (sites are arranged arid to mesic, top down). San Fernando Creek and Aransas River both receive water from waste water treatment plants. SD, standard deviation.

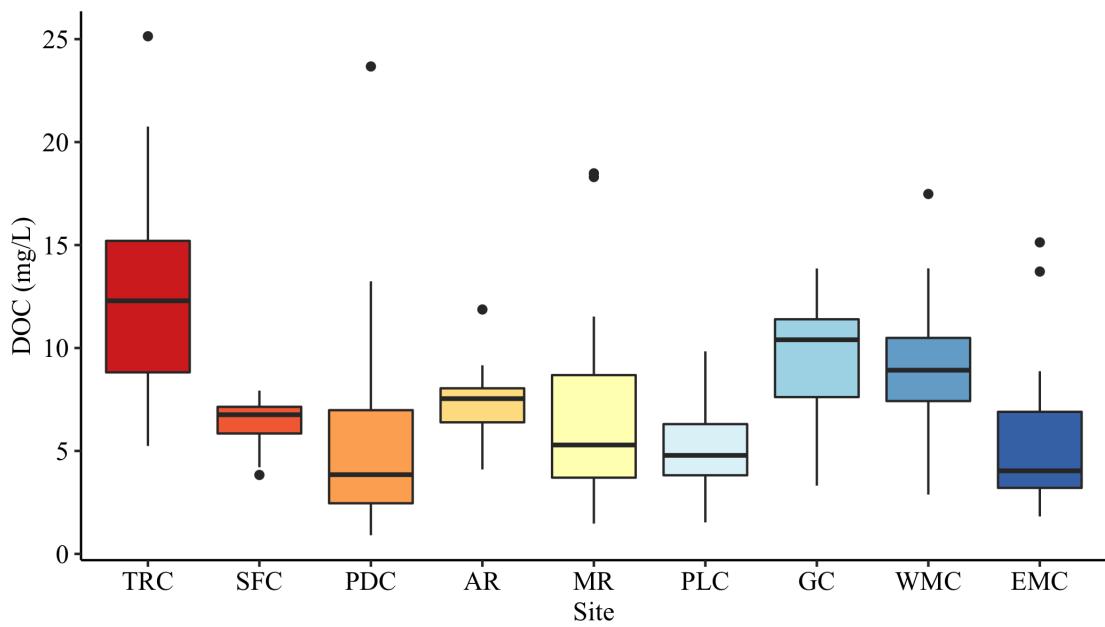


Figure 11: *Dissolved Organic Carbon*. Sites are arranged arid to mesic left to right. Dissolved organic carbon appears to increase as precipitation increases (left to right). However, TRC and EMC do not follow this pattern. The boxes are the middle 50 quartile (25 to 75), the line is the median, the tails are 1.5X interquartile range, and any points falling outside of the line are considered outliers.

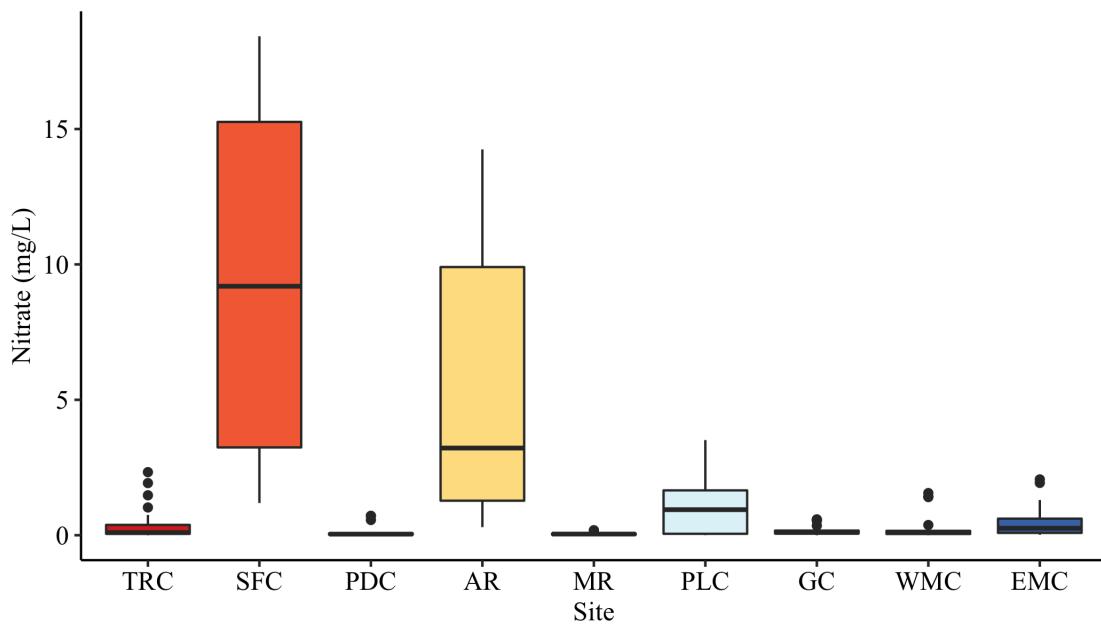


Figure 12: *Nitrate*. There does not appear to be a trend in nitrate across the precipitation gradient (Sites are arranged arid to mesic, left to right), however, SFC and AR had concentrations 20-185x higher than other study sites. The boxes are the middle 50 quartile (25 to 75), the line is the median, the tails are 1.5X interquartile range, and any points falling outside of the line are considered outliers.

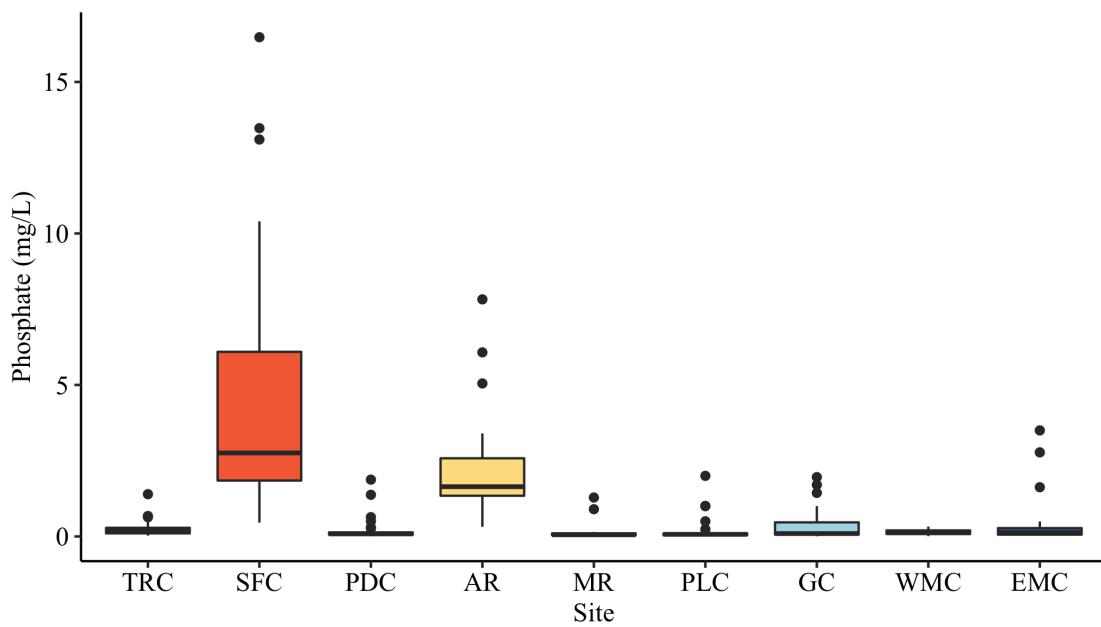


Figure 13: *Soluble Reactive Phosphorous*. There does not appear to be a trend in soluble reactive phosphorous across the precipitation gradient (Sites are arranged arid to mesic, left to right), however, SFC and AR had concentrations 10-35x higher than other study sites. The boxes are the middle 50 quartile (25 to 75), the line is the median, the tails are 1.5X interquartile range, and any points falling outside of the line are considered outliers.

Discharge

Across the precipitation and land use gradients, average discharged ranged from $0.03 \text{ m}^3 \text{ s}^{-1}$ to $3.00 \text{ m}^3 \text{ s}^{-1}$, with WMC having the highest discharge, and PDC the flashiest (Table 4). Across the gradients, discharge greatly varied between sites and had quick responses to storm events (Figure 14).

Table 4: *Summary of Site Discharge*

Site	Mean Discharge ($\text{m}^3 \text{ s}^{-1}$)	Median Discharge ($\text{m}^3 \text{ s}^{-1}$)	CV (%)
TRC	0.03	0.00	447.32
SFC	0.19	0.03	1586.92
PDC	0.12	0.00	1112.93
AR	0.37	0.10	551.65
MR	2.49	0.13	578.40
PLC	1.17	0.03	760.08
GC	0.71	0.01	909.21
WMC	3.00	0.37	433.70
EMC	0.90	0.04	457.34

Note: Mean, median, and Coefficient of Variation (CV) of site discharge across the precipitation gradient (sites are arranged arid to mesic, top down).

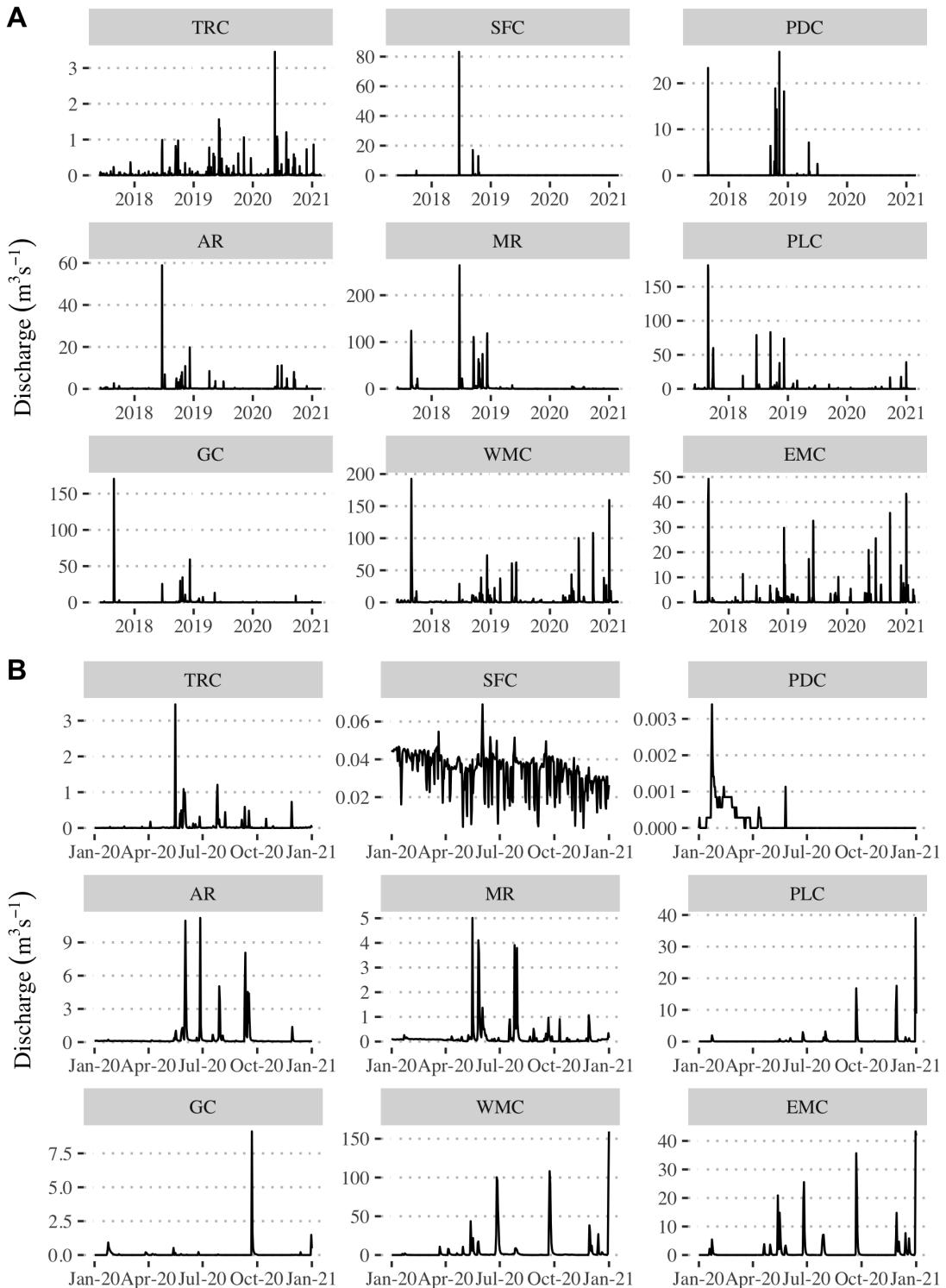


Figure 14: Site Discharge. Sites are arranged arid to mesic left to right and top to bottom. Discharge appears to increase along the gradients, however they are punctuated by sharp increases due to rainfall. Note the different y-axis. Figure A is discharge over the study period, while figure B is 2020.

Principal Component Analysis and Structural Equation Model

The PCA based on percentages of watershed land use categories identified two gradients in these sites. Land use-PC1, explaining 44.1% of the variation, and was explained by wetlands, shrubs, and grasslands to cropland and developed land, while land use-PC2, explaining 29% of the variation, ordered streams along a gradient of forest and pasture relative to other land uses (Figure 15). PC values were used as a proxy for watershed land use in the structural equation model to evaluate distal and proximal drivers of GPP and ER.

I used a structural equation model to parse out the drivers of GPP and ER. I used the proximal drivers, average monthly precipitation, the presence of WWTP in the watershed, and land use PC1 and PC2 and distal drivers, discharge (CV), DOC, nitrate, and phosphate to explain the variability in monthly GPP and ER. I was unable to find a statistically significant model for the drivers of GPP and ER (Figure 16). However, when GPP and ER were removed from the model, there was a statistically significant model (Figure 17). The results of the second SEM without GPP and ER indicated that land use PC1 and PC2 are strongly driving NO₃-N, PO₄-P, DOC, and turbidity, while monthly average precipitation is weakly driving NO₃-N and DOC.

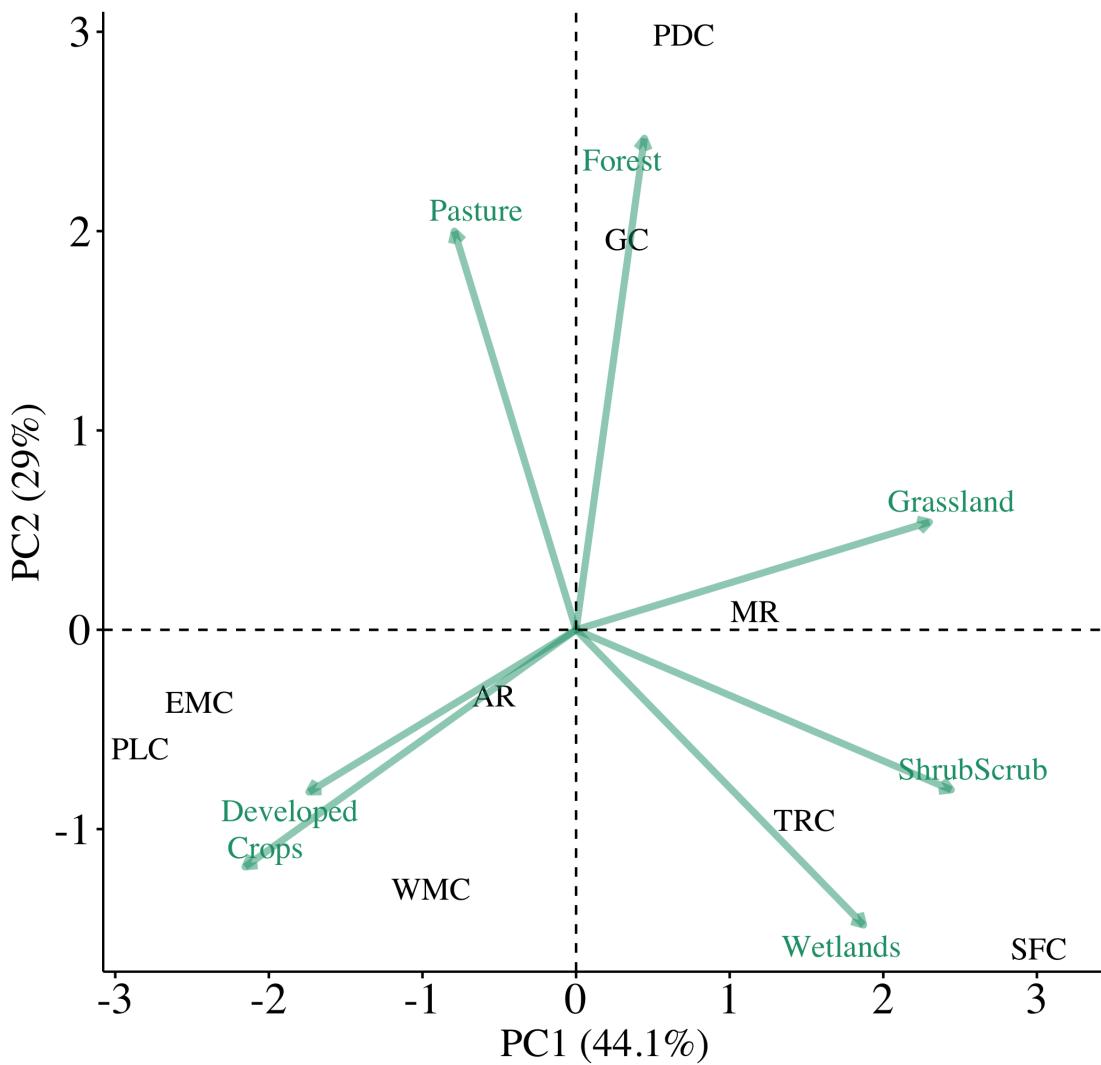


Figure 15: *Principal Component Analysis*. Principal component 1 ordered streams along a gradient of wetlands, shrubs, and grasslands to cropland and developed land, while principal component 2 grouped forest and pasture together.

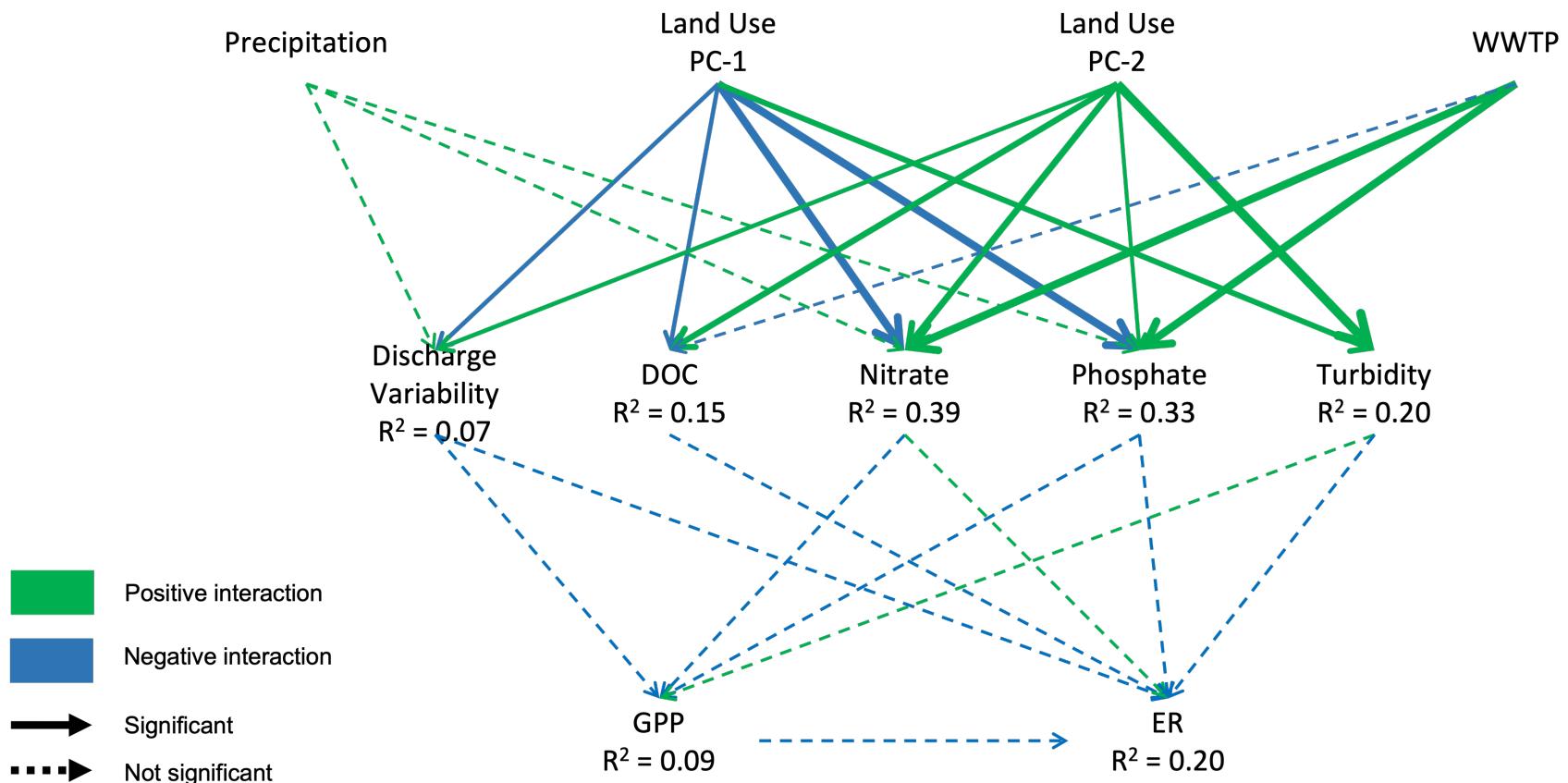


Figure 16: SEM 1. The land use PCs (PC1 and PC2) and precipitation gradient had a strong impact on the proximal drivers (discharge, turbidity, DOC, nitrate, and phosphate), however, this interaction did not reach gross primary production or ecosystem respiration.

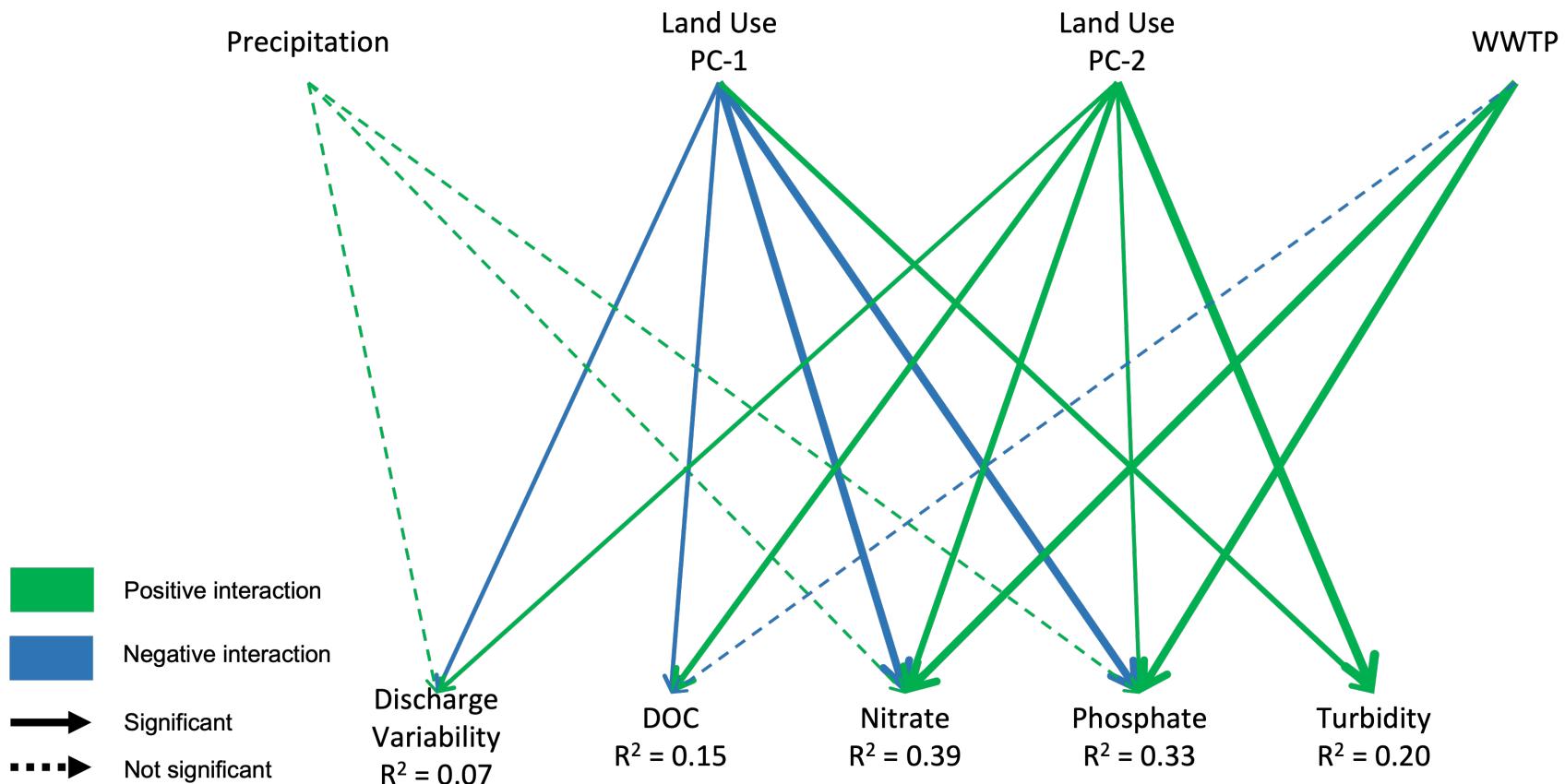


Figure 17: SEM 2. The land use PCs (PC1 and PC2) and precipitation gradient had a strong impact on proximal drivers (discharge, turbidity, DOC, nitrate, and phosphate).

CHAPTER IV

Discussion

Across the coupled land use and precipitation regime gradients, all streams were heterotrophic with rates of ER exceeding GPP. Sites had very low GPP (0.12 to $0.78 \text{ g O}_2 \text{ m}^{-2} \text{ d}^{-1}$) compared to ER across the coupled gradients, with no strong apparent seasonal trends and more daily and year to year variation. There was no apparent trend in nutrient concentrations or GPP. However, ER and DOC generally increased as agricultural land increased and non-agricultural vegetation decreased, moving from semi-arid to mesic.

Ecosystem Metabolism

Texas coastal plain streams appear to have relatively low GPP compared to other stream ecosystems (Figure 7). For instance, mean GPP in tropical streams with an open canopy was $2.09 \text{ g O}_2 \text{ m}^{-2} \text{ d}^{-1}$ and in a small forested head water stream in Tennessee mean GPP was $1.4 \text{ g O}_2 \text{ m}^{-2} \text{ d}^{-1}$ peaking at $10.80 \text{ g O}_2 \text{ m}^{-2} \text{ d}^{-1}$ [45, 60]. Sub-alpine streams appear to have greater GPP compared to the Texas coastal plain streams as well where GPP from 12 Austrian sub-alpine streams peaked at $25 \text{ g O}_2 \text{ m}^{-2} \text{ d}^{-1}$ [69]. Agricultural streams elsewhere also have greater GPP, where in six mid-western row-crop draining streams with high light availability and nutrients, mean GPP was $4.6 \text{ g O}_2 \text{ m}^{-2} \text{ d}^{-1}$ peaking at $22.0 \text{ g O}_2 \text{ m}^{-2} \text{ d}^{-1}$ [29]. In comparison, 33 Austrian streams with a mix of forested, agriculture, and urban land uses were slightly similar to slightly higher than Texas coastal plain streams where GPP ranged from 0.01 to $3.3 \text{ g O}_2 \text{ m}^{-2} \text{ d}^{-1}$ [27]. Rates of GPP from these Texas coastal streams were most similar to those of closed canopy tropical streams ($0.57 \text{ g O}_2 \text{ m}^{-2} \text{ d}^{-1}$), [45]. Canopy cover could explain some of the limitation of light, for sites where canopy cover was low, turbidity likely decreased light reaching the benthos, where most of the primary production would take place (average turbidity ranged

from 15-141 NTU). This suggest these streams were likely light limited, resulting in low rates of GPP [35, 36, 45]. Another contributing factor to low GPP in these ecosystems may be caused by sandy substrate and frequent bed movement. Across the coupled gradients, a majority of sites had sandy substrate. In a desert stream in Arizona, low GPP (0.15 to 0.29 g O₂ m⁻² d⁻¹) was attributed to bed movement caused by sandy substrate disrupting primary producers [67]. Again in a rural Australian stream, low GPP (0 to 0.5 g O₂ m⁻² d⁻¹) was also attributed to bed movement caused by sandy substrate [6]. In streams with high bed movement, GPP is often suppressed due to disturbance to primary producers [6, 67, 68].

Within sites, daily variation of GPP exceeded that of seasonal variation (Figure 10). There was not strong seasonal variation or a peak of GPP in the spring or summer within sites. The lack of seasonal trends in GPP appears to be uncommon in other stream ecosystems. For instance, in a small forested Tennessee stream GPP peaked during spring before leaf out (0.01 to 10.80 g O₂ m⁻² d⁻¹), which was attributed to an increase in light due to longer days in spring prior to canopy leaf out [60]. In 12 Austrian sub-alpine streams GPP peaked in spring after snow melt (0.01 to 25 g O₂ m⁻² d⁻¹) which was also attributed to increased light [69]. In 6 mid-western row-crop drained streams, GPP also peaked in the spring (0.1 to 22.0 g O₂ m⁻² d⁻¹) which was also attributed to high light availability [29]. Again, in an analysis of 222 stream and rivers across the United States, seasonal changes in light and flow regimes were found to be the strongest drivers of GPP [10]. In the subtropical Texas coastal plains region, where there is a more subtle shift in seasons, compared to temperate ecosystems, along with high turbidity in these streams, may be attributed to low GPP and lack of strong seasonal peaks in GPP seen in other stream ecosystems.

ER rates from these Texas coastal plain streams were lower, but within range (-0.4 to -29.0 g O₂ m⁻² d⁻¹) of estimates of ER from other stream ecosystems [11]. The median ER rates across these Texas coastal plain streams were similar to estimates of ER from an agriculturally impacted tropical stream in Costa Rica (-0.5 to -0.8 g O₂ m⁻² d⁻¹) [52]. However, median ER of all sites was lower than estimates of ER from tropical streams with a mix of open and closed canopy (-4.30 g O₂ m⁻² d⁻¹), six mid-western row-crop drained streams (-0.9 to -34.8 g O₂ m⁻² d⁻¹), eight streams with a mix of agriculture, urban, and reference land uses across the United States (-2 to -8 g O₂ m⁻² d⁻¹), a small forested head water stream in Tennessee (-0.99 to -16.01 g O₂ m⁻² d⁻¹), and in 12 streams across an Austrian sub-alpine catchment (-0.04 to -54.2 g O₂ m⁻² d⁻¹) [11, 29, 45, 48, 60, 69]. As nutrients and DOC concentrations were relatively high to fuel microbial metabolism (Table 3), I would have expected greater rates of ER; however, rates of ER were on the lower end of the range reported from other ecosystems [11, 29, 48, 60, 69]. These lower than expected rates of ER may be explained by the lack of hyporehic exchange caused by low channel slope. Streams with low slope have decreased hyporehic exchange where an estimated 50-85% of ER fluxes originate [25, 49, 50, 64].

DOC and Nutrients

Across most sites, DOC concentrations increased along the precipitation gradient. This trend was expected, as increasing DOC concentrations are linked to increases of terrestrial primary production [41, 46, 47]. However, the driest site, TRC and the second most mesic site, EMC did not follow this pattern. TRC is dominated by a dense, intact riparian zone comprised of native shrub vegetation, anoxic stream water (DO < 0.5 mg L⁻¹) 75% of the time, and an average discharge of 0.03 m³/s. With possible low hyporheic exchange,

lack of mineralization of DOC may have caused the DOC concentrations to be higher than found at other sites. The second site that did not follow the pattern was EMC, this site has a watershed that is dominated by agriculture and has a sandy riparian zone, this may have led to a decrease in DOC compared to other sites. The sandy sediment in the riparian zone contains less organic carbon than riparian zones composed of soil [15]. The increase in DOC across the precipitation gradient did not drive an increase in ER. A temporal mismatch in the monthly sampling schedule potentially caused the inability to link interactions between DOC and ER.

Nutrient concentrations did not drive variation in GPP and ER. All sites, except SFC, had similar concentrations of ammonium and nitrate, with no apparent trend across the gradients (Table 3). Sites receiving WWTP effluent had increased level of nitrate. SFC is predominantly waste water dependent, likely contributing to increased nitrate and phosphate concentrations. This increase in nutrients may have lead to SFC having the second highest ER for these coastal streams ($-2.60 \text{ g O}_2 \text{ m}^{-2} \text{ d}^{-1}$). Generally, increases in nutrient concentrations fuel microbial respiration and lead to increased ER [57]. However, the results from the SEM (Figure 16) indicate there was not a significant impact of nutrient concentrations on GPP or ER. Previous studies on eight and nine streams with a mix of agriculture, urban, and reference land uses across the United States and Puerto Rico and 83 streams across the global tropics have also been unable to relate rates of ecosystem metabolism to nutrient concentrations [11, 45, 48]. The findings from this study and others suggest weekly or monthly nutrient measurements may be insufficient for linking nutrient concentrations to changes in ecosystem metabolism and more frequent measurements of nutrient concentrations are needed to link the effects of nutrients to daily estimates of GPP

and ER [11, 27].

Discharge

Across the precipitation and land use gradients, WMC had the highest discharge, while SFC had the most flow variability (Table 4). All sites exhibited quick increases in discharge from frequent precipitation events, with equally quick decreases after precipitation events. Frequent precipitation events, which increase stream discharge, leads to scouring of primary producers and increases in turbidity, which may reduce GPP [35, 66]. However, the low GPP in the Texas coastal streams may already be light limited without increased turbidity from high flows.

Precipitation and Land use Gradients

With monthly measurements of nutrients, DOC, and turbidity, there was a strong influence of land use proximal drivers of ecosystem metabolism, with land use driving changes in nitrate, phosphate, ammonium, and turbidity. However, there was not an influence of DOC, nitrate, phosphorous, ammonium, and turbidity on GPP and ER. The inability to find a link between proximal drivers and ecosystem metabolism suggest the snap-shot sampling of nutrients, DOC, and turbidity was too limited to detect responses of ecosystem metabolism to changes in proximal drivers [11]. The low variation in GPP and ER (Table II) may have also prevented linking drivers to ecosystem metabolism. Additionally, these streams had intact riparian zones and were likely light limited, which may have limited the response of ecosystem metabolism to changes in land use [10, 29, 40].

Conclusion

While I was able to parse out the effect of regional drivers (land use and precipitation regimes) on proximal drivers of ecosystem metabolism (ie. nutrients, DOC, and turbidity), I was unable to elucidate the combined effects of precipitation and land use gradients on stream ecosystem metabolism. This suggest the two coupled gradients, land use and precipitation regime, may mask the combined effects on stream ecosystem metabolism. Future work should focus on the use of high frequency measurements of proximal drivers to attempt to parse out drivers of ecosystem metabolism in subtropical streams.

A majority of research on stream ecosystem metabolism comes from temperate regions, with tropical and subtropical regions being understudied [45]. These subtropical Texas coastal plains streams provide valuable insight into how subtropical streams may differ from their more studied temperate counterparts. These low estimates of GPP suggest that Texas coastal streams likely rely heavily on allochthonous rather than autochthonous carbon sources as a basal resource. These are slow, flat streams, which have low GPP and low to moderate ER. These streams do appear to function differently than their more temperate counterpart. But in light of global change, teasing apart what drives ecosystem metabolism will be of importance given that GPP and ER modulate carbon, nutrient fluxes, and even basal food resources.

REFERENCES

- [1] J.A. Aitkenhead-Peterson, W.H. McDowell, and J.C. Neff, *Sources, Production, and Regulation of Allochthonous Dissolved Organic Matter Inputs to Surface Waters*, Aquatic Ecosystems, Elsevier, 2003, pp. 25–70.
- [2] Jeremy M. Alberts, Jake J. Beaulieu, and Ishi Buffam, *Watershed Land Use and Seasonal Variation Constrain the Influence of Riparian Canopy Cover on Stream Ecosystem Metabolism*, *Ecosystems* **20** (2017), no. 3, 553–567, ISBN: 1002101600409 Publisher: Springer US.
- [3] Alison P. Appling, Robert O. Hall, Maite Arroita, and Charles B. Yackulic, *stream-Metabolizer: Models for Estimating Aquatic Photosynthesis and Respiration*, 2018.
- [4] Alison P. Appling, Jordan S. Read, Luke A. Winslow, Maite Arroita, Emily S. Bernhardt, Natalie A. Griffiths, Robert O. Hall, Judson W. Harvey, James B. Heffernan, Emily H. Stanley, Edward G. Stets, and Charles B. Yackulic, *The metabolic regimes of 356 rivers in the United States*, *Scientific Data* **5** (2018), no. 1, 180292.
- [5] Maite Arroita, Arturo Elosegi, and Robert O. Hall, *Twenty years of daily metabolism show riverine recovery following sewage abatement*, *Limnology and Oceanography* **64** (2019), no. S1, S77–S92.
- [6] Bonnie L. Atkinson, Michael R. Grace, Barry T. Hart, and Kellie E. N. Vanderkruk, *Sediment instability affects the rate and location of primary production and respiration in a sand-bed stream*, *Journal of the North American Benthological Society* **27** (2008), no. 3, 581–592 (en).
- [7] Tom J. Battin, Louis A. Kaplan, Stuart Findlay, Charles S. Hopkinson, Eugenia Martí, Aaron I. Packman, J. Denis Newbold, and Francesc Sabater, *Biophysical controls on*

- organic carbon fluxes in fluvial networks*, Nature Geoscience **1** (2008), no. 2, 95–100.
- [8] Jake J. Beaulieu, Clay P. Arango, David A. Balz, and William D. Shuster, *Continuous monitoring reveals multiple controls on ecosystem metabolism in a suburban stream*, Freshwater Biology **58** (2013), no. 5, 918–937.
- [9] E. S. Bernhardt, J. B. Heffernan, N. B. Grimm, E. H. Stanley, J. W. Harvey, Maite Arroita, Alison P. Appling, M. J. Cohen, W. H. McDowell, Robert O. Hall, J. S. Read, B. J. Roberts, E. G. Stets, and C. B. Yackulic, *The metabolic regimes of flowing waters*, Limnology and Oceanography **63** (2018), no. S1, S99–S118.
- [10] Emily S. Bernhardt, Phil Savoy, Michael J. Vlah, Alison P. Appling, Lauren E. Koenig, Robert O. Hall, Maite Arroita, Joanna R. Blaszczak, Alice M. Carter, Matt Cohen, Judson W. Harvey, James B. Heffernan, Ashley M. Helton, Jacob D. Hosser, Lily Kirk, William H. McDowell, Emily H. Stanley, Charles B. Yackulic, and Nancy B. Grimm, *Light and flow regimes regulate the metabolism of rivers*, Proceedings of the National Academy of Sciences **119** (2022), no. 8, e2121976119 (en).
- [11] Melody J. Bernot, Daniel J. Sobota, Robert O. Hall, Patrick J. Mulholland, Walter K. Dodds, Jackson R. Webster, Jennifer L. Tank, Linda R. Ashkenas, Lee W. Cooper, Clifford N. Dahm, Stanley V. Gregory, Nancy B. Grimm, Stephen K. Hamilton, Sherri L. Johnson, William H. McDowell, Judith L. Meyer, Bruce Peterson, Geoffrey C. Poole, H. Maurice Valett, Clay Arango, Jake J. Beaulieu, Amy J. Burgin, Chelsea Crenshaw, Ashley M. Helton, Laura Johnson, Jeff Merriam, B. R. Niederlehner, Jonathan M. O'Brien, Jody D. Potter, Richard W. Sheibley, Suzanne M. Thomas, and Kym Wilson, *Inter-regional comparison of land-use effects on stream metabolism*, Freshwater Biology **55** (2010), no. 9, 1874–1890.

- [12] Melody J. Bernot, Jennifer L. Tank, Todd V. Royer, and Mark B. David, *Nutrient uptake in streams draining agricultural catchments of the midwestern United States*, Freshwater Biology **51** (2006), no. 3, 499–509.
- [13] Stefan Bertilsson and Jeremy B Jones, *Supply of Dissolved Organic Matter to Aquatic Ecosystems*, Aquatic Ecosystems, Elsevier, 2003, pp. 3–24.
- [14] Joanna R. Blaszcak, Joseph M. Delesantro, Dean L. Urban, Martin W. Doyle, and Emily S. Bernhardt, *Scoured or suffocated: Urban stream ecosystems oscillate between hydrologic and dissolved oxygen extremes*, Limnology and Oceanography **64** (2019), no. 3, 877–894.
- [15] C. Boix-Fayos, E. Nadeu, J. M. Quiñonero, M. Martínez-Mena, M. Almagro, and J. de Vente, *Sediment flow paths and associated organic carbon dynamics across a Mediterranean catchment*, Hydrology and Earth System Sciences **19** (2015), no. 3, 1209–1223 (en).
- [16] Derek B. Booth and C. Rhett Jackson, *Urbanization of aquatic systems: Degradation thresholds, stormwater detection, and the limits of mitigation*, Journal of the American Water Resources Association **33** (1997), no. 5, 1077–1090.
- [17] Joan P. Casas-Ruiz, Núria Catalán, Lluís Gómez-Gener, Daniel von Schiller, Biel Obrador, Dolly N. Kothawala, Pilar López, Sergi Sabater, and Rafael Marcé, *A tale of pipes and reactors: Controls on the in-stream dynamics of dissolved organic matter in rivers*, Limnology and Oceanography **62** (2017), S85–S94.
- [18] Timothy P. Covino, Emily S. Bernhardt, and James B. Heffernan, *Measuring and interpreting relationships between nutrient supply, demand, and limitation*, Freshwater Science **37** (2018), no. 3, 448–455.

- [19] I. F. Creed, L. E. Band, N. W. Foster, I. K. Morrison, J. A. Nicolson, R. S. Semkin, and D. S. Jeffries, *Regulation of nitrate-N release from temperate forests: A test of the N flushing hypothesis*, Water Resources Research **32** (1996), no. 11, 3337–3354.
- [20] C. J. Davis, C. H. Fritsen, E. D. Wirthlin, and J. C. Memmott, *High rates of primary productivity in a semi-arid tailwater: implications for self-regulated production*, River Research and Applications **28** (2012), no. 10, 1820–1829.
- [21] Laura A. De Cicco, David Lorenz, Robert M. Hirsch, William Watkins, and Mike Johnson, *data retrieval: R packages for discovering and retrieving water data available from u.s. federal hydrologic web services*, Reston, VA, 2021.
- [22] Benoît O.L. Demars, J. Russell Manson, Jon S. Ólafsson, Gísli M. Gíslason, Rakel Gudmundsdóttir, Guy Woodward, Julia Reiss, Doris E. Pichler, Jes J. Rasmussen, and Nikolai Friberg, *Temperature and the metabolic balance of streams*, Freshwater Biology **56** (2011), no. 6, 1106–1121.
- [23] Ottmar Edenhofer and al et., *Technical summary in: Climate change 2014: Mitigation of climate change. contribution of working group iii to the fifth assessment report of the intergovernmental panel on climate change. technical report*, February 2014.
- [24] Christina Fasching, Amber J. Ulseth, Jakob Schelker, Gertraud Steniczka, and Tom J. Battin, *Hydrology controls dissolved organic matter export and composition in an Alpine stream and its hyporheic zone*, Limnology and Oceanography **61** (2016), no. 2, 558–571.
- [25] Christine S. Fellows, Maurice H. Valett, and Clifford N. Dahm, *Whole stream metabolism in two montane streams: Contribution of the hyporheic zone*, Limnology and Oceanography **46** (2001), no. 3, 523–531 (en).

- [26] Stuart G. Fisher, Lawrence J. Gray, Nancy B. Grimm, and David E. Busch, *Temporal Succession in a Desert Stream Ecosystem Following Flash Flooding*, Ecological Monographs **52** (1982), no. 1, 93–110.
- [27] Thomas Fuß, Barbara Behounek, Amber J. Ulseth, and Gabriel A. Singer, *Land use controls stream ecosystem metabolism by shifting dissolved organic matter and nutrient regimes*, Freshwater Biology **62** (2017), no. 3, 582–599.
- [28] Herncin E. Garcia and Louis I. Gordon, *Oxygen solubility in seawater: Better fitting equations*, Limnology and Oceanography **37** (1992), no. 6, 1307–1312.
- [29] Natalie A. Griffiths, Jennifer L. Tank, Todd V. Royer, Sarah S. Roley, Emma J. Rosi-Marshall, Matt R. Whiles, Jake J. Beaulieu, and Laura T. Johnson, *Agricultural land use alters the seasonality and magnitude of stream metabolism*, Limnology and Oceanography **58** (2013), no. 4, 1513–1529.
- [30] Nancy B. Grimm, David Foster, Peter Groffman, J. Morgan Grove, Charles S. Hopkinson, Knute J. Nadelhoffer, Diane E. Pataki, and Debra P.C. Peters, *The changing landscape: ecosystem responses to urbanization and pollution across climatic and societal gradients*, Frontiers in Ecology and the Environment **6** (2008), no. 5, 264–272.
- [31] PRISM Climate Group, *Parameter-elevation regressions on independent slopes model*, Oregon State University.
- [32] Robert Jr O. Hall, Michelle A. Baker, Christopher D. Arp, and Benjamin J. Koch, *Hydrologic control of nitrogen removal, storage, and export in a mountain stream*, Limnology and Oceanography **54** (2009), no. 6, 2128–2142 (en), _eprint: <https://aslopubs.onlinelibrary.wiley.com/doi/pdf/10.4319/lo.2009.54.6.2128>.

- [33] Robert O. Hall, Jennifer L. Tank, Michelle A. Baker, Emma J. Rosi-Marshall, and Erin R. Hotchkiss, *Metabolism, Gas Exchange, and Carbon Spiraling in Rivers*, Ecosystems **19** (2016), no. 1, 73–86.
- [34] Robert O. Hall and Amber J. Ulseth, *Gas Exchange in Streams and Rivers*, Wiley Interdisciplinary Reviews: Water (2019), no. June, 1–18.
- [35] Robert O. Hall, Charles B. Yackulic, Theodore A. Kennedy, Michael D. Yard, Emma J. Rosi-Marshall, Nicholas Voichick, and Kathrine E. Behn, *Turbidity, light, temperature, and hydropeaking control primary productivity in the Colorado River, Grand Canyon*, Limnology and Oceanography **60** (2015), no. 2, 512–526.
- [36] Sarah A. S. Honious, Rebecca L. Hale, James J. Guilinger, Benjamin T. Crosby, and Colden V. Baxter, *Turbidity Structures the Controls of Ecosystem Metabolism and Associated Metabolic Process Domains Along a 75-km Segment of a Semiarid Stream*, Ecosystems (2021), n/a–n/a (en).
- [37] Erin R. Hotchkiss and Robert O. Hall, *High rates of daytime respiration in three streams: Use of $\delta^{18}\text{O}_{\text{O}_2}$ and O_2 to model diel ecosystem metabolism*, Limnology and Oceanography **59** (2014), no. 3, 798–810.
- [38] William A. House and Melanie S. Warwick, *Hysteresis of the solute concentration/discharge relationship in rivers during storms*, Water Research **32** (1998), no. 8, 2279–2290.
- [39] Oihana Izagirre, Urko Agirre, Miren Bermejo, Jesús Pozo, and Arturo Elosegi, *Environmental controls of whole-stream metabolism identified from continuous monitoring of Basque streams*, Journal of the North American Benthological Society **27** (2008), no. 2, 252–268.

- [40] Kathi Jo Jankowski, Linda A. Deegan, Christopher Neill, Hillary L. Sullivan, Paulo Ilha, Leonardo Maracahipes-Santos, Nubia Marques, and Marcia N. Macedo, *Land Use Change Influences Ecosystem Function in Headwater Streams of the Lowland Amazon Basin*, Water **13** (2021), no. 12, 1667 (en).
- [41] Jeremy B. Jones, Stuart G. Fisher, and Nancy B. Grimm, *A long-term perspective of dissolved organic carbon transport in Sycamore Creek, Arizona, USA*, Hydrobiologia **317** (1996), no. 3, 183–188 (en).
- [42] Gary M. Lovett, Jonathan J. Cole, and Michael L. Pace, *Is net ecosystem production equal to ecosystem carbon accumulation?*, Ecosystems **9** (2006), no. 1, 152–155.
- [43] David A. Lytle and N. Le Roy Poff, *Adaptation to natural flow regimes*, Trends in Ecology and Evolution **19** (2004), no. 2, 94–100.
- [44] Ziad A. Malaeb, J. Kevin Summers, and Bruce H. Pugesek, *Using structural equation modeling to investigate relationships among ecological variables*, Environmental and Ecological Statistics **7** (2000), no. 1, 93–111.
- [45] Nicholas S. Marzolf and Marcelo Ardón, *Ecosystem metabolism in tropical streams and rivers: a review and synthesis*, Limnology and Oceanography (2021), lno.11707 (en).
- [46] M. Meybeck, *Carbon, nitrogen, and phosphorus transport by world rivers*, American Journal of Science **282** (1982), no. 4, 401–450 (en).
- [47] P J Mulholland, C N Dahm, M B David, D M DiToro, T R Fisher, H F Hemond, I Kogel-Knabner, M H Meybeck, J L Meyer, and J R Sedell, *Group report 4: What are the temporal and spatial variations of organic acids at the ecosystem level*, (1989).

- [48] P J Mulholland, C S Fellows, J. L. Tank, Nancy B. Grimm, J. R. Webster, S K Hamilton, E Marti, L. Ashkenas, W. B. Bowden, W. K. Dodds, W. H. McDowell, M. J. Paul, and B. J. Peterson, *Inter-biome comparison of factors controlling stream metabolism*, Freshwater Biology **46** (2001), no. 11, 1503–1517.
- [49] Patrick J. Mulholland, Erich R. Marzolf, Jackson R. Webster, Deborah R. Hart, and Susan P. Hendricks, *Evidence that hyporheic zones increase heterotrophic metabolism and phosphorus uptake in forest streams*, Limnology and Oceanography **42** (1997), no. 3, 443–451 (en).
- [50] Markus W. Naegeli and Urs Uehlinger, *Contribution of the Hyporheic Zone to Ecosystem Metabolism in a Prealpine Gravel-Bed-River*, Journal of the North American Benthological Society **16** (1997), no. 4, 794–804.
- [51] Howard T. Odum, *Primary Production in Flowing Waters*, Limnology and Oceanography **1** (1956), no. 2, 102–117.
- [52] Aline Ortega-Pieck, Alexander K. Fremier, and Cailin Huyck Orr, *Agricultural influences on the magnitude of stream metabolism in humid tropical headwater streams*, Hydrobiologia **799** (2017), no. 1, 49–64 (en).
- [53] Daniel Padfield, Chris Lowe, Angus Buckling, Richard Ffrench-Constant, Simon Jennings, Felicity Shelley, Jón S. Ólafsson, and Gabriel Yvon-Durocher, *Metabolic compensation constrains the temperature dependence of gross primary production*, Ecology Letters **20** (2017), no. 10, 1250–1260.
- [54] Margaret A. Palmer and Catherine M. Febria, *Ecology: The heartbeat of ecosystems*, **336**, no. 6087, 1393–1394.
- [55] Daniel M. Perkins, Gabriel Yvon-Durocher, Benoît O.L. Demars, Julia Reiss, Doris E.

- Pichler, Nikolai Friberg, Mark Trimmer, and Guy Woodward, *Consistent temperature dependence of respiration across ecosystems contrasting in thermal history*, Global Change Biology **18** (2012), no. 4, 1300–1311.
- [56] R Core Team, *R: A language and environment for statistical computing*, R Foundation for Statistical Computing, Vienna, Austria, 2021.
- [57] Alonso Ramírez, Catherine M. Pringle, and Luisenrique Molina, *Effects of stream phosphorus levels on microbial respiration: Phosphorus levels and microbial respiration*, Freshwater Biology **48** (2003), no. 1, 88–97 (en).
- [58] Peter A. Raymond, James E. Saiers, and William V. Sobczak, *Hydrological and biogeochemical controls on watershed dissolved organic matter transport: pulse-shunt concept*, Ecology **97** (2016), no. 1, 5–16.
- [59] Peter A. Raymond, Christopher J. Zappa, David Butman, Thomas L. Bott, Jody Potter, Patrick Mulholland, Andrew E. Laursen, William H. McDowell, and Denis Newbold, *Scaling the gas transfer velocity and hydraulic geometry in streams and small rivers*, Limnology and Oceanography: Fluids and Environments **2** (2012), no. 1, 41–53.
- [60] Brian J. Roberts, Patrick J. Mulholland, and Walter R. Hill, *Multiple Scales of Temporal Variability in Ecosystem Metabolism Rates: Results from 2 Years of Continuous Monitoring in a Forested Headwater Stream*, Ecosystems **10** (2007), no. 4, 588–606.
- [61] Yves Rosseel, *lavaan: An R package for structural equation modeling*, Journal of Statistical Software **48** (2012), no. 2, 1–36.
- [62] Phil Savoy, *StreamLight: An R package for estimating stream lighting conditions*, 2021.

- [63] A. H. Sawyer, L. A. Kaplan, O. Lazareva, and H. A. Michael, *Hydrologic dynamics and geochemical responses within a floodplain aquifer and hyporheic zone during Hurricane Sandy*, Water Resources Research **50** (2014), no. 6, 4877–4892.
- [64] Jack A. Stanford and J. V. Ward, *An ecosystem perspective of alluvial rivers: Connectivity and the hyporheic corridor*, Journal of the North American Benthological Society **12** (1993), no. 1, 48–60.
- [65] U. S. Geological Survey, *USGS Water Data for the Nation*.
- [66] Urs Uehlinger, *Resistance and resilience of ecosystem metabolism in a flood-prone river system*, Freshwater Biology **45** (2000), no. 3, 319–332.
- [67] Urs Uehlinger, Markus Naegeli, and Stuart G. Fisher, *A heterotrophic desert stream? The role of sediment stability.*, Western North American Naturalist **62** (2002), no. 4, 488–473.
- [68] Urs Uehlinger and Markus W. Naegeli, *Ecosystem Metabolism, Disturbance, and Stability in a Prealpine Gravel Bed River*, Journal of the North American Benthological Society **17** (1998), no. 2, 165–178.
- [69] Amber J. Ulseth, Enrico Bertuzzo, Gabriel A. Singer, Jakob Schelker, and Tom J. Battin, *Climate-Induced Changes in Spring Snowmelt Impact Ecosystem Metabolism and Carbon Fluxes in an Alpine Stream Network*, Ecosystems **21** (2018), no. 2, 373–390.
- [70] Amber J. Ulseth and Anne E. Hershey, *Natural abundances of stable isotopes trace anthropogenic N and C in an urban stream*, Journal of the North American Benthological Society **24** (2005), no. 2, 270–289.

- [71] Tracy N. Wiegner, Louis A. Kaplan, J. Denis Newbold, and Peggy H. Ostrom, *Contribution of dissolved organic C to stream metabolism: A mesocosm study using ^{13}C -enriched tree-tissue leachate*, Journal of the North American Benthological Society **24** (2005), no. 1, 48–67.
- [72] Craig E. Williamson, Walter Dodds, Timothy K. Kratz, and Margaret A. Palmer, *Lakes and streams as sentinels of environmental change in terrestrial and atmospheric processes*, Frontiers in Ecology and the Environment **6** (2008), no. 5, 247–254.
- [73] Jessica C. Y. Wong and Dudley Dudley Williams, *Sources and seasonal patterns of dissolved organic matter (DOM) in the hyporheic zone*, Hydrobiologia **647** (2010), no. 1, 99–111.

APPENDIX A

Metabolism Data

Below are graphs of temporal variation for all sites for GPP (green lines), ER (orange lines), and NEP (black lines) across the coupled gradients. Sites are arranged arid to mesic top down.

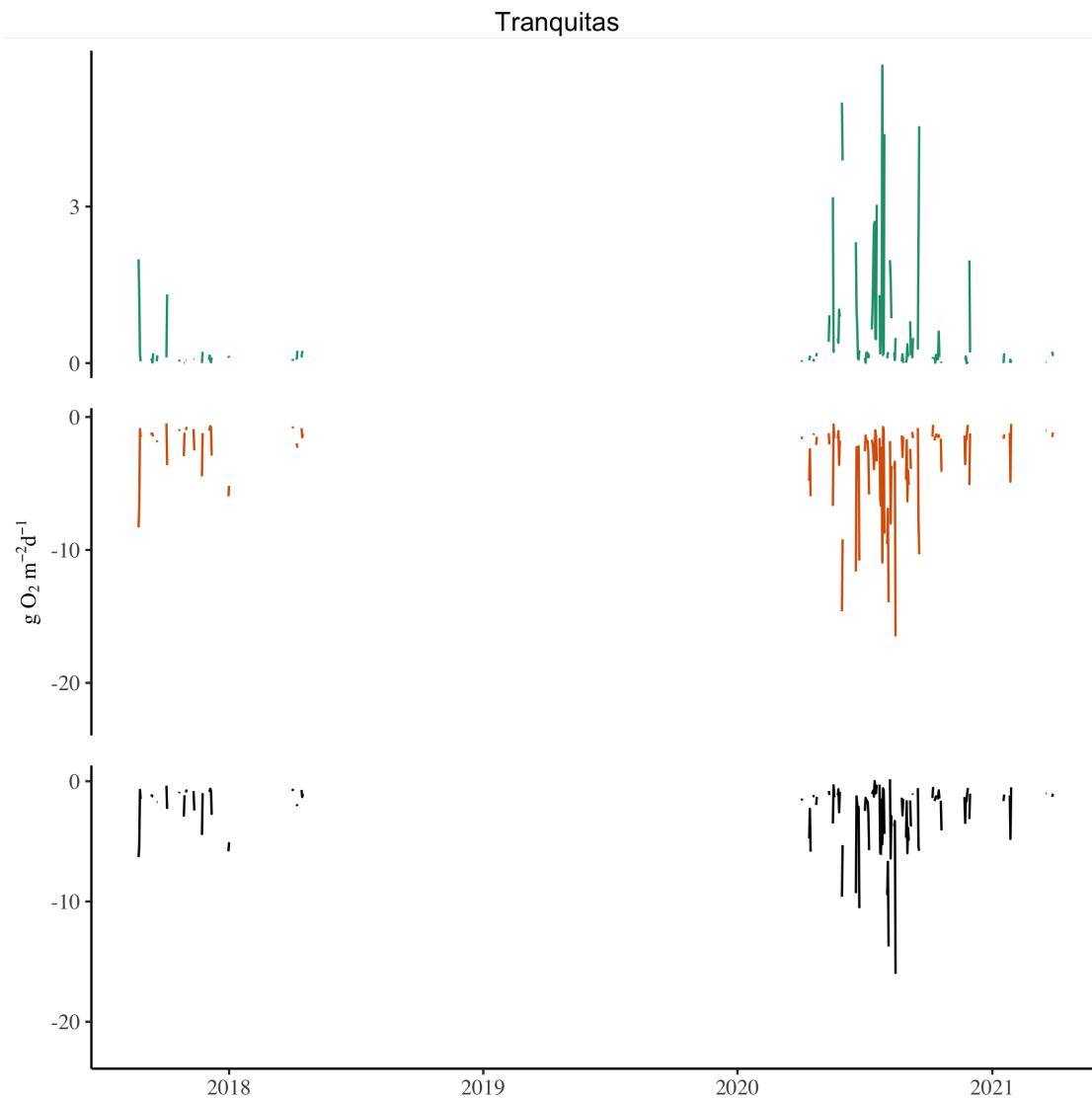


Figure 18: Tranquitas Creek.

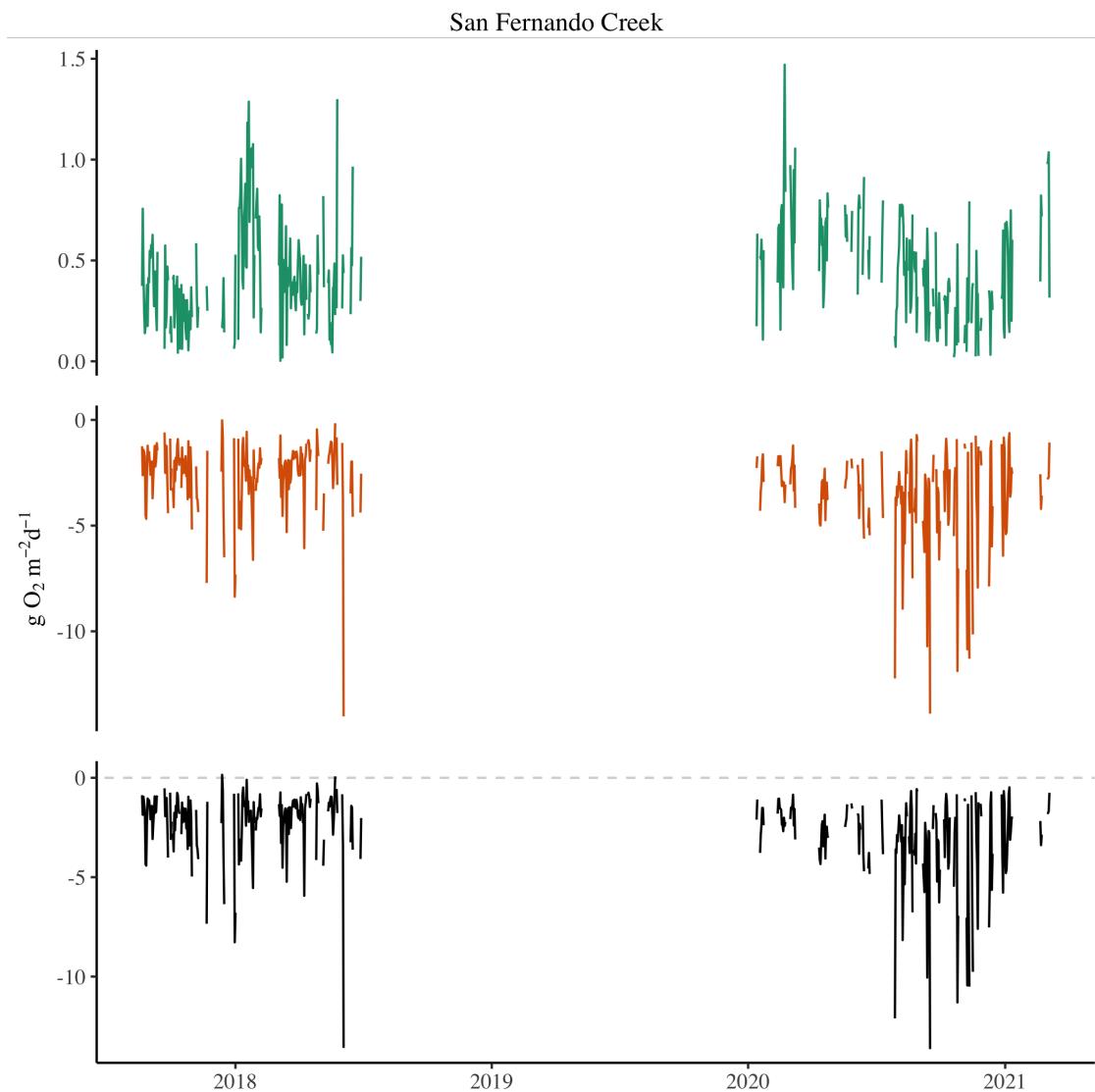


Figure 19: San Fernando Creek

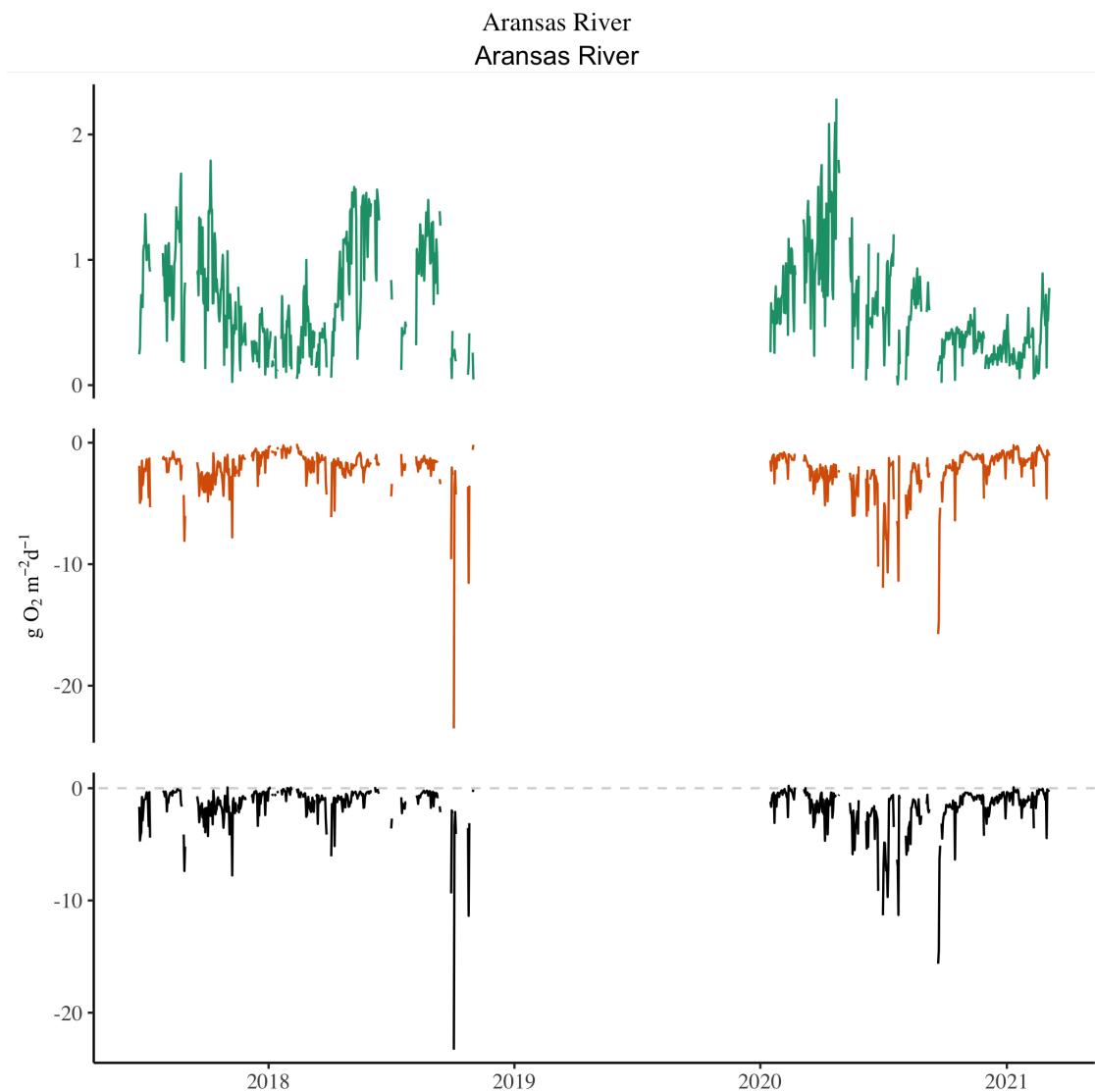


Figure 20: Aransas River

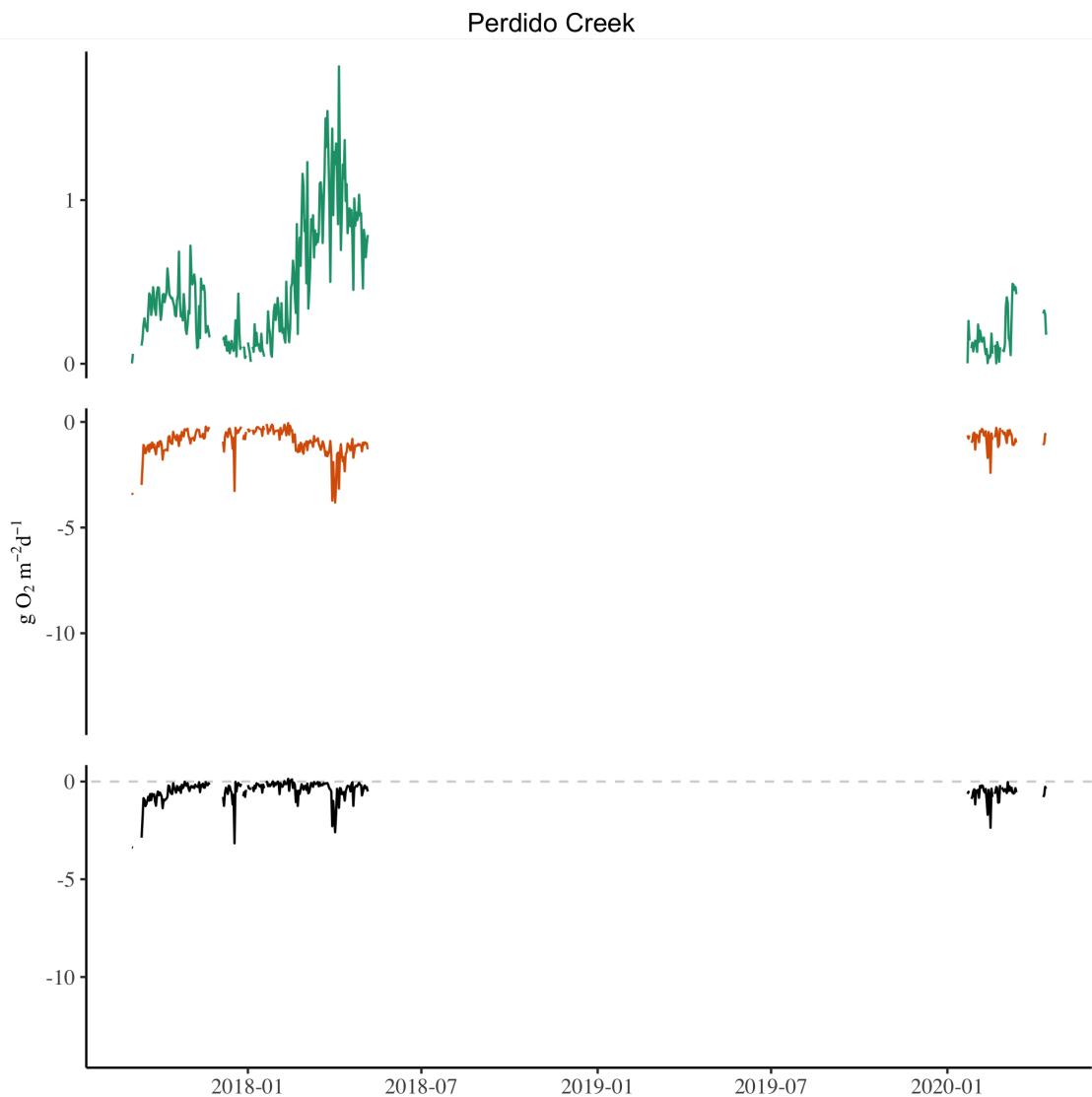


Figure 21: Perdido Creek

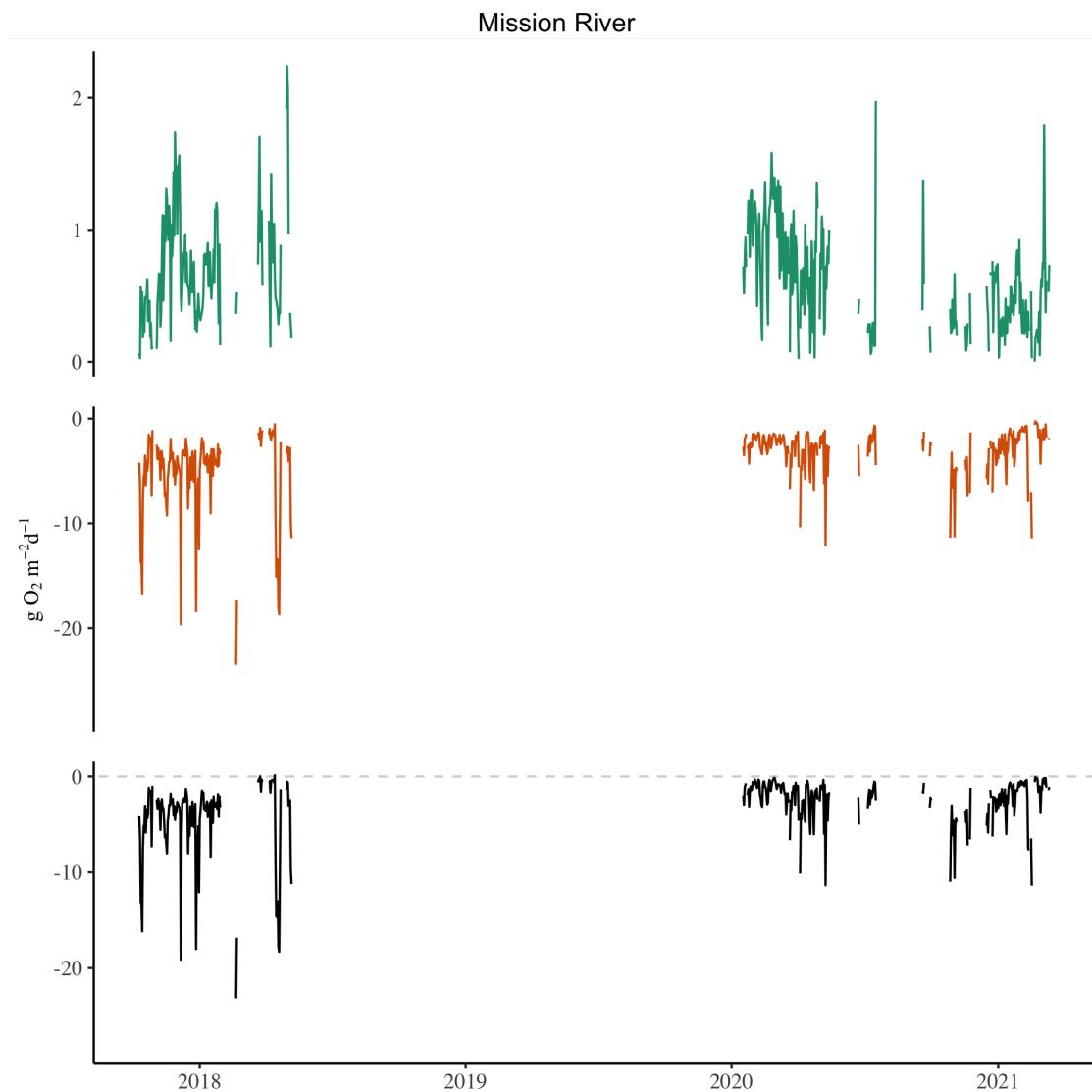


Figure 22: Mission River

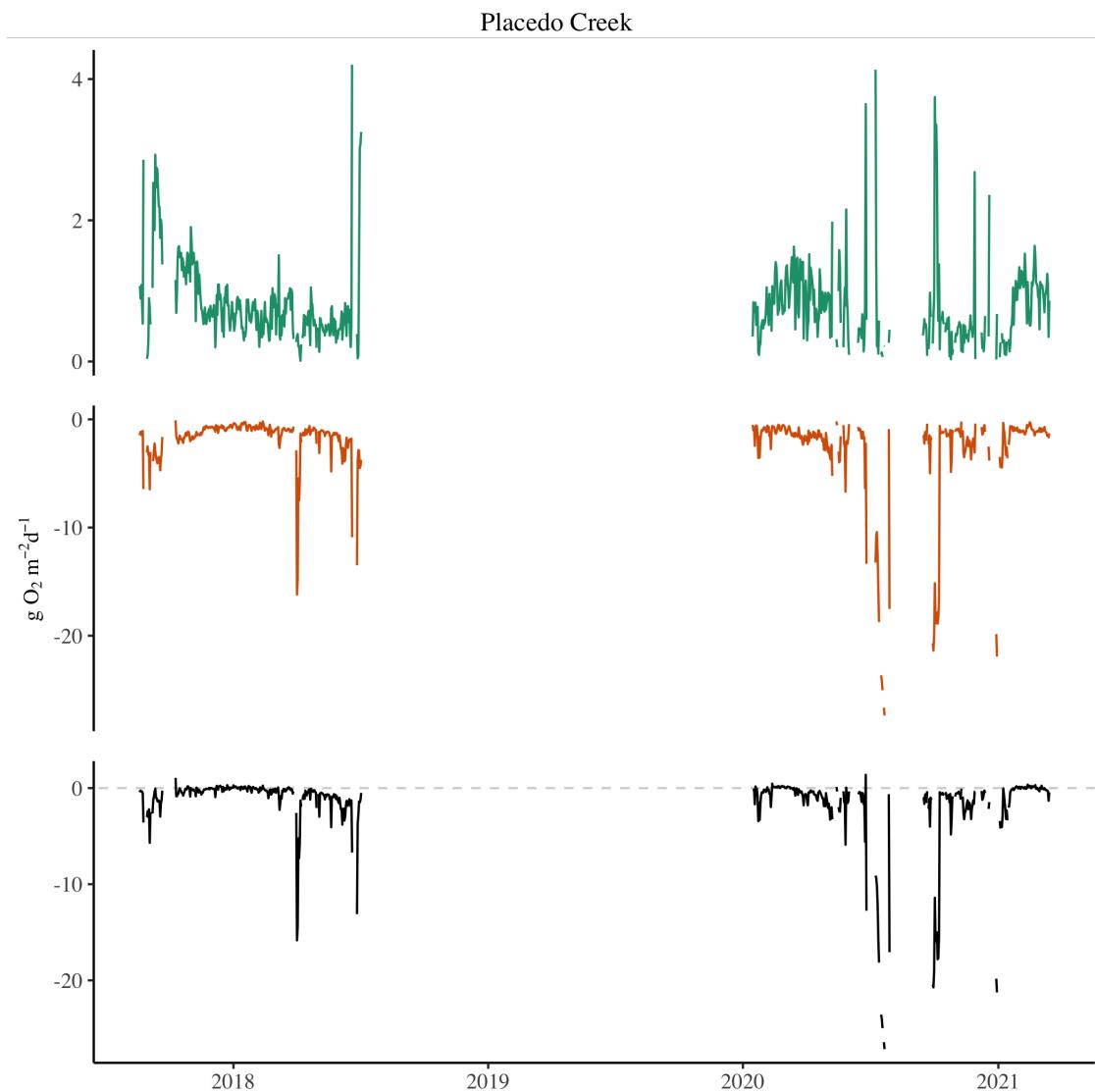


Figure 23: Placedo Creek

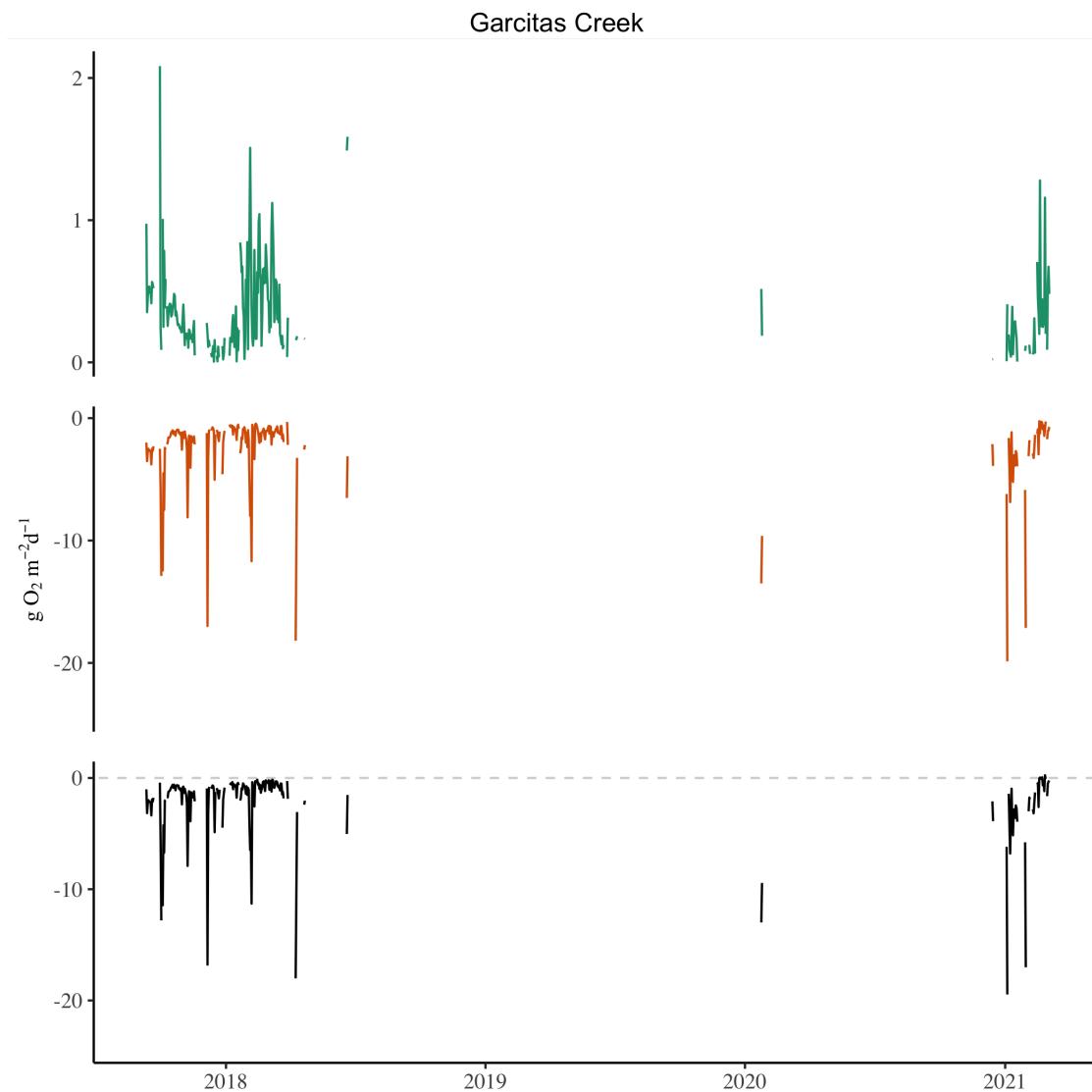


Figure 24: Garcitas Creek

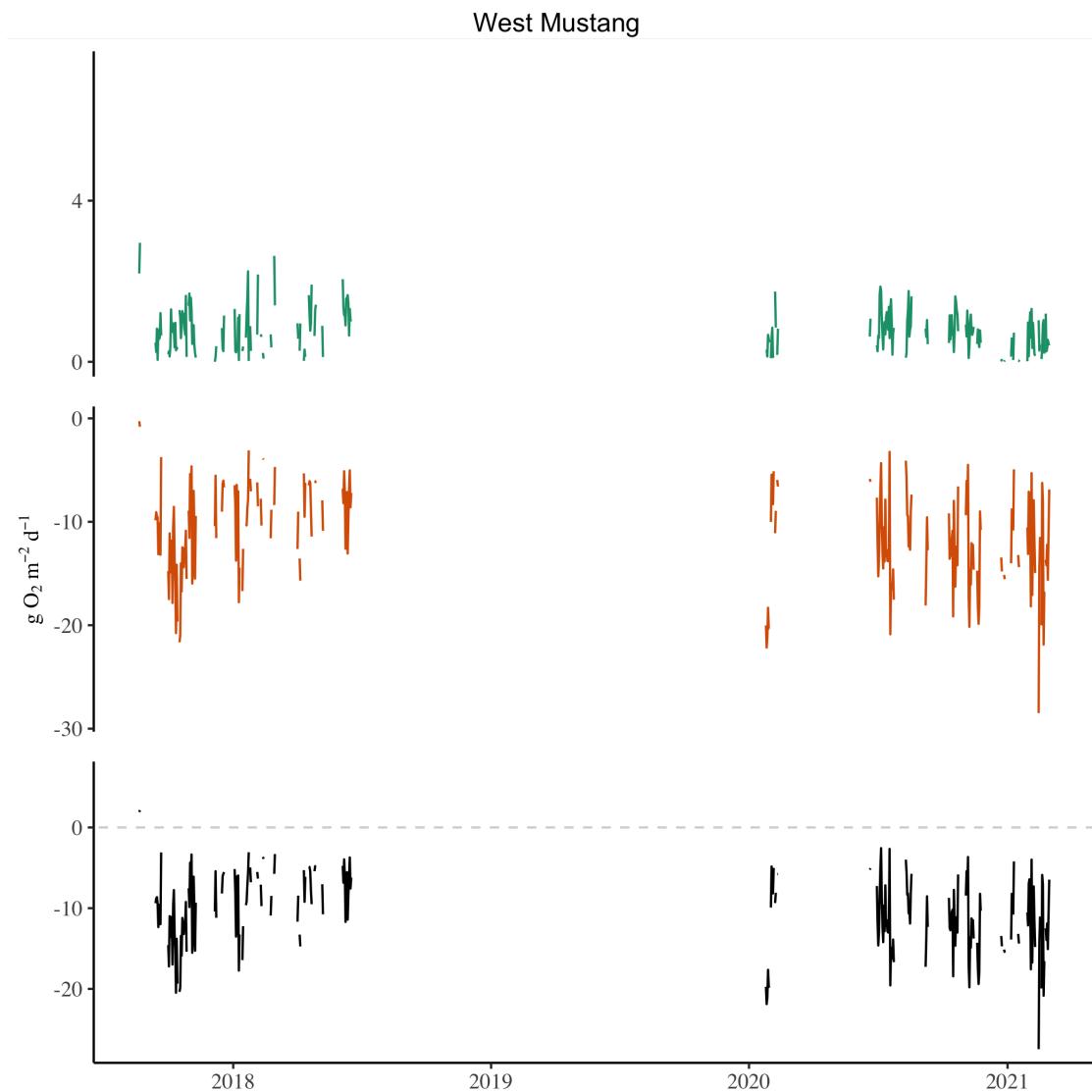


Figure 25: West Mustang Creek

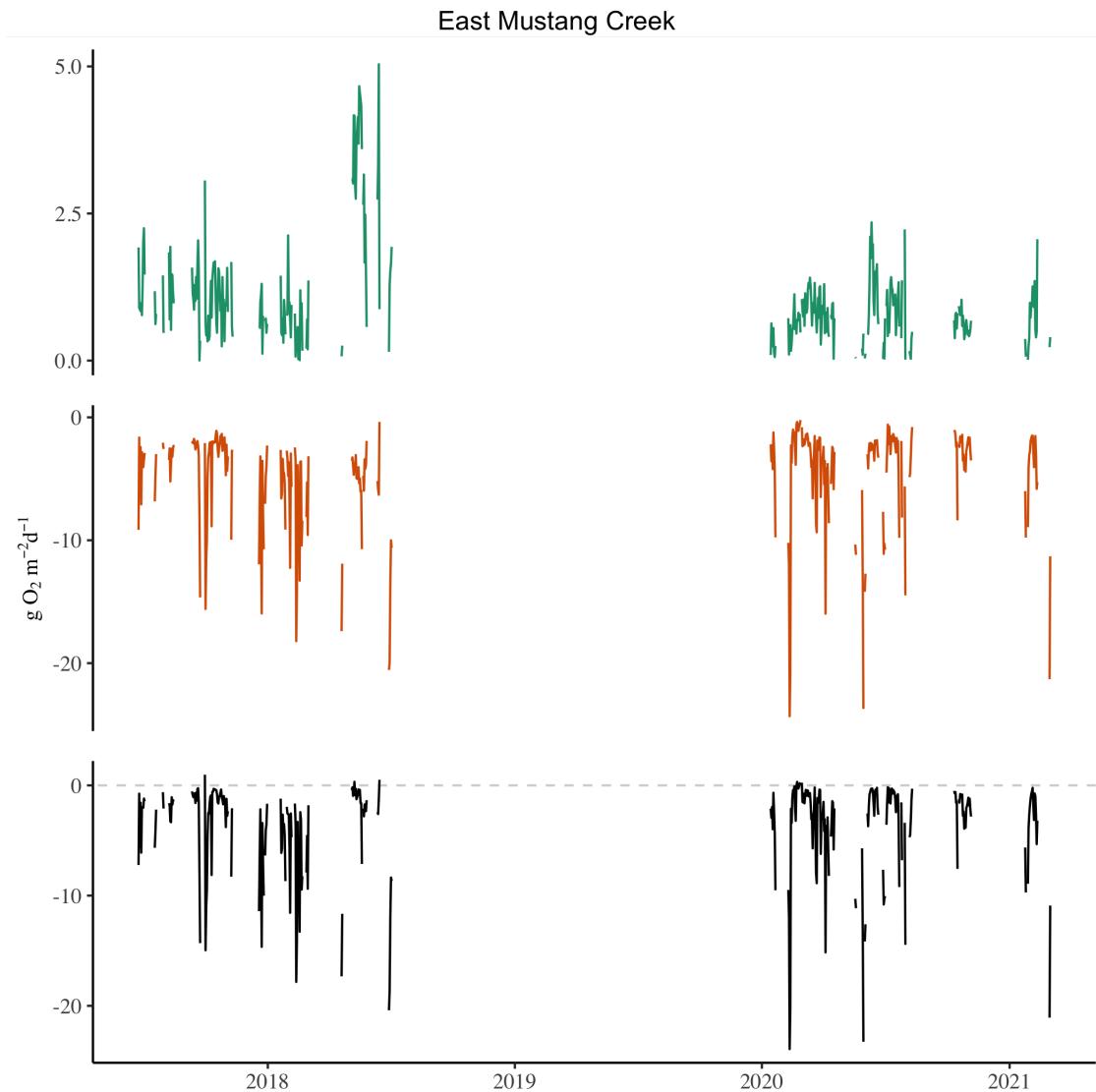


Figure 26: East Mustang Creek

VITA

Connor L. Brown

EDUCATION

M.S., Biology 2019-Present Sam Houston State University, Huntsville, Texas Thesis:
Ecosystem metabolism of coastal Texas streams across precipitation regimes and land use gradients.

Relevant Coursework: Ichthyology, Invertebrate Zoology, Biogeography, Biostatistics, Hydrology, Stream Ecology

B.S., Natural Resources Management 2016-2018 Texas Tech University, Lubbock, Texas
Concentration: Aquatic and Fisheries Biology

Minor: Geographic Information Science and Technology

Relevant Coursework: Freshwater Bioassessment, Watershed Planning, Fisheries Conservation and Management, Introduction to Geographic Information Systems, Advanced Geographic Information Systems, Cartographic Design, Spatial Analysis, GPS Mapping, Aerial Photo Interpretation, Integrated Natural Resources Management Skills, Wildlife and Vegetation Techniques, Diversity of Life, Genetics, Introduction to Conservation Science.

PUBLICATIONS

Brown, C. L. Delaune, K. D., Pease, A. A. 2022. *Benthic Macroinvertebrate Assemblage Structure in Salinized Reaches of the Lower Pecos River, Texas.* (In Review.). The Southwestern Naturalist

EXPERIENCE

2020-2021 Graduate Research Assistant

Stream and Biogeochemistry Lab, Department of Biological Sciences, Sam Houston State University.

Managed data collection, analyzed time series data, estimated ecosystem metabolism using R, and collected macroinvertebrates and fish for the NSF Funded project Thresholds in Ecosystem Responses to Rainfall Gradients (TERRG).

2019 Graduate Research Assistant

Texas Research Institute for Environmental Studies, Sam Houston State University

Worked on a funded grant from the Texas Military Department to collect invertebrate and habitat data, identified terrestrial and aquatic invertebrates, and pinned specimens.

2019-2020 Teaching Assistant

Department of Biological Sciences, Sam Houston State University

Taught three sections of Ecology Lab and Environmental Science. This included giving a lecture over the material, leading lab activities, and assisting in students' knowledge of ecology and environmental science.

2016-2018 Undergraduate Researcher

Department of Natural Resources Management, Texas Tech University

Proposed and conducted a research project on the Pecos River. Field work included setting up Hester-Dendy samplers at three sites along the Pecos and taking habitat measurements. Lab work included sorting macroinvertebrates and identifying them using dichotomous keys.

2016 Undergraduate Internship

Department of Natural Resources Management, Texas Tech University

Worked closely with a graduate student on their dissertation with both field and lab work. Field work included setting up transects, collecting macroinvertebrates, fish, water sampling, as well as taking habitat measurements. Lab work included using dichotomous keys to identify macroinvertebrates as well as extracting environmental DNA from water samples.

PRESENTATIONS

Brown, C. L., Carvallo, F., Frazier, C., Groff, C.M., Jenkins, V., Kinard, S. K., Solis, A.T., Strickland, B., Hogan, J. D., Patrick, C. J., Whiles, M. R., Zanden, H. V., Ulseth, A. J., 2021. Ecosystem metabolism of coastal Texas streams across precipitation and land use gradients. Society for Freshwater Science.

Brown, C. L., Delaune, K. D., Pease, A. A., 2018. Spatial and Temporal Variation in Benthic Macroinvertebrate Assemblages Structure in Salinized Reaches of the Pecos River. Desert Fishes Council, Death Valley, California.

Brown, C. L., Delaune, K. D., Pease, A. A., 2018. Macroinvertebrate community structure on the lower Pecos River. Southwestern Association of Naturalists, San Marcos, Texas.