To my parents, Dale and Melissa
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TABLE OF CONTENTS

<p>| ACKNOWLEDGMENTS | ........................................................................................................ | 4 |
| LIST OF TABLES | ........................................................................................................ | 11 |
| LIST OF FIGURES | ........................................................................................................ | 12 |
| LIST OF OBJECTS | ........................................................................................................ | 15 |
| LIST OF ABBREVIATIONS | ................................................................................................. | 16 |
| ABSTRACT | ........................................................................................................ | 17 |
| CHAPTER 1 | INTRODUCTION | ........................................................................................................ | 21 |
| | Spring Ecosystems | ........................................................................................................ | 21 |
| | Applying Multiscale Modeling to Understand Ecosystem Dynamics | ........................................................................................................ | 26 |
| | Research Objectives and Chapter Summaries | ........................................................................................................ | 28 |
| CHAPTER 2 | LINKING CHANGES IN RIVER DISCHARGE TO CLIMATIC SHIFTS | THROUGH A REINTERPRETATION OF THE BUDYKO FRAMEWORK | ........................................................................................................ | 34 |
| | Budyko Hypothesis | ........................................................................................................ | 34 |
| | Properties and Interpretation of the Parametric Budyko Equations | ........................................................................................................ | 37 |
| | Interpreting Budyko Curves | ........................................................................................................ | 38 |
| | Budyko’s interpretation of the “original” curves | ........................................................................................................ | 38 |
| | Current interpretations of the parametric Budyko framework | ........................................................................................................ | 39 |
| | Alternative interpretation of the parametric Budyko framework | ........................................................................................................ | 41 |
| | Extending the Budyko Hypothesis to Account for Intra-Annual Climate Variability | ........................................................................................................ | 43 |
| | Methods | ........................................................................................................ | 45 |
| | Analytical Solution for the Catchment-Specific Parameter | ........................................................................................................ | 45 |
| | Extending the Original Budyko Hypothesis | ........................................................................................................ | 47 |
| | Statistical Emergence of Budyko Curves | ........................................................................................................ | 50 |
| | Predictive Power of the Extended Budyko Hypothesis | ........................................................................................................ | 52 |
| | Results | ........................................................................................................ | 55 |
| | Statistical Emergence of Budyko Curves | ........................................................................................................ | 55 |
| | Predictive Power of the Extended Budyko Hypothesis | ........................................................................................................ | 55 |
| | Discussion | ........................................................................................................ | 57 |
| | Analytical Solution for the Catchment-Specific Parameter | ........................................................................................................ | 58 |
| | Extending the Original Budyko Hypothesis | ........................................................................................................ | 59 |
| | Statistical Emergence of Budyko Curves | ........................................................................................................ | 61 |
| | Predictive Power of the Extended Budyko Hypothesis | ........................................................................................................ | 63 |</p>
<table>
<thead>
<tr>
<th>Section</th>
<th>Page</th>
</tr>
</thead>
<tbody>
<tr>
<td>Summary and Conclusions</td>
<td>64</td>
</tr>
<tr>
<td>3 USING TRACERS TO QUANTIFY AND PREDICT HETEROGENEITY OF TRANSIENT STORAGE</td>
<td>71</td>
</tr>
<tr>
<td>Hydraulic Transport</td>
<td>71</td>
</tr>
<tr>
<td>Methods</td>
<td>73</td>
</tr>
<tr>
<td>Methodology for Quantification of Transient Storage Membership</td>
<td>73</td>
</tr>
<tr>
<td>Site Descriptions</td>
<td>75</td>
</tr>
<tr>
<td>Rainbow River reach</td>
<td>75</td>
</tr>
<tr>
<td>Silver River reach</td>
<td>75</td>
</tr>
<tr>
<td>Alexander Springs Creek reach</td>
<td>76</td>
</tr>
<tr>
<td>Data Collection</td>
<td>76</td>
</tr>
<tr>
<td>Dye tracing</td>
<td>76</td>
</tr>
<tr>
<td>Roving sampling and eco-geomorphological feature characterization</td>
<td>77</td>
</tr>
<tr>
<td>Sample processing</td>
<td>79</td>
</tr>
<tr>
<td>Quantitative Analysis of Dye Traces and Roving Samples</td>
<td>81</td>
</tr>
<tr>
<td>ADS model</td>
<td>81</td>
</tr>
<tr>
<td>Breakthrough curve calibration</td>
<td>83</td>
</tr>
<tr>
<td>Transient storage classification</td>
<td>84</td>
</tr>
<tr>
<td>Probabilistic Transient Storage Model</td>
<td>85</td>
</tr>
<tr>
<td>Model description</td>
<td>85</td>
</tr>
<tr>
<td>Model calibration</td>
<td>86</td>
</tr>
<tr>
<td>Predicting transient storage in experimental reach cross sections</td>
<td>87</td>
</tr>
<tr>
<td>Results</td>
<td>88</td>
</tr>
<tr>
<td>Quantitative Analysis of Dye Traces and Roving Samples</td>
<td>88</td>
</tr>
<tr>
<td>Breakthrough curve calibration</td>
<td>88</td>
</tr>
<tr>
<td>Transient storage classification</td>
<td>88</td>
</tr>
<tr>
<td>Probabilistic Transient Storage Model</td>
<td>89</td>
</tr>
<tr>
<td>Model calibration</td>
<td>89</td>
</tr>
<tr>
<td>Predicting transient storage in experimental reach cross sections</td>
<td>90</td>
</tr>
<tr>
<td>Discussion</td>
<td>90</td>
</tr>
<tr>
<td>Quantitative Analysis of Dye Traces and Roving Samples</td>
<td>90</td>
</tr>
<tr>
<td>Breakthrough curve calibration</td>
<td>90</td>
</tr>
<tr>
<td>Transient storage classification</td>
<td>91</td>
</tr>
<tr>
<td>Probabilistic Transient Storage Model</td>
<td>92</td>
</tr>
<tr>
<td>Model calibration</td>
<td>92</td>
</tr>
<tr>
<td>Predicting transient storage in experimental reach cross sections</td>
<td>93</td>
</tr>
<tr>
<td>Applications for the predictive model</td>
<td>93</td>
</tr>
<tr>
<td>Summary and Conclusions</td>
<td>94</td>
</tr>
<tr>
<td>4 HYDRODYNAMIC CONTROLS ON PRIMARY PRODUCERS COMMUNITIES IN SPRING-FED RIVERS</td>
<td>109</td>
</tr>
<tr>
<td>Primary Producers and Hydrodynamics</td>
<td>109</td>
</tr>
<tr>
<td>Data and Methods</td>
<td>111</td>
</tr>
<tr>
<td>Observational and Experimental Datasets</td>
<td>111</td>
</tr>
</tbody>
</table>
Text A-2 ................................................................................................................................. 167

B SUPPORTING INFORMATION FOR CHAPTER 3 ..................................................... 177

Overview ............................................................................................................................... 177
Method .................................................................................................................................. 177
Result ..................................................................................................................................... 178

C SUPPORTING INFORMATION FOR CHAPTER 4 ...................................................... 179

Overview ............................................................................................................................... 179
Text C-1 ................................................................................................................................. 180
  Gulf Coast Springs Survey ................................................................................................. 180
    General description of dataset ....................................................................................... 180
    Data collection and processing methodology ............................................................... 180
    Data format ...................................................................................................................... 180
    Site locations .................................................................................................................. 180
    Funding sources ............................................................................................................. 181
  Gum Slough Filamentous Algae Survey ......................................................................... 181
    General description of dataset ....................................................................................... 181
    Data collection and processing methodology ............................................................... 181
    Data format ...................................................................................................................... 182
    Site locations .................................................................................................................. 182
    Funding sources ............................................................................................................. 182
  Synoptic Biological Springs Study ................................................................................. 182
    General description of dataset ....................................................................................... 182
    Data collection and processing methodology ............................................................... 182
    Site locations .................................................................................................................. 183
    Funding sources ............................................................................................................. 183
  CRISPS SAV Groundtruthing Survey .......................................................................... 184
    General description of dataset ....................................................................................... 184
    Data collection and processing methodology ............................................................... 184
    Site locations .................................................................................................................. 185
    Funding sources ............................................................................................................. 185
  CRISPS Hydraulics and Hydrodynamics Periphyton Survey ........................................ 185
    General description of dataset ....................................................................................... 185
    Data collection and processing methodology ............................................................... 186
    Site locations .................................................................................................................. 187
    Funding sources ............................................................................................................. 187
Text C-2 ................................................................................................................................. 187
  Explicit Posterior Distributions for Primary Producer Cover Datasets .................... 187
  Explicit Posterior Distributions for Primary Producer Biomass Datasets ................ 193
  Sampling of Posterior Distributions ................................................................................ 195
Text C-3 ................................................................................................................................. 195
# LIST OF TABLES

<table>
<thead>
<tr>
<th>Table</th>
<th>Description</th>
<th>Page</th>
</tr>
</thead>
<tbody>
<tr>
<td>2-1</td>
<td>Previously proposed functional forms for the Budyko hypothesis.</td>
<td>66</td>
</tr>
<tr>
<td>3-1</td>
<td>Calibrated ADS model parameters for each of the 5 experimental efforts.</td>
<td>100</td>
</tr>
<tr>
<td>3-2</td>
<td>Calibrated statistically significant parameters of the probabilistic transient storage model.</td>
<td>103</td>
</tr>
<tr>
<td>A-1</td>
<td>Existing relationships for the catchment-specific parameter in terms of biophysical features.</td>
<td>170</td>
</tr>
<tr>
<td>A-2</td>
<td>Selected (E_0) estimation methods.</td>
<td>172</td>
</tr>
<tr>
<td>A-3</td>
<td>Illustration of why the condition, (C &gt; D &gt; 0), holds true for Equations A-4 and A-10 for arid climates and Equations S6 and S12 for humid climates.</td>
<td>174</td>
</tr>
<tr>
<td>C-1</td>
<td>Summary of the visual classification scales used with the corresponding datasets.</td>
<td>207</td>
</tr>
<tr>
<td>Figure</td>
<td>Illustration</td>
<td>Description</td>
</tr>
<tr>
<td>--------</td>
<td>--------------</td>
<td>------------------------------------------------------------------------------</td>
</tr>
<tr>
<td>1-1</td>
<td></td>
<td>Illustration of algal proliferation within spring run ecosystems.</td>
</tr>
<tr>
<td>1-2</td>
<td></td>
<td>Comparison of different spring run primary producer communities.</td>
</tr>
<tr>
<td>1-3</td>
<td></td>
<td>Conceptual multiscale modeling for a springshed. On the springshed scale,</td>
</tr>
<tr>
<td></td>
<td></td>
<td>distributions of rainfall ($P$) and potential evaporation ($E0$) govern the</td>
</tr>
<tr>
<td></td>
<td></td>
<td>discharge generation process.</td>
</tr>
<tr>
<td>2-1</td>
<td></td>
<td>Development of an expression for catchment $E$ in terms of the intra-annual,</td>
</tr>
<tr>
<td></td>
<td></td>
<td>time-dependent average values of $P$, $Pta$, and $E0$, $E0ta$ for two</td>
</tr>
<tr>
<td></td>
<td></td>
<td>catchments with different correlation structure between $Pta$ and $E0ta$.</td>
</tr>
<tr>
<td>2-2</td>
<td></td>
<td>Results of the of parameterizing Equation 2-18 using three intra-annual</td>
</tr>
<tr>
<td></td>
<td></td>
<td>distributions for $Pta$ and $E0ta$.</td>
</tr>
<tr>
<td>2-3</td>
<td></td>
<td>Empirical and predicted estimates of $E$ for the 426 MOPEX catchments.</td>
</tr>
<tr>
<td>2-4</td>
<td></td>
<td>Uncertainty in predictive estimates of $E$ relative to empirically derived</td>
</tr>
<tr>
<td></td>
<td></td>
<td>values for the 426 MOPEX catchments.</td>
</tr>
<tr>
<td>3-1</td>
<td></td>
<td>Rainbow River reach used in this study.</td>
</tr>
<tr>
<td>3-2</td>
<td></td>
<td>Silver River reach used in this study.</td>
</tr>
<tr>
<td>3-3</td>
<td></td>
<td>Alexander Springs Creek reach used in this study.</td>
</tr>
<tr>
<td>3-4</td>
<td></td>
<td>UF scientific divers performing an approximate instantaneous pulse injection</td>
</tr>
<tr>
<td></td>
<td></td>
<td>of the conservative tracer solute Rhodamine WT dye into the outflow of the</td>
</tr>
<tr>
<td></td>
<td></td>
<td>spring vent.</td>
</tr>
<tr>
<td>3-5</td>
<td></td>
<td>Custom built apparatus for collecting water samples from any depth within</td>
</tr>
<tr>
<td></td>
<td></td>
<td>the study reach.</td>
</tr>
<tr>
<td>3-6</td>
<td></td>
<td>Simulated breakthrough curves from the calibrated ADS model for each of the</td>
</tr>
<tr>
<td></td>
<td></td>
<td>5 experimental efforts of this study.</td>
</tr>
<tr>
<td>3-7</td>
<td></td>
<td>ADS model zone classification of subset of roving samples for Alexander</td>
</tr>
<tr>
<td></td>
<td></td>
<td>Springs Creek.</td>
</tr>
<tr>
<td>3-8</td>
<td></td>
<td>ADS model zone classification of subset of roving samples for the Silver</td>
</tr>
<tr>
<td></td>
<td></td>
<td>River.</td>
</tr>
<tr>
<td>3-9</td>
<td></td>
<td>ADS model zone classification of subset of roving samples for the Rainbow</td>
</tr>
<tr>
<td></td>
<td></td>
<td>River.</td>
</tr>
</tbody>
</table>
3-10 Probability distributions for each of the statistically significant model parameters of the probabilistic transient storage model. 

3-11 Plot of the calibrated probabilistic transient storage model.

3-12 Cross section created from transects measurements in Alexander Springs Creek.

3-13 Cross section created from transects measurements in the Rainbow River.

3-14 Cross section created from transects measurements in the Silver River.

3-15 Comparison of predicted storage/adveective zone behavior cross section map to the measured velocity field cross section map for the Silver River.

4-1 Conceptual summary of the methods used in the observational and experimental components of Chapter 4.

4-2 Summary of observational critical velocity threshold results.

4-3 Representative results of periphyton accrual during flow suppression experiments.

4-4 Results of flow manipulation experiments.

5-1 Silver River reach used in this study.

5-2 Breakthrough curves for the four dye traces conducted on the upper reach with their associated discharges.

5-3 Plot of $Q$ vs. $Ar$.

5-4 Stage-discharge curve for the Silver River for years 2000-2018.

5-5 Comparison of a predicted Silver River velocity profile to measured velocity profile for a depth of 2 meters.

5-6 Comparison of a predicted Silver River velocity profile to measured velocity profile for a depth of 1.2 meters.

5-7 $vmHQ$ vs. $Q$ for a range of discharges.

5-8 Comparison of the critical threshold discharge, 15.5 m$^3$/s, to the Silver River discharge time series.

5-9 Long-term rainfall and potential evapotranspiration distributions for the Silver River springshed.

5-10 Temporally varying $P$ and $E0$ for the Silver River springshed.
Timing of the temporally varying $P$ and $E_0$ for the Silver River springshed...... 148

Comparison of temporally varying predicted fraction of rain becoming recharge, $P - EP$, (green) to temporally varying observed fraction of rain becoming spring discharge (blue), for the Silver River springshed................. 149

The parametric Budyko equation plotted in Budyko space as a function of $E_0/P$ for different values of the catchment-specific parameter, $n$.................... 169

Illustration of the semicircular contour in the complex plane, used to evaluate Equation A-36........................................................................................................... 173

Comparison of numerically calculated values of $n$ to finite series approximations of Equation A-56 for an arid catchment......................... 175

Comparison of numerically calculated values of $n$ to finite series approximations of Equation A-57 for a humid catchment......................... 175

Comparison of numerically calculated values of $w$ to finite series approximations of Equation A-58 for an arid catchment......................... 176

Comparison of numerically calculated values of $w$ to finite series approximations of Equation A-59 for a humid catchment......................... 176

Flow velocity profiles before (blue) and after (red) the deployment of the flow control structure................................................................. 208

Images of the flow control structures used in the flow suppression prior to deployment in the field........................................................................ 209

Illustration of canopy motion due to traveling vortices (i.e., monami). ........... 210

A rooted VP blade model as a cantilever beam undergoing simple elastic bending with the coordinate system and geometry of the VP blade referenced in Text S4................................................................. 211

Corresponding periphyton biomass and cover measurements from the Synoptic Biological Springs Study dataset...................................................... 211

Corresponding macroalgae biomass and cover measurements from (a) the Gulf Coast Springs Survey and (b) the Synoptic Biological Springs Study dataset........................................................................................................ 212

Corresponding VP biomass and cover measurements from (a) the Gulf Coast Springs Survey and (b) the Synoptic Biological Springs Study dataset........ 212
<table>
<thead>
<tr>
<th>Object</th>
<th>Description</th>
<th>Page</th>
</tr>
</thead>
<tbody>
<tr>
<td>C-1</td>
<td>Flow control structures deployed in the field</td>
<td>212</td>
</tr>
<tr>
<td>C-2</td>
<td>Flow restoration process to the treatment sites.</td>
<td>212</td>
</tr>
<tr>
<td>C-3</td>
<td>Illustration of monami behavior in the Silver River</td>
<td>213</td>
</tr>
<tr>
<td>Abbreviation</td>
<td>Definition</td>
<td></td>
</tr>
<tr>
<td>--------------</td>
<td>------------</td>
<td></td>
</tr>
<tr>
<td>ADS</td>
<td>Advection dispersion with transient storage</td>
<td></td>
</tr>
<tr>
<td>AZ</td>
<td>Adveective zone</td>
<td></td>
</tr>
<tr>
<td>CRSIPS</td>
<td>Collaborative Research Initiative on Sustainability and Protection of Springs</td>
<td></td>
</tr>
<tr>
<td>E</td>
<td>Actual evapotranspiration</td>
<td></td>
</tr>
<tr>
<td>EFM</td>
<td>Electromagnetic flow meter</td>
<td></td>
</tr>
<tr>
<td>$E_0$</td>
<td>Potential evapotranspiration</td>
<td></td>
</tr>
<tr>
<td>GPS</td>
<td>Global positioning system</td>
<td></td>
</tr>
<tr>
<td>MOPEX</td>
<td>Model Parameter Estimation Project</td>
<td></td>
</tr>
<tr>
<td>NOAA</td>
<td>National Oceanic and Atmospheric Administration</td>
<td></td>
</tr>
<tr>
<td>NSE</td>
<td>Nash-Sutcliffe efficiency</td>
<td></td>
</tr>
<tr>
<td>P</td>
<td>Precipitation</td>
<td></td>
</tr>
<tr>
<td>PET</td>
<td>Potential evapotranspiration</td>
<td></td>
</tr>
<tr>
<td>pH</td>
<td>Power of hydrogen</td>
<td></td>
</tr>
<tr>
<td>ppb</td>
<td>Parts per billion</td>
<td></td>
</tr>
<tr>
<td>PPCS</td>
<td>Primary producer community</td>
<td></td>
</tr>
<tr>
<td>Q</td>
<td>Discharge</td>
<td></td>
</tr>
<tr>
<td>SAV</td>
<td>Submerged aquatic vegetation</td>
<td></td>
</tr>
<tr>
<td>SZ</td>
<td>Storage zone</td>
<td></td>
</tr>
<tr>
<td>USGS</td>
<td>United States Geological Survey</td>
<td></td>
</tr>
<tr>
<td>VP</td>
<td>Aquatic rooted vascular plants</td>
<td></td>
</tr>
<tr>
<td>WT</td>
<td>Water tracing</td>
<td></td>
</tr>
</tbody>
</table>
LINKING LANDSCAPE HYDROLOGIC PROCESSES TO SPRING ECOSYSTEM DYNAMICS

By

Nathan George Frederick Reaver

December 2018

Chair: David Andrew Kaplan
Major: Environmental Engineering Sciences

In many of Florida’s spring-fed rivers, cover of benthic and periphytic algae has increased, and in some cases replaced, the once-dominant aquatic rooted vascular plant communities. These shifts in primary producer communities have occurred contemporaneously with observed increases in nitrogen concentration and declines in the discharge of many springs. One hypothesized driver of observed vegetation shifts is a reduction in the hydraulic control of algal abundance, induced by declines in spring discharge. This dissertation aims to test this hypothesis using a multi-scale observational, experimental, and modeling approach.

First, I investigated the landscape-scale drivers of discharge (i.e. flow) generation using the Budyko framework. The Budyko framework posits that the primary drivers of long-term average catchment evaporation and discharge as the available water (i.e. rainfall) and energy (i.e. sunlight, wind, and temperature) supplies to the landscape. The framework suggests a semi-empirical function of average rainfall and potential evaporation (i.e. the Budyko curve) to describe the central tendency of long-term average catchment evaporation and discharge over a large number of catchments. However, this curve cannot explain why an individual catchment deviates from it.
Through a reinterpretation of the Budyko framework, I developed an evapotranspiration model that can predict the average discharge produced from a landscape using the distributions of rainfall and potential evapotranspiration. This is a substantial improvement over the current framework both practically and conceptually, because it improves predictive power without increasing the data burden required to estimate average catchment and provides a completely physical basis (vs. semi-empirical) for the occurrence of the Budyko curve and deviations of individual catchments from it. I validated the predictive ability of this model using data from 426 US catchments.

To link landscape-scale discharge-generation processes with reach-scale hydraulic processes, I conducted hydraulic tracer experiments in three spring-fed rivers. Using these results, I developed a predictive model for determining the location of river transient storage as a function of reach scale biophysical properties. Transient storage zones are areas within a river with low velocity and long residence times for water and associated dissolved solutes. These zones play an important role in the transport, cycling, and ultimate fate of reactive solutes such as nutrients and dissolved oxygen. Predicting where in a river transient storage is likely to occur can help to improve the modeling of riverine ecosystem dynamics by better constraining the timing and magnitude of the fluxes of solutes to and from ecosystem components. Additionally, I conducted multiple tracer experiments on a single spring-fed river, the Silver River, which allowed me to develop specific quantitative relationships between river discharge and flow velocities in the spring.

To connect reach scale hydraulic processes to primary producer community structure and dynamics, I used field observations from 16 spring-fed rivers to test for
critical threshold velocities for rooted vascular plants, benthic algae, and periphyton abundance. Critically, only periphyton exhibited a critical threshold behavior, with lower abundances occurring above a flow velocity of ~0.22 m/s. This threshold velocity agrees well with experimentally and theoretically obtained values of 0.20 and 0.23 m/s, respectively. Additionally, experimental results suggest that transitions from high to low periphyton abundances when the critical threshold velocity is crossed are not hysteretic. This means that if flow is restored above the critical threshold velocity, high periphyton abundance does not persist. Overall, this nexus of theory, observation, and experimental findings suggest that hydrodynamic controls are critical for structuring flowing water ecosystems by shifting the competitive balance between primary producers.

Finally, I combined the results from the landscape-, river reach-, and primary producer-scale analyses into a multiscale modeling framework. I applied this framework to the Silver River and its springshed to quantify the cascading effects of landscape scale changes in climate to changes in spring discharge, reach-scale velocities, velocities experienced by primary producers, and ultimately on spring run algal abundance. Model results suggest that observed primary producer community shifts in the Silver River can be associated with corresponding discharge declines driven by declines in aquifer recharge due to landscape-scale changes in rainfall and potential evapotranspiration. However, this process cannot fully describe the magnitude and timing of the observed declines in the Silver River. Further investigation is required, and I propose a multiple hypothesis testing methodology to accomplish this. Overall results suggest that the restoration of spring discharge and spring run flow velocity can reverse
shifts in primary producer communities in springs where the dominant driver of algal abundance is hydraulic control.
"The blue ether of another world"
—William Bartram

"Each is a little ecologic jewel in which geology and biology have created a masterwork of natural art"
—Archie Carr

Springs and the rivers their outflows feed, are highly productive, clear-water ecosystems fed by groundwater discharge [Scott et al., 2004]. North Florida has one of the highest concentrations of springs and spring-fed rivers in the world [FSTF, 2000], sourced from the Floridan Aquifer, one of the largest and most productive aquifers in the world [Miller, 1990]. The Floridan Aquifer and its associated springs are vital ecological, cultural, and economic resources [Bonn and Bell, 2003; Borisova et al., 2014; Dunbar et al., 1989; Huth and Morgan, 2011; Laist and Reynolds III, 2005].

The description by Archie Carr given above captures the concept of springs as ecosystems particularly well, highlighting how the interactions between biological organisms and their physical surroundings results in the environment that we observe. Springs are also particularly well-suited for the general study of ecosystem behaviors, drivers and dynamics due to several of their unique properties. First, almost all of the discharge to a spring comes from a single vent or small group of vents opening from the
aquifer; as such, springs can be treated as if having a point source in many cases. This means that the inputs to the ecosystem are easier to quantify than in other ecosystems, which can have a large range of inputs from multiple sources. Additionally, water temperature and chemistry remain relatively constant in springs [Heffernan et al., 2010b; Odum, 1957a; b]. As approximate chemostats, springs are thus ideal ecosystems in which to study ecosystem dynamics, which in large part motivated pioneering work on whole ecosystem metabolism [Odum, 1956].

In addition to their ecological value, springs also provide a “window” into the health of Floridan Aquifer, which is the primary drinking water supply for over 10 million people [Marella and Berndt, 2005]. The condition of spring ecosystems is closely tied to the quantity and quality of water discharge from the Floridan Aquifer. In recent years, many of Florida’s springs have been showing signs of undesirable ecological changes. Benthic and periphytic algae abundance are increasing in a majority of Florida springs [Stevenson et al., 2004], and in some cases, algae are replacing the once-dominant aquatic rooted vascular plant communities. Examples of an aquatic rooted vascular plant-dominated spring run ecosystem compared to one with increased periphytic algae abundance and an algal-dominated spring run ecosystem are given in Figure 1-1 and Figure 1-2, respectively.

Notably, these shifts in primary producer communities have occurred contemporaneously with observed increases in nitrogen concentration and declines in the discharge of many springs [FSTF, 2000]. The root cause (or causes) of observed primary producer shifts continue to be investigated, and multiple plausible hypotheses have been advanced, such as eutrophication due to increased nitrate levels in springs.
Nitrate levels have steadily increased in spring discharges over the past several decades in large part due to use of inorganic fertilizer [Brown et al., 2008]. This hypothesis suggests that increased nitrate levels allow proliferation of algae by removing a nutrient limitation. However, nitrate concentrations and algal cover have been shown to be uncorrelated [Heffernan et al., 2010a], and spring ecosystem primary production does not appear to be nutrient limited even under natural levels of nitrate [UFWI, 2017]. A closely connected hypothesis for primary producer shifts is inhibition of submerged aquatic macrophytes by increased energy expenditure due to elevated nitrate concentrations and subsequently being outcompeted by algae. However, experimental results suggest that this mechanism is unlikely to produce the observed primary producer shifts [UFWI, 2017].

Another hypothesis is inhibition of grazing control on algae through the reduced abundance or activity algae consumers within the spring ecosystem [Heffernan et al., 2010a]. One proposed mechanism of grazer inhibition is the increasing frequency of hypoxia in many springs [Liebowitz et al., 2014]. Many of the dominant algal grazers are not highly mobile (e.g. snails) and are therefore cannot escape during low dissolved O$_2$ events. A possible mechanism for the increased frequency of hypoxia for springs with short runs and closely associated with larger rivers is the increased occurrence of flow reversals [Hensley and Cohen, 2017]. These flow reversal events can decrease dissolved O$_2$, decrease light availability through the introduction of water highly enriched in dissolved organic carbon, and substantially lower pH. These disturbances are known to have negative impacts on the submerged aquatic macrophytes and algal grazers. Additionally, it has been proposed that recreation pressure removes submerged aquatic
macrophytes through trampling or dislodging of sediments and allow algae to replace them [Brown et al., 2008].

In this dissertation, I focus on the hydraulic control hypothesis, which posits that discharge and flow velocity are important drivers of primary producer community structure. In the case of Florida springs specifically, the hydraulic control hypothesis states that reductions in spring discharge are directly associated with observations of increased algal abundance. Hydrodynamics are known to play an important role in structuring primary producer communities in lotic (flowing-water) ecosystems [Biggs, 1996; Biggs and Stokseth, 1996; Franklin et al., 2008; Jowett and Biggs, 2010]. Higher flow velocities can increase nutrient delivery rate by thinning the diffusive boundary layer over primary producer surfaces, increasing their productivity [Biggs, 1996; Biggs and Stokseth, 1996; Larned et al., 2004; Nepf, 2012a; b; Saravia et al., 1998]. However, if velocities are too high, primary producers can be dislodged from the substrate or be prevented from colonizing [Franklin et al., 2008; Ghosh and Gaur, 1998; Ryder et al., 2006; Wellnitz and Rader, 2003]. Lotic primary producers include rooted vascular plants (VP), macroalgae, and periphyton [O'Hare, 2015], and for all communities, biomass is generally negatively correlated with velocity [Biggs, 1996; Biggs and Stokseth, 1996]. This negative correlation of primary producers with velocity has been observed directly in spring runs [Hoyer et al., 2004; King, 2014]. As such, reductions in flow velocity have the potential to drive substantial variation in the primary producer community structure of spring ecosystems.

Reductions in flow velocity within spring runs are driven largely by declines in spring discharge. The cause of spring discharge decline has yet to be determined,
conclusively. However, there are several hypotheses which can reproduce the behaviors associated with the observed spring discharges, however, these hypotheses each use very different mechanisms:

- Changes of the effective springshed areas have occurred over time, shrinking the capture area of some springs and reducing the associated aquifer recharge volumes.

- The structure and proximity of the Floridan Aquifer to the ocean causes significant deep aquifer storage of freshwater with long lag times between changes in aquifer recharge (e.g., due to long-term precipitation trends like the Atlantic Multidecadal Oscillation) and observed changes in spring discharge.

- Declines in spring discharge have reduced in velocities spring runs, allowing increased aquatic vegetation within the spring run channel. The increased hydraulic resistance imposed by this vegetation causes a backwater effect, increasing the elevation of the water over the spring vent, which reduces the pressure gradient between the aquifer and the river, causing a suppression of flow.

- Changes in climate and/or land use within the Silver Springs springshed has changed the average evapotranspiration from the basin, and therefore recharge into the aquifer.

- Increased aquifer pumping for human and agricultural uses over time

  Notably, impacts of increased aquifer pumping, can manifest as several of the other hypothesized drivers (e.g., changes in springshed area, changes in deep aquifer storage, and changes to the average evapotranspiration from the basin). Therefore, any methodology applied to test these hypotheses must also consider the effects of aquifer pumping.

  Critically, the processes and interactions embedded within the hydraulic control hypothesis span a large range of spatial and temporal scales, from the landscape, to the river reach, to the organism (primary producers). As such, a comprehensive testing of this hypothesis inherently requires a multiscale modeling approach. In this
dissertation, I seek to rigorously test the algal hydraulic control hypothesis using a multi-scale observational, experimental, and modeling approach.

**Applying Multiscale Modeling to Understand Ecosystem Dynamics**

Multiscale modeling is a process to understand a system’s behavior at one scale using information or models from different scales [Famiglietti and Wood, 1994a; Horstemeyer, 2009]. Passing of information between scales can be unidirectional or bidirectional, depending on the nature of the modeling process. It could be argued that almost all physical processes fall under the purview of multiscale phenomena [Weinan, 2011], though in the study of ecosystems and their dynamics, multiscale interactions are particularly evident. From biogeochemical processing of nutrients on the molecular level by microbes [Falkowski et al., 2008], to forests impacting the radiative balance of the Earth through changes in albedo [Ni and Woodcock, 2000], ecological interactions among organisms as well as between organisms and their abiotic environment occur across various scales.

A clear example where the multiscale modeling approach is being utilized is the integration of the biosphere into climate models to produce Earth system models [Bonan and Doney, 2018]. Climate models themselves are multiscale models, simulating smaller scale phenomena, such as cloud formation [Xu et al., 2017], in the context of larger scales, such as atmospheric circulation. Including ecosystem processes furthers this multiscale approach. Ecosystem process models that occur at the organism scale are imbedded within the larger climate model [Bonan, 2008]. Information about matter (e.g. H₂O, CO₂, etc.) and energy flows (e.g. heat, sunlight, etc.) into and out of the smaller ecosystem models (e.g. soil carbon decomposition model of permafrost) is passed bidirectionally to the larger scale climate models. The
parameterization of such multiscale models requires accurate scientific understanding of the biophysical processes at all of the scales. For processes that are only partially or poorly understood, experimentation and observation is required to better constrain model parameters within that scale’s model [Melillo et al., 2017]

While it is evident that Earth system models exchange information bidirectionally across multiple scales, it is also possible to have multiscale modeling frameworks that exchange information unidirectionally. Famiglietti and Wood [1994a; 1994b] provide an example of this unidirectional multiscale modeling approach. They developed a local scale model of the hydrologic cycle for a point within a catchment, incorporating relevant local biophysical features (e.g. vegetation cover, soil characteristics, etc.). This model was used to parametrize a much simpler macroscale model of the regional hydrologic cycle based on lumped statistical representations of the land surface (i.e. aggregation of biophysical features at the local scale). To ensure that the simplified regional model replicated the aggregate behavior of many point-like local scale models, both models were tested for parity at an intermediate scale, the catchment scale. The predictions of the hydrologic fluxes from aggregation of the local scale models and the regional scale model matched the observed data. This suggested that the simplified regional scale model did capture the aggregate behavior of the underlying and more complex dynamics of smaller scale processes, when it was informed by information from that smaller scale.

In the case of the algal hydraulic control hypothesis in springs, the strongest influencing processes can be divided conceptually into three levels: landscape scale, river reach scale, and organism scale. Physical processes at each scale directly
influence the levels below, while feedbacks from smaller scales may potentially impact processes at larger scales. The discharge generating processes for springs occur on the landscape scale (~1 km to 100 km). Processes impacting the hydraulics of spring-fed rivers occur at the reach scale (~100 m to 1 km), but are in part controlled by spring discharge generated from the larger landscape scale. Interactions between primary producers and hydraulic flows occur on the scale of the organism and its immediate surroundings (~1 mm to 100 m). Figure 1-3 provides a conceptual illustration of these three scales and the relationships between them that influence the algal hydraulic control hypothesis. In this dissertation, dominant processes and the relevant relationships between each scale are investigated, culminating in a linkage of landscape hydrologic process to the structure and dynamics of spring ecosystems.

**Research Objectives and Chapter Summaries**

As noted above, the overarching goal of this dissertation is to test the algal hydraulic control hypothesis using a multi-scale observational, experimental, and modeling approach. Specific objectives of this study were to:

- Characterize the dominant drivers and controls of watershed long-term average discharge generation.
- Develop relationships between river discharge and reach-scale hydraulics characteristics.
- Characterize and test relationships between reach-scale flow characteristics and primary producer abundance.
- Combine interactions between landscape, reach, and organism scales into a multiscale modeling framework to test hypothesized drivers of spring ecosystem structure and dynamics at each scale.

The specific methods used to meet these objectives, and the results and conclusions of each, are described in each dissertation chapter, briefly summarized below.
In Chapter 2, I investigated the drivers and controls of discharge generation at the landscape scale using the Budyko framework, which quantifies evapotranspiration in terms of water and energy inputs to a landscape. Through a reinterpretation of this framework I developed a “supply-demand limited” evapotranspiration model requiring only rainfall and potential evaporation data as inputs, to predict the average discharge produced from a landscape. I validated the predictive ability of this model using 426 catchments. This chapter is a general contribution to landscape hydrology, however, the results are applicable to any basin, and therefore can be used to test climate-driven flow-generation questions for springs.

In Chapter 3, I present the findings of hydraulic tracer field experiments I conducted on three spring-fed rivers, the Silver River, Rainbow River, and Alexander Springs Creek. I used these results to develop a general spring-fed river predictive model of reach scale flow properties.

In Chapter 4, I use field observations from 16 different spring-fed rivers to investigate the relationships between reach scale flow velocities and the abundance of the dominant primary producers in spring ecosystems, specifically testing for critical threshold velocities for rooted vascular plants, benthic algae, and periphyton abundance. Additionally, I present the findings from a field experiment I conducted studying periphyton growth dynamics. Finally, I develop a mechanistic model from first principles, which predicts the existence and magnitude of critical threshold velocities determined for periphyton and benthic algae in the observational and experimental studies.
In Chapter 5, I combined the results from the previous three chapters into a multiscale modeling framework. I apply this model to a spring-fed river, the Silver River, to test the hypothesis that spring ecosystem primary producer community shifts are due to a reduction in the hydraulic control of algal abundance, induced by declines in discharge. A final conclusion chapter summarizes the findings and significance of the overall study and proposes future work.
Figure 1-1. Illustration of algal proliferation within spring run ecosystems. Aquatic rooted vascular plant-dominated primary producer community in the Silver River, FL (left panel) compared to another location in the Silver River with increased periphyton abundance (right panel). Photos courtesy of author.

Figure 1-2. Comparison of different spring run primary producer communities. Aquatic rooted vascular plant-dominated primary producer community in the Silver River, FL (left panel) compared a benthic algae-dominated primary producer
community in the Manatee Spring Run, FL (right panel). Photos courtesy of author.

Figure 1-3. Conceptual multiscale modeling for a springshed. On the springshed scale, distributions of rainfall \((P)\) and potential evaporation \((E_0)\) govern the discharge generation process. The springshed scale informs the next smaller scale, the spring run (i.e. reach) scale by supplying discharge information. Within the spring scale, flow velocity is governed by reach-scale hydraulic transport properties, which are informed by both discharge information from the larger scale and primary producer structure information at the next smaller scale, the primary producer scale. At the primary producer scale, the behavior of primary producers is governed by properties of the individual organisms interacting with the local flow velocity environment, which is informed from
reach-scale flow velocity information. This multiscale cascade of information allows for predictions about primary producer structure as a function of discharge generating process on the landscape scale.
CHAPTER 2
LINKING CHANGES IN RIVER DISCHARGE TO CLIMATIC SHIFTS THROUGH A REINTERPRETATION OF THE BUDYKO FRAMEWORK

Budyko Hypothesis

The Budyko hypothesis posits that a catchment’s long-term mean evapotranspiration ($\bar{E}$) is primarily dependent on the aridity index, the ratio of mean rainfall depth ($\bar{P}$) to mean potential evapotranspiration ($\bar{E}_0$). Functional forms of this relationship are known as Budyko equations or curves. While Budyko curves are able to reproduce mean $\bar{E}$ as a function of aridity across multiple catchments, they are unable to explain differences in $\bar{E}$ among individual catchments with the same $\bar{P}$ and $\bar{E}_0$. Two parametric Budyko equations have been developed to explain these deviations, each containing an empirically determined catchment-specific parameter ($n$ or $w$). Variation in $n$ and $w$ has been interpreted to represent differences in catchment biophysical features, however, this interpretation does not explicitly arise from the derivation of the parametric equations, which are inherently underdetermined and thus cannot be used to predict $\bar{E}$. To illustrate this, we developed analytical solutions for $n$ and $w$ in terms of $\bar{E}$, $\bar{P}$, and $\bar{E}_0$. Furthermore, we hypothesized that intra-annual climate variability is sufficient to explain the behavior of individual catchments without invoking landscape biophysical characteristics. To test this hypothesis, we extended the original Budyko hypothesis using a physically-based expression for $\bar{E}$ based on the intra-annual variability of $P$ and $E_0$. Using this expression, we showed that Budyko “curves” emerge statistically based solely on probabilistic representations of $P$ and $E_0$. The predictive power of the new expression was demonstrated using 426 U.S. catchments from the Model Parameter
Estimation Project database, with 82% of catchments falling within prediction uncertainty intervals.

Understanding the fate of precipitated water is essential to catchment hydrology. Over long time periods, it is reasonable to assume that short-term changes in catchment storage average to zero ($\overline{\Delta S} = 0$), such that long-term average rainfall is partitioned into either evapotranspiration or discharge from the catchment, yielding

$$\overline{P} = \overline{E} + \overline{Q}$$  \hspace{1cm} (2-1)

where $P$ is precipitation, $E$ is evapotranspiration, $Q$ is catchment discharge, and the overbar indicates mean values. Budyko [1974] recognized the primary drivers of long-term average catchment evaporation as the available water and energy supplies, characterized respectively by $\overline{P}$ and potential evapotranspiration, $\overline{E_0}$, and formulated the hypothesis that catchment $\overline{E}$ is a function of $\overline{P}$ and $\overline{E_0}$,

$$\overline{E} = f_0(\overline{P}, \overline{E_0})$$  \hspace{1cm} (2-2)

Several explicit functional forms of $f_0$ have been proposed (Table 2-1). While these formulations are able to match the central tendency of $\overline{E}$ over a large numbers of catchments reasonably well, they are fundamentally unable to explain differences in $\overline{E}$ that may be observed between catchments with identical $\overline{P}$ and $\overline{E_0}$ [Yang et al.]. This is due to the constraint imposed by Equation 2-2, where a well-defined function can only have a single output for given inputs. This constrains any formulae for $f_0$ to be parameter-free, preventing it from explaining variance in $\overline{E}$ for a given $\overline{P}$ and $\overline{E_0}$. 
The original Budyko hypothesis has been modified to explain the deviation of individual catchments from the explicit Budyko curves by invoking a function that is implicit in \( \bar{E} \) [Yang et al., 2008],

\[
\bar{E} = f_1(\bar{P}, \bar{E}_0, \bar{E}) \tag{2-3}
\]

where for a given \( \bar{P} \) and \( \bar{E}_0 \), there may be more than one value of \( \bar{E} \) that satisfies Equation 2-3. Using the hypothesized relationship given by Equation 2-3 and appropriate physical boundary conditions, it is possible to analytically derive explicit forms of \( f_1 \). It has been shown that there are at least two possible analytical solutions to Equation 2-3. The first of these solutions was independently discovered twice [Choudhury, 1999; Mezentsev, 1955] prior to its analytical derivation from Equation 2-3 [Yang et al., 2008] and is given by

\[
\frac{\bar{E}}{\bar{P}} = \frac{\frac{\bar{E}_0}{\bar{P}}}{1 + \left(\frac{\bar{E}_0}{\bar{P}}\right)^n} \tag{2-4}
\]

where \( n \) is a parameter specific to each catchment. With slightly different assumptions about the structure and boundary conditions of \( f_1 \), a different parametric form of the Budyko equation can be derived [Fu, 1981; Zhang et al., 2004],

\[
\frac{\bar{E}}{\bar{P}} = 1 + \frac{\bar{E}_0}{\bar{P}} - \left(1 + \left(\frac{\bar{E}_0}{\bar{P}}\right)^w\right)^{\frac{1}{w}} \tag{2-5}
\]

where \( w \) is a catchment-specific parameter. Both solutions contain a single unknown “catchment-specific parameter” (\( n \) or \( w \)). Equations 2-4 and 2-5 express the evaporative ratio \( \left(\frac{\bar{E}}{\bar{P}}\right) \) as a function of the aridity index \( \left(\frac{\bar{E}_0}{\bar{P}}\right) \), however, equivalent forms for both equations exist which express the R-Index \( \left(\frac{\bar{E}}{\bar{E}_0}\right) \) [Yao, 1974] as a function of the humidity.
index \( \left( \frac{\bar{P}}{\bar{E}_0} \right) \) [Hulme et al., 1992]. These alternative forms are important for the
development of explicit analytical solutions for \( n \) and \( w \) (Section 2.1). The alternative
forms of Equations 2-4 and 2-5 are given in Appendix A as Equations A-5 and A-11,
respectively. We refer to all of these expressions as the "parametric Budyko equations."

**Properties and Interpretation of the Parametric Budyko Equations**

The catchment-specific parameter arises due to the implicit nature of Equation 2-3, which implies that there are unknown factors, other than \( \bar{P} \) and \( \bar{E}_0 \) and specific to
each catchment, that impact \( \bar{E} \). These unknown factors are represented by \( n \) and \( w \).

Two catchments that experience the same \( \bar{P} \) and \( \bar{E}_0 \), but have a different \( n \) or \( w \), will
have different \( \bar{E} \). Higher values of \( n \) and \( w \) correspond to a higher fraction of \( \bar{P} \)
becoming \( \bar{E} \), with \( \bar{E} \) approaching \( \bar{E}_0 \) in energy-limited systems, and \( \bar{E} \) approaching \( \bar{P} \) in
water-limited systems (i.e. as \( n \) or \( w \) approaches \( \infty \)). The lower limiting values that \( n \)
and \( w \) can take are 0 and 1, respectively. Mathematically, the value of the catchment-
specific parameter describes a family of curves in Budyko space (Figure A-1 in
Appendix A). The two forms of the catchment-specific parameter are approximately
linearly related [Yang et al., 2008], where,

\[
w \equiv n + 0.72
\]  

The original and parametric Budyko curve equations have been extensively
studied, utilized, and extended within the catchment hydrology literature (Section 1.3).
However, key questions about their interpretation remain. Specifically, do explicit curves
originate from fundamental catchment hydrologic processes or are they conceptual
tools that have been empirically applied to explain observed patterns in catchment
behavior? If the latter is the case, how much emphasis should be ascribed to the explicit
“curve concept”? At the center of this question is the meaning of the catchment-specific parameter of the parametric Budyko equations; what do \( n \) and \( w \) really represent?

These questions have important implications for both the theoretical understanding and practical utility of the Budyko framework.

**Interpreting Budyko Curves**

**Budyko’s interpretation of the “original” curves**

To begin to answer these questions, it is illuminating to review the original interpretation offered by Budyko [1974], in which he considered the explicit curves to be semi-empirical. Specifically, the physical basis for explicit curves is dictated by the conservation of mass and energy (i.e. the curves could never cross the water and energy limits in Budyko space) and the fact that the curves must approach the energy and water limits for increasing humidity (i.e. \( \frac{E_0}{P} \rightarrow 0 \)) and aridity (i.e. \( \frac{E_0}{P} \rightarrow \infty \)), respectively. The empirical nature of these curves comes from the choice of functional form as they transition from the energy limit to the water limit. Any functional form that satisfies the previous two conditions (and provides a good fit to observed data) could thus be a reasonable choice. Indeed, Budyko’s own explicit formulation was simply the geometric mean of the Schreiber and Ol’Dekop formulae (Table 2-1), which provided a slightly better fit to observed data. These interpretations are suggested in Budyko’s own words:

> It is apparent … that the dependence that lies at the base of this equation is in general determined by two limiting conditions, one of which is based on the idea of the valve mechanism of the turbulent exchange of sensible heat in the surface layer of air, and the other on the obvious fact of the smallness of the run-off coefficient in conditions of arid climate. The choice of one or another interpolation function for the transition from the first of these conditions to the second is not very important, since, over most of the range of variation in the parameters of the relationship equation, the
appropriate relation deviates little from one or the other boundary condition. [Budyko, 1974] (p. 325-326)

From this interpretation, it is clear that the explicit curves resulting from the original Budyko hypothesis, while constrained at their limits by fundamental physical laws, have been empirical in nature and not derived from catchment hydrologic processes. This suggests that the concept of an explicit curve is not necessarily required to explain the behavior observed in actual catchments. However, attempts to extend and generalize the Budyko framework (i.e. the parametric Budyko equations) have retained the idea of an explicit curve. Adherence to this curve concept may have unintended consequences, particularly for the interpretation of the catchment-specific parameter and analytical methods derived from the original and parametric Budyko framework [Milly et al., 2018; Roderick and Farquhar, 2011; Shen et al., 2017; Wang and Hejazi, 2011; W Wang et al., 2016; Yang and Yang, 2011; Zhang et al., 2016; Zhou et al., 2016]. In summary, while the curve concept in the parametric Budyko framework is a mathematically valid approach to describe the central tendency of $\overline{E}$ across many catchments, it does not have an explicit physical meaning. In this context, we explore current interpretations of the parametric Budyko framework and hypothesize a possible alternative interpretation.

**Current interpretations of the parametric Budyko framework**

The catchment-specific parameter of the parametric Budyko framework has generally been interpreted as a lumped quantity that represents the influence of all catchment biophysical features other than $\overline{P}$ and $\overline{E_0}$ [C Wang et al., 2016]. Numerous studies have found relationships between the catchment-specific parameter and various biophysical features [Abatzoglou and Ficklin, 2017; Cong et al., 2015; Donohue et al.,
2012; Li et al., 2013; Shao et al., 2012; Xing et al., 2018a; Xu et al., 2013; Yang et al., 2007; Yang et al., 2009; Yang et al., 2016; Zhang et al., 2018]. The explicit expressions for \( n \) or \( w \) developed in these studies are summarized in Table A-1 in Appendix A. These relationships suggest that the catchment-specific parameter is indeed related to biophysical features, with all features falling into one of three categories: (1) climate variability; (2) catchment physical processes; and (3) vegetation structure and function [Donohue et al., 2012]. Importantly, these relationships are all statistical or derived from curve fitting, which makes it difficult to develop a mechanistic understanding of causal relationships between the catchment-specific parameter and relevant biophysical features. To date, there has not been an explicit derivation of the catchment-specific parameter in terms of biophysical features.

Current interpretations of the catchment-specific parameter can be grouped into four general categories: (1) the catchment-specific parameter is related to biophysical features, and it is possible to discern and understand that relationship (references in Table A-1 and C Wang et al. [2016]); (2) the catchment-specific parameter is related to biophysical features, but it may not be possible to determine an explicit relationship, therefore it should be treated probabilistically [Greve et al., 2015; Gudmundsson et al., 2016; Singh and Kumar, 2015]; (3) the catchment-specific parameter and the parametric forms of the Budyko equation contradict the Budyko hypothesis [Gentine et al., 2012; Sposito, 2017a; b]; and (4) the catchment-specific parameter is an arbitrary constant that is generated as a part of the solution to Equation 2-3, but it has no \textit{a priori} physical meaning [Greve et al., 2015; Sposito, 2017b].
The idea that the catchment-specific parameter is related to biophysical features (i.e., interpretation 1) has been widely embraced by the catchment hydrology community, which has developed methods to determine the sensitivity of rainfall partitioning to climate and/or landscape changes for individual catchments [Fernandez and Sayama, 2015; Liang et al., 2015; Roderick and Farquhar, 2011; Sun et al., 2014; W Wang et al., 2016; Xing et al., 2018b; Yang and Yang, 2011; Yang et al., 2018; G Zhou et al., 2015; X Zhou et al., 2015]. A common extension of this interpretation is that the curves associated with a given n or w have intrinsic physical meaning. From this perspective, a catchment with a given set of biophysical features will have a corresponding n or w, and the curve associated with that n or w represents the behavior of that catchment under any climatic condition (i.e. any aridity index). If the climate changes for that catchment, but its overall biophysical features remain constant, this interpretation posits that the catchment will only move along the curve associated with the specific n or w. This interpretation has led to methods to decompose anthropogenic and climatic impacts on the rainfall partitioning [Huang et al., 2016; Jaramillo et al., 2018; Jiang et al., 2015; Liang et al., 2015; Mo et al., 2018; Sun et al., 2014; Wang and Hejazi, 2011; Xing et al., 2018b]. While compelling for projecting future climate and land-use changes on catchment hydrology, unsupported assumptions underlying this interpretation may lead to spurious conclusions.

**Alternative interpretation of the parametric Budyko framework**

We note that in the derivations of both forms of the parametric Budyko equations (Equations 2-4 and 2-5), n and w arise as arbitrary constants from mathematical necessity rather than being introduced in relation to any physically relevant quantities
[Fu, 1981; Yang et al., 2008; Zhang et al., 2004]. Specifically, they arise as “separation constants” that are used when solving partial differential equations by the method of separation of variables. The most basic interpretation of the catchment-specific parameter, therefore, is that it is an arbitrary constant required for the solutions of Equation 2-3 to satisfy the boundary conditions of the catchment water and energy balance, while still allowing catchments to have different values of \( \bar{E} \) for a given \( \bar{P} \) and \( \bar{E}_0 \). This means that the catchment-specific parameter and catchment \( \bar{E} \) completely determine each other, and it is not possible to solve for one without the other. As such, the dependence of the catchment-specific parameter on biophysical features is directly derived from the dependence of \( \bar{E} \) on those same features.

This interdependence makes the parametric Budyko equations inherently under-determined (i.e., there are fewer equations than unknowns). Without \textit{a priori} knowledge of the value of the catchment-specific parameter, estimation of catchment \( \bar{E} \) from \( \bar{P} \) and \( \bar{E}_0 \) is not possible using the parametric Budyko equations. The same is true for estimating changes in \( \bar{E} \) from changes in \( \bar{P} \) and \( \bar{E}_0 \). This severely limits the practical applications of the parametric Budyko framework, as it will always require outside information in order to constrain \( \bar{E} \). In other words, if the catchment-specific parameter is unknown, \( \bar{E} \) must be determined using another method outside of the parametric Budyko framework.

From this perspective, \( n \) and \( w \) are actually proxy variables for \( \bar{E} \), where the parametric Budyko equations can be interpreted as coordinate transformations between the Cartesian Budyko space, with coordinates \( \left( \frac{\bar{E}_0}{\bar{P}}, \frac{\bar{E}}{\bar{P}} \right) \), and “Budyko curve space”, with coordinates \( \left( \frac{\bar{E}_0}{\bar{P}}, n \right) \) or \( \left( \frac{\bar{E}_0}{\bar{P}}, w \right) \). Coordinate transformations translate between different
descriptions of the same space, but do not add information. The parametric Budyko equations only describe how to represent Budyko space in terms of $\frac{E_0}{P}$ and monotonically increasing Budyko-like curves, rather than specific $\frac{E_0}{P}$, $\frac{E}{P}$ pairs. This is a result of imposing the conceptual framework of an explicit curve on Budyko space. While the parametric equations are a mathematically valid way to describe Budyko space, they do not substantially add to the understanding of catchment rainfall partitioning and, in fact, may be having the opposite effect as efforts to understand $n$ and $w$ in terms of biophysical features increase (Table A-1 in Appendix A). However, since $n$ and $w$ are proxies for $E$, it is likely more fruitful to investigate the relationship between $E$ and biophysical features directly, rather than using $n$ or $w$ as an intermediate and potentially confounding step. To explicitly illustrate the complete dependence of $n$ and $w$ on $E$, we developed analytical solutions for both catchment-specific parameters in terms of $E$, $P$, and $E_0$, providing a formal link between the parametric Budyko framework and other models of these parameters.

**Extending the Budyko Hypothesis to Account for Intra-Annual Climate Variability**

The importance of intra-annual variation in $P$ and $E_0$ and their impact on $E$ has been noted by many authors [Donohue et al., 2010; Feng et al., 2012; Koster and Suarez, 1999; Milly, 1994; Potter and Zhang, 2009; Potter et al., 2005; Thornthwaite, 1948]. Indeed, Budyko himself recognized the importance of the “annual march of potential evaporation and precipitation”, even commenting specifically on how climate distributions impact $E$:

Systematic deviations from the mean dependence presented by the equation of relationship are observed. The character of these deviations depends on the features of the annual march of potential evaporation and
precipitation. With a parallel change in monthly values of potential evaporation and precipitation, the mean annual values of the ratio of evaporation to precipitation increase slightly. With the inverse changes of potential evaporation and precipitation (when the increase of potential evaporation during its annual march coincides with a decline in precipitation), mean values of the ratio of evaporation to precipitation decrease. [Budyko, 1974] (p. 326)

In other words, catchments where evaporative supply and demand are positively correlated will have higher $\bar{E}$ and those that are negatively correlated, given the same aridity index (and identical biophysical features). However, neither the original nor parametric Budyko formulations adequately addresses these deviations. To address this short-coming, we hypothesized that intra-annual climate variability is sufficient to explain observed $\bar{E}$ in individual catchments without invoking landscape biophysical characteristics. To test this hypothesis, we extended the original Budyko hypothesis to develop a simple, physically-based expression for $\bar{E}$ in terms of only catchment average daily rainfall and potential evapotranspiration distributions. This expression can describe any point in Budyko space without invoking differences in catchment biophysical features or relying on the concept of an explicit Budyko curve form. We used this expression for $\bar{E}$ to probabilistically simulate large numbers of plausible catchments and to illustrate how Budyko-like curves emerge statistically as the central tendency of these simulations. Finally, the predictive power of the expression was tested using data from 426 U.S. catchments from the Model Parameter Estimation Project (MOPEX) database [Schaake et al., 2006], and the range of uncertainty in estimates of $\bar{E}$ driven by choice of potential evapotranspiration model was quantified.
Methods

Analytical Solution for the Catchment-Specific Parameter

Given that Equations 2-4 and 2-5 can be used to solve for \( n \) and \( w \) numerically, the development of an analytical solution for the catchment-specific parameter is not explicitly required to understand the interpretation outlined in Section 1.3.3. However, the analytical solution is useful for demonstrating the direct dependence of the catchment-specific parameter on \( \bar{E} \) and provides a link between the parametric Budyko framework and other models of catchment hydrology. The starting points for developing explicit solutions for \( n \) and \( w \) are Equations 2-4 and 2-5, which can be algebraically manipulated into the following,

\[
(e^n)^{\ln \left( \frac{\bar{E}}{\bar{P}} \right)} - (e^n)^{\ln \left( \frac{\bar{E}}{\bar{P}} \right)} = 1
\]  

(2-7)

and

\[
(e^w)^{\ln \left( \frac{\bar{E} + \bar{P} - \bar{E}}{\bar{P}} \right)} - (e^w)^{\ln \left( \frac{\bar{E}}{\bar{P}} \right)} = 1
\]  

(2-8)

Equations 2-7 and 2-8 have the following general form,

\[
y^C + zy^D = 1
\]  

(2-9)

where \( C \) and \( D \) are constants, \( z \) is an arbitrary numeric variable, and \( y \) is a function of \( z \).

With the constraint, \( C > D > 0 \), Equation 2-9 has a solution of the form [Hochstadt, 2012] (p. 81-84),

\[
y(z) = \frac{1}{C} \sum_{r=0}^{\infty} \frac{(-1)^r z^r \Gamma \left( \frac{1 + Dr}{C} \right)}{r! \Gamma \left( \frac{1 + Dr}{C} + 1 - r \right)}
\]  

(2-10)

where \( r \) is an integer index variable, and \( \Gamma(\cdot) \) is the gamma function. It can be shown that Equations 2-7 and 2-8 fulfill the necessary constraints (i.e. \( C > D > 0 \)) for arid
climates (i.e. \( E_0 > \overline{P} \)) and the equivalent R-Index and humidity index forms (Equations A-10 and A-12 in Appendix A) do so for humid climates (i.e. \( E_0 < \overline{P} \)), which leads to the following general solution for the catchment-specific parameter,

\[
n|w = \ln \left( \frac{1}{\ln(G)} \sum_{r=0}^{\infty} \frac{\Gamma \left( \frac{1 + \ln(H)}{\ln(G)} \right)}{\Gamma \left( r + 1 \right)} r \left( \frac{1 + \ln(H)}{\ln(G)} + 1 - r \right) \right)
\]  

(2-11)

where \( G_n = \left\{ \frac{E_0}{E}, \frac{P}{E} \right\} \), \( G_w = \left\{ \frac{E_0 + P - E}{P}, \frac{E_0 + P - E}{E_0} \right\} \), and \( H_{n,w} = \left\{ \frac{E_0}{P}, \frac{P}{E_0} \right\} \). The first and second terms inside the braces apply to arid and humid climates, respectively. For critical point climates, where \( E_0 = \overline{P} \), Equations 2-7 and 2-8 can be solved algebraically, giving,

\[
n|w = \frac{\ln(2)}{\ln(\Omega)}
\]  

(2-12)

where \( \Omega_n = \frac{E_0}{E} \) and \( \Omega_w = 2 - \frac{E}{E_0} \).

Complete derivations of Equations 2-11 and 2-12, with descriptions of their behaviors are presented in Appendix A. Note that Equations 2-11 and 2-12 are explicit expressions of \( n \) and \( w \) in terms of only \( E \), \( P \), and \( E_0 \) such that for given values of \( P \) and \( E_0 \), \( n \) and \( w \) are completely determined by \( E \). In order to relate \( n \) and \( w \) to catchment biophysical features, a model that describes \( E \) in terms of those features is required. However, these equations are general expressions, so any “valid” model for catchment \( E \), \( P \), or \( E_0 \) can be applied, allowing \( n \) and \( w \) to be expressed in terms of any specific models for \( E \), \( P \), or \( E_0 \) and their associated parameters.
Extending the Original Budyko Hypothesis

Here we aim to generalize and extend the Budyko hypothesis by postulating that $\bar{E}$ is a function of intra-annual, time-dependent (e.g. daily) average values of $P$ and $E_0$ (rather than their long-term annual average) such that,

$$\bar{E} = f_2[\bar{P}(t)_a, \bar{E}_0(t)_a]$$  \hspace{1cm} (2-13)

where $\bar{P}(t)_a$ and $\bar{E}_0(t)_a$ are functions describing how the long-term average values of $P$ and $E_0$ vary with time $t$ over the course of a year. Example time series of the long-term average value of $P$ and $E_0$ over the course of a year are illustrated in Figure 2-1a. Given $\bar{P}(t)_a$ and $\bar{E}_0(t)_a$, the simplest physically-based model for intra-annual, time dependent average $E$, $\bar{E}(t)_a$, is given by,

$$\bar{E}(t)_a = \begin{cases} \bar{E}_0(t)_a, & \bar{E}_0(t)_a < \bar{P}(t)_a \\ \bar{P}(t)_a, & \bar{E}_0(t)_a \geq \bar{P}(t)_a \end{cases}$$  \hspace{1cm} (2-14)

Equation 2-14 is a “supply-demand limited” evapotranspiration model, simply stating that the long-term average $E$ at a given time will be equal to the evapotranspiration driver (i.e. $P$ or $E_0$) that is, on average, most limiting (Figure 2-1b,e). To find an expression for $\bar{E}$, we take the average value of the function $\bar{E}(t)_a$. However, the temporal order of $\bar{E}(t)_a$ does not matter for computing the annual average (Figure 2-1c,f), and therefore we can rearrange $\bar{E}(t)_a$ so that all values where $\bar{E}_0(t)_a < \bar{P}(t)_a$ are consecutive, followed by all values where $\bar{E}_0(t)_a \geq \bar{P}(t)_a$. This separation allows us to divide the average of $\bar{E}(t)_a$ into two component integrals,

$$\bar{E} = \frac{1}{\tau} \int_0^{t_P} \bar{E}_0(t)_{a, t_P} dt + \frac{1}{\tau} \int_{t_P}^{\tau} \bar{P}(t)_{a, t_E} dt$$  \hspace{1cm} (2-15)
where $\overline{E_0}(t)_{a,t_p}$ are all values of $\overline{E_0}(t)_a$ for $\overline{E_0}(t)_a < \overline{P}(t)_a$, $\overline{P}(t)_{a,t_{E_0}}$ are all values of $\overline{P}(t)_a$ for $\overline{E_0}(t)_a \geq \overline{P}(t)_a$, $\tau$ is the averaging interval, in this case, a year, and $t_p$ is the total amount of time that $\overline{E_0}(t)_a < \overline{P}(t)_a$ (Figure 2-1c,f). Equation 2-15 can be rearranged as,

$$\overline{E} = \left(\frac{t_p}{\tau}\right) \left[ \frac{1}{t_p} \int_0^{t_p} \overline{E_0(t)_{a,t_p}} dt \right] + \left(1 - \frac{t_p}{\tau}\right) \left[ \frac{1}{\tau - t_p} \int_{t_p}^{\tau} \overline{P(t)_{a,t_{E_0}}} dt \right]$$

(2-16)

The two bracketed integrals in Equation 2-16 represent the average values of $\overline{E_0(t)_{a,E_0<P}}$ and $\overline{P(t)_{a,E_0>P}}$, allowing us to rewrite Equation 2-16 as,

$$\overline{E} = \left(\frac{t_p}{\tau}\right) \langle \overline{E_0(t)_{a,t_p}} \rangle + \left(1 - \frac{t_p}{\tau}\right) \langle \overline{P(t)_{a,t_{E_0}}} \rangle$$

(2-17)

where the angular brackets represent the average.

Since only the relative relationship of the climate drivers $\overline{P(t)_a}$ and $\overline{E_0(t)_a}$ is important, rather than their specific temporal order, Equation 2-17 can be considered probabilistically. Indeed, as an alternative to thinking of the climatic drivers as two independent temporal functions, they may be considered as a single bivariate probability density function of catchment climate. As such, each of the variables in Equation 2-17 can be interpreted in terms of probability distributions, giving,

$$\overline{E} = \left(Pr_{E_0<P}\right) \langle \overline{E_0(t)_{a,t_p}} \rangle + \left(1 - Pr_{E_0<P}\right) \langle \overline{P(t)_{a,t_{E_0}}} \rangle$$

(2-18)

where $Pr_{E_0<P}$ is the probability that $\overline{E_0_a} < \overline{P}_a$ is observed in a catchment, $\langle \overline{E_0(t)_{a,t_p}} \rangle$ is the average value of $\overline{E_0}_a$ when $\overline{E_0}_a < \overline{P}_a$, and $\langle \overline{P(t)_{a,t_{E_0}}} \rangle$ is the average value of $\overline{P}_a$ when $\overline{E_0}_a > \overline{P}_a$.

Equation 2-18 suggests that if the distribution of the climate drivers of a catchment are known, $\overline{E}$ can be predicted. The parameters $Pr_{E_0<P}$, $\langle \overline{E_0(t)_{a,t_p}} \rangle$, and
\( \langle P(t)_{a,tE_0} \rangle \) can be easily calculated from theoretical climatic distributions or empirical distributions generated from measurements of \( P \) and \( E_0 \). Notably, Equation 2-18 is valid for any climatic distribution, since it does not impose any assumptions about the distribution type for \( P \) and \( E_0 \). Additionally, it is conceptually able to represent any point within Budyko space without a fitting parameter. Instead, variation in \( \bar{E} \) can be interpreted as resulting from differences in the timing and magnitude of evaporative supply and demand between catchments. Moreover, Equation 2-18 does not impose an explicit functional curve for catchments to “follow”, but it can be directly linked to the parametric Budyko framework through Equation 2-11.

Finally, implicit in Equation 2-18 is the assumption that the distributions of climate drivers are spatially uniform across the catchment area, however, it is straightforward to extend this framework to account for spatial variation. We start by generalizing the average of \( \bar{E}_a \) to include both time and space

\[
\bar{E} = \frac{1}{\Delta t} \frac{1}{A_t} \int_0^{A_t} \int_0^\tau \bar{E}(t, A)_{a} dt dA
\]

(2-19)

where \( A \) is area, and \( A_t \) is the total catchment area. While Equation 2-19 is conceptually useful, it is practically difficult to define the space- and time-dependent functions for \( \bar{E}(t, A)_{a} \). This can be addressed by discretizing \( A \) in Equation 2-19 into sub-basins over which climate is relatively uniform,

\[
\bar{E} = \frac{1}{A_t} \sum_{j=1}^{N} \bar{E}_A_j \Delta A_j
\]

(2-20)

where \( N \) is the number of sub-basins, \( E_A \) is Equation 2-18 computed for each sub-basin \( j \) and \( \Delta A \) is the sub-basin area, with \( \sum_{j=1}^{N} \Delta A_j = A_t \).
Statistical Emergence of Budyko Curves

While the concept of an explicit Budyko curve is subjective, observed data from real catchments do fall in a relatively narrow band of Budyko space. In this work, we tested our extended Budyko hypothesis in reproducing this behavior by parameterizing Equation 2-18 with a large collection of intra-annual distributions of $\overline{P}(t)_a$ and $\overline{E}_0(t)_a$. To do so, we simulated 10,000 series of $\overline{P}(t)_a$ and $\overline{E}_0(t)_a$ from three different classes of distributions and compared the resulting $\frac{\overline{E}}{\overline{P}}$ and $\frac{\overline{E}_0}{\overline{P}}$ ratios with both non-parametric Budyko curves and the “best fit” parametric Budyko curve (i.e., Equation 2-4 with $n = 1.8$ [Donohue et al., 2012]).

Based on natural climatic seasonality, it is expected that for most catchments, $\overline{P}(t)_a$ and $\overline{E}_0(t)_a$ will follow an approximate sine-wave pattern with a yearly period. Varying the amplitude, phase, and vertical offset of these sine-waves captures the general behavior of nearly all observed climates (e.g. wet and dry seasonal, temperate, tropical, etc.), as well as rare or unobserved climates (e.g. a climate where $\overline{E}_0(t)_a$ is always larger than $\overline{P}(t)_a$). To test the dependency of the development of “Budyko curve behavior” on the choice of climate distribution, we also explored normal and gamma distributions of $\overline{P}(t)_a$ and $\overline{E}_0(t)_a$. The general procedure used for each class of distributions was as follows:

- Simulated distributions of $\overline{P}(t)_a$ and $\overline{E}_0(t)_a$ were generated by drawing 10,000 sets of distribution parameters (e.g. amplitude, phase, etc.) from uniform distributions.
- $\overline{E}$ was calculated for each of the simulated distributions using Equation 2-18.
- The ratios $\frac{\overline{E}}{\overline{P}}$ and $\frac{\overline{E}_0}{\overline{P}}$ were calculated for each simulated distribution.
• Corresponding pairs of \( \frac{E}{P} \) and \( \frac{E_0}{P} \) were ranked by \( \frac{E_0}{P} \) from lowest to highest, and a moving median (i.e. the central tendency) was computed for the rank-ordered values of \( \frac{E}{P} \).

• Corresponding pairs of \( \frac{E}{P} \) and \( \frac{E_0}{P} \) were plotted in Budyko space, along with the Schreiber curve (Table 2-1), Ol’Dekop curve (Table 2-1), “best fit” parametric Budyko curve, and the moving median for comparison.

A moving median was used to reduce sensitivity to extreme values compared to the mean, with a sampling window large enough (301) to provide smoothing of the data without loss of resolution in \( \frac{E_0}{P} \). The parameters for Equation 2-18 were calculated empirically from the simulated distributions.

For the first numerical experiment, each distribution for \( \tilde{P}(t)_a \) and \( \overline{E_0}(t)_a \) consisted of a sine wave with a period of 365 days, with negative values truncated to zero, and three parameters, amplitude (\( \psi \)), phase (\( \varphi \)), and offset (\( Y \)). \( \tilde{P}(t)_a \) and \( \overline{E_0}(t)_a \) distributions were simulated by randomly drawing values for \( \psi \), \( \varphi \), and \( Y \) from uniform distributions (\( U \)) all with minimum values of zero, and maximum values of 5 for \( \psi \) and \( Y \), and \( \pi \) for \( \varphi \) to allow \( \tilde{P}(t)_a \) and \( \overline{E_0}(t)_a \) to be completely in or out of phase. The form of the simulated distributions for both \( \tilde{P}(t)_a \) and \( \overline{E_0}(t)_a \) is,

\[
\tilde{X}(t)_a = \begin{cases} 
(\psi_X)\sin\left(\frac{2\pi}{365} t + \varphi_X\right) + Y_X, \tilde{X}(t)_a \geq 0 \\
0, \quad \tilde{X}(t)_a < 0
\end{cases}
\] (2-21)

where \( X = P|E_0 \). Two additional numerical experiments were performed, where \( \tilde{P}(t)_a \) and \( \overline{E_0}(t)_a \) were drawn from normal (truncated between 0 and \( \infty \)) and gamma distributions, whose parameters were determined from uniform distributions between 0 and 5.
Predictive Power of the Extended Budyko Hypothesis

We tested the predictive ability of Equation 2-18 using data from the MOPEX database. Empirical estimates of $\bar{E}$ and empirical distributions for $\bar{P}(t)_a$ and $\bar{E}_0(t)_a$ were determined for each catchment using MOPEX hydrometerological data. The empirical distributions for $\bar{P}(t)_a$ and $\bar{E}_0(t)_a$ were used to parametrize Equation 2-18 and produce predictive estimates of $\bar{E}$. The empirical and predictive estimates of $\bar{E}$ were compared to quantify the predictive power of Equation 2-18. Finally, prediction uncertainty intervals for Equation 2-18 were generated based on the uncertainty in estimates of $\bar{E}_0(t)_a$.

Each catchment within the MOPEX database has up to 54 years of daily discharge and rainfall measurements from 1948 to 2003. We used these data to estimate $\bar{E}$ from,

$$\bar{E}_e = \bar{P}_e - \bar{Q}_e$$

(2-22)

where the subscript $e$ indicates the empirical means of the daily measurements. Catchments with fewer than 10 years of data (5 of 431) were excluded. Intra-annual, time-dependent average values of $P$, $\bar{P}(t)_a$, were computed from daily rainfall measurements. The MOPEX dataset also contains daily $E_0$ estimates, generated by fitting single-frequency Fourier series to monthly average pan evaporation estimates from digitized NOAA Evaporation Atlas maps [Farnsworth et al., 1982; Schaake et al., 2006]. However, estimates of $E_0$ from pan evaporation data are not suitable for all climates [Kahler and Brutsaert, 2006], and may not accurately represent $E_0$ across the widely ranging climates covered by the MOPEX database. Additionally, a decreasing trend in measured pan evaporation data has been observed over the past 50 years.
[Brutsaert and Parlange, 1998; Roderick and Farquhar, 2002], making the MOPEX extrapolation (>50 years) questionable.

To account for this uncertainty, we developed three additional estimates of $E_0$ using data from the MOPEX database, including maximum and minimum daily temperatures and catchment latitude. Selected methods included the Thornthwaite model [Tabari et al., 2011; Thornthwaite, 1948] and two versions of the Hamon model [Chang et al., 2016; Hamon, 1961; 1963; Lu et al., 2005], which require the smallest number of assumptions for complete parameterization and produce estimates of $E_0$ similar to more data-intensive methods such as FAO Penman-Monteith [Allen et al., 1998; Lu et al., 2005; Tabari et al., 2011]. The equations used from these three methods are summarized in Table A-2 in Appendix A. Our reported $\bar{E}_0(t)_a$ values are the means of the four estimates from the MOPEX-provided values and the other three models.

Predictive estimates of $\bar{E}$, $\bar{E}_p$, were calculated for each catchment using Equation 2-18, with parameters calculated from the empirical distributions of $\bar{P}(t)_a$ and $\bar{E}_0(t)_a$ described in Section 2.3. It is important to note that Equation 2-18 was not calibrated to $\bar{E}_e$; indeed, the values $\bar{E}_p$ are model predictions made using different information than that used to compute $\bar{E}_e$. The relationship between $\bar{E}_e$ and $\bar{E}_p$ was assessed based on the Nash-Sutcliffe model efficiency coefficient (NSE) [Nash and Sutcliffe, 1970]. Prediction error of Equation 2-18 was assessed using the root-mean-square error (RMSE).

Finally, we assessed sources of errors in our estimates of $\bar{E}$. Differences between $\bar{E}_p$ and $\bar{E}_e$ can be caused by errors in either value. For example, the coarse
spatial resolution in the MOPEX database requires the climate over each catchment to be considered as uniform. MOPEX catchments have a wide range of areas (\(\sim 70 \text{ km}^2\) to \(\sim 10300 \text{ km}^2\)), possibly making this assumption invalid for some catchments and potentially impacting both \(\overline{E_e}\) and \(\overline{E_p}\) (Equation 2-20). Additionally, both values would be affected by systematic measurement errors in any climate driver variables. Much of this uncertainty cannot be accurately quantified for the MOPEX dataset, and we have taken the data “as is”.

Despite this limitation, we are able to quantify some of the uncertainty that impacts \(\overline{E_p}\), specifically the uncertainty in \(\overline{E_0(t)}_a\) resulting from the method used in its estimation. Empirical or limited data methods to estimate \(E_0\) do not provide accurate estimates for all types of catchments. For example, some methods are better for humid climates, while others are better for arid climates [Zhao et al., 2013]. Also, the calibrated empirical parameters can vary substantially between catchments [Bautista et al., 2009].

Our choice of the three additional \(E_0\) estimation methods attempted to minimize these impacts given the available data, however, it is very likely that some persisted. We can assess how the variation in our estimated empirical distributions of \(\overline{E_0(t)}_a\) impacts the predictions made by Equation 2-18. To do so, we created distributions for each catchment for the minimum and maximum estimates of daily \(E_0, \overline{E_0(t)}_{a,l}\) and \(\overline{E_0(t)}_{a,u}\), based on the lowest and highest estimate of the four \(E_0\) methods for each day of the year. Since each \(E_0\) distribution is plausible, \(\overline{E_0(t)}_{a,l}\) and \(\overline{E_0(t)}_{a,u}\) represent the lower and upper possible distributions given the available data and methods used. Equation 2-18 was parameterized using \(\overline{E_0(t)}_{a,l}, \overline{E_0(t)}_{a,u}\), and \(\overline{P(t)}_a\), producing a plausible range of \(\overline{E_p}\) which were compared to \(\overline{E_e}\) for each catchment.
Results

Statistical Emergence of Budyko Curves

The results of parameterizing Equation 2-18 using three intra-annual distributions for $\bar{P}(t)_a$ and $\bar{E}_0(t)_a$ (Section 2.3) are shown in Figure 2-2, where the data have been plotted in Budyko space. Each black circle represents a single simulated catchment (e.g. a random draw of parameters for Equation 2-21). The “original” Budyko curves (i.e., the Schreiber and Ol’Dekop curves; Table 2-1), along with the “best fit” parametric Budyko curve (i.e., Equation 2-4 with $n = 1.8$) is also plotted in each panel. The central tendency of the aggregated simulated catchments is represented by the moving median. For the truncated sinusoidal distributions (Figure 2-2a), the central tendency of the simulated catchments showed strong resemblance to the standard Budyko curve across the majority of Budyko space, with the best agreement to the best-fit parametric form. For the most arid ($\frac{\bar{E}_0}{\bar{P}} > 2.3$) and humid ($\frac{\bar{E}_0}{\bar{P}} < 0.4$) catchments, the moving median tended to underestimate $\bar{E}$ relative to the standard curves. The normal and gamma distributions filled the Budyko space to differing degrees (Figures 2-2b, 2-2c), but the central tendencies for all three distributions were also strikingly similar to the standard curve ($0.80 < \text{NSE} < 0.99$ between all pair comparisons).

Predictive Power of the Extended Budyko Hypothesis

The empirical and predicted estimates of $\bar{E}$ for the 426 MOPEX catchments are plotted in Budyko space in Figure 2-3a. Discrepancies between the empirical (Equation 2-22) and predictive estimates (Equation 2-18) appear as the vertical distance between corresponding green and black circles in the figure. Again, the best fit parametric Budyko curve is shown for reference. The general “Budyko curve behavior” is evident in
both the empirical and predictive estimates. The largest discrepancies between empirical and predictive estimates occur in arid catchments ($\frac{E_0}{P} > 1$). Figure 2-3b shows good agreement between empirical and modeled estimates of $\bar{E}$ ($NSE = 0.62$ and $RMSE = 0.27$ mm/day), with the greatest disagreement between the model and observations at low $\bar{E}$ ($<1.5$ mm/day). The proportion of catchments with $E_p < 1.5$ mm/day is relatively small (histogram inset in Figure 2-3b).

Finally, uncertainty in predictive estimates of $\bar{E}$ relative to empirically derived values is illustrated in Figure 2-4a. Catchments are ranked by $E_p$, from highest to lowest (red line). The corresponding upper and lower plausible values (orange lines), define prediction uncertainty intervals for each catchment. Values of $E_e$ for each catchment are also plotted (black circles), allowing for comparison to the prediction uncertainty intervals. Proximity of $E_e$ to the red line indicates better agreement with $E_p$. For $E_e$ values between the upper and lower plausible values of $E_p$, we can say that the discrepancy between $E_p$ and $E_e$ is within the prediction uncertainty interval of Equation 2-18, given the uncertainty in $E_0(t)$. Values of $E_e$ outside of the upper and lower plausible values of $E_p$ suggest that there are likely unknown errors within the data, invalid assumptions in the methods used to parameterize Equation 2-18, or that the “supply-demand limited” model (Equation 2-14) used to derive Equation 2-18 is invalid for those catchments. Overall, 350 of the 426 MOPEX catchments (82%) fall within the prediction uncertainty intervals. The spatial distribution of the catchments that fall inside and outside of this range is shown in Figure 2-4b.
Discussion

The original Budyko hypothesis (Equation 2-2) and resulting non-parametric curves (Table 2-1) provide an overarching framework for understanding catchment hydrology in terms of energy and water balances. The retention of the “curve concept” when the Budyko hypothesis was extended to explain deviations from mean catchment behavior resulted in the parametric Budyko equations (Equations 2-4 and 2-5). In recent years, profound efforts (Table A-1 in Appendix A) have been invested in developing an understanding of the catchment-specific parameter \((n\) or \(w\)) of the parametric Budyko equations, with the aim of producing a framework that is both capable of explaining variance in rainfall partitioning and also is predictable based on catchment physical properties. In this work, we contend that parametric Budyko equations are fundamentally underdetermined, with statistically or model fitted values of \(n\) and \(w\) resulting directly from estimates or measurements of \(\bar{E}\) and therefore lacking predictive power.

To address this shortcoming, this study hypothesized that intra-annual climate variability is sufficient to explain \(\bar{E}\) in individual catchments without invoking landscape biophysical characteristics. To test this hypothesis, we extended the original Budyko framework by developing an expression for \(\bar{E}\) as a function of only time-varying rainfall and potential evapotranspiration (Equation 2-18). The extended Budyko hypothesis and Equation 2-18 remain true to the original Budyko hypothesis in that they describe \(\bar{E}\) in terms of the governing climatic drivers, \(P\) and \(E_0\). Additionally, Equation 2-18 is derived from a simple, physically-based, “supply-demand limited” evapotranspiration model (Equation 2-14). This approach does not impose a “Budyko curve”, yet it is able to
reproduce the Budyko-type behavior observed across real catchments (Figures 2-2 and 2-3).

**Analytical Solution for the Catchment-Specific Parameter**

Equation 2-11 shows that $n$ and $w$ are completely determined by $\bar{E}$, $\bar{E}_0$, and $\bar{P}$. Since $n$ and $w$ only depend on $\bar{E}$, $\bar{E}_0$, and $\bar{P}$, it becomes obvious that their dependence on catchment biophysical features (if present) is due to the dependence of $\bar{E}$, $\bar{E}_0$, or $\bar{P}$ on those features. In short, this means that $\bar{E}$, $\bar{E}_0$, and $\bar{P}$ must always be determined before $n$ or $w$ can be estimated, which is the case for all of the relationships presented in Table A-1 of Appendix A. Each of the previous studies that attempted this, estimated $\bar{E}$ either empirically (i.e., $\bar{E} = \bar{P} - \bar{Q}$) or using a model, after which $n$ or $w$ is numerically calibrated to that estimated $\bar{E}$, and the calibrated $n$ or $w$ is fit to a proposed model.

Practically, $n$ and $w$ could be eliminated from each of these studies by fitting the proposed models to the estimated values of $\bar{E}$ directly, bypassing the parametric Budyko framework altogether. The resulting models would likely be easier to interpret, as they would be relating catchment biophysical features to a real quantity, $\bar{E}$, rather than to an ambiguous parameter.

Furthermore, the functional form of Equation 2-11 highlights the ambiguous nature of $n$ and $w$. The relationships between $n$, $w$, $\bar{E}$, $\bar{E}_0$, and $\bar{P}$ are composed of logarithms of infinite series for the non-trivial cases. This highly nonlinear relationship defies an intuitive understanding of how $n$ and $w$ should vary with changes to $\bar{E}$, $\bar{E}_0$, or $\bar{P}$. The complicated nature of Equation 2-11 is the result of imposing the explicit “Budyko curve” concept onto the more general “Budyko space”. As such, $n$, $w$, and the parametric Budyko equations can be viewed as artifacts of the explicit Budyko curve.
concept being ascribed more physical meaning than is justifiable based on their foundational underpinnings. In other words, the catchment-specific parameters, \( n \) and \( w \), are mathematically valid ways of describing Budyko space, but they are intrinsically physically meaningless. The increasingly common interpretation of \( n \) and \( w \) as catchment biophysical parameters may therefore be unjustified and misleading, as any physical meaning of \( n \) and \( w \) must be due to their dependence on \( \bar{E}, \bar{E}_0, \) and \( \bar{P} \) through Equation 2-11.

We should be clear that the general “Budyko curve behavior” observed across multiple catchments is a valid, well documented, physical phenomenon. However, the concept of an explicit curve has always been semi-empirical and should not be ascribed undue physical meaning. Our aim is to show that the solutions given in Equation 2-11, along with the interpretation of parametric Budyko equations as coordinate transformations, can help link the large body of work and understanding within the parametric Budyko framework with other areas of catchment hydrology.

**Extending the Original Budyko Hypothesis**

Our extended Budyko framework remains grounded in the original Budyko hypothesis, stating that catchment \( \bar{E} \) is governed by the properties of the climatic drivers, \( P \) and \( E_0 \). The main result of this extension, Equation 2-18, is able to produce any point within Budyko space without imposing empirical curves or invoking specific biophysical features from the catchment. Additionally, Equation 2-18 arises from a simple, physically-based, “supply-demand limited” evaporation model (Equation 2-14). Though Equation 2-18 is able to produce any point within Budyko space without invoking catchment physical features, it does not necessarily suggest that catchment
features are unimportant in driving catchment hydrology, particularly at shorter time scales. In general, we know that catchment physical features (soils, slopes, geology, land cover, etc.) affect rainfall-runoff processes [Dunne et al., 1991; Gerten et al., 2004; McGuire et al., 2005; Qazi et al., 2017; Rogger et al., 2017], particularly at the scale of individual storms [Milly and Eagleson, 1988; Yao et al., 2016]. However, differences in the evapotranspiration-available water storage between most catchments is likely small enough that the “supply-demand limited” evapotranspiration model we proposed (Equation 2-14) is valid to characterize the long-term average “annual march” of $\bar{E}_0$ and $\bar{P}$. We note that Equation 2-14 would not be valid for short-term (i.e. daily) estimates of $\bar{E}$, since storage dynamics become more important at shorter time scales [Spence et al., 2009; Wittenberg, 1999].

A large part of the allure of the original Budyko hypothesis is its generality and simplicity, enabling estimation of $\bar{E}$ using only relatively easy to measure climate variables (i.e. $\bar{E}_0$ and $\bar{P}$) without knowing anything about the physical composition of the catchment. Equation 2-18 retains this quality. The same data that would be used to parametrize $\bar{E}_0$ and $\bar{P}$ in the original Budyko equations (i.e. daily or monthly measurements of $P$ and $E_0$) can be used to parameterize $Pr_{E_0<P}$, $\langle \bar{E}_0(t)_{a,P} \rangle$, and $\langle \bar{P}(t)_{a,E_0} \rangle$ of Equation 2-18. This relation can potentially produce more accurate estimates of $\bar{E}$ without requiring any additional data burden over the original Budyko equations. Additionally, Equation 2-18 can be used to develop runoff elasticities using methods similar to Roderick and Farquhar [2011] and W Wang et al. [2016], or to project $\bar{E}$ and $\bar{Q}$ under future climates (i.e. future $\bar{P}(t)_a$ and $\bar{E}_0(t)_a$).
For shorter time scales, where the assumptions of Equation 2-14 and Equation 2-18 are invalid, $\overline{E}$ can be estimated directly using models that take into account the relevant dynamics at that scale (e.g. [Porporato et al., 2004; Rodriguez-Iturbe et al., 1999]). Using models for $\overline{E}$ that directly incorporate biophysical features allows for changes in rainfall partitioning to be directly attributed to specific landscape changes in a physically-based manner, as opposed to filtering the attribution through a convoluted and circular coordinate transformation between $\overline{E}$ and $n$ or $w$. It may also be possible to determine the temporal and spatial scales in which catchment specific features become important by comparing results of Equation 2-18 and biophysical models for $\overline{E}$.

Specifically, $\overline{E}$ could be estimated for different time and spatial scales for both classes of models to find the scale-dependent divergence behavior between estimates from both.

**Statistical Emergence of Budyko Curves**

For the extended Budyko hypothesis and Equation 2-18 to be validated as physically representative of real-world catchments, they must be able to generate “Budyko curve behavior” without any arbitrary boundary condition constraints. As shown in Figure 2-2, the median behavior of the simulated catchments under three widely varying $\overline{P}(t)_a$ and $\overline{E}_0(t)_a$ distribution classes were very similar to the “standard” Budyko curves (and to each other). It is striking that the median behavior of all simulated catchments was so similar, even though the underlying climate distributions were very different. This suggests that the functional form of the underlying climatic distributions is not central to the generation of “Budyko curve behavior” and supports the probabilistic formulation of Equation 2-18. This analysis implies that the general “Budyko curve
behavior” is the statistical central tendency of catchments over a wide range of climates. Therefore, it should be expected that most observed catchments will be distributed close to this central tendency, as observed in real catchments (citations in Tables 2-1 and A-1) [Zhang et al., 2001]. Overall, these results suggest that “Budyko curve behavior” is an emergent statistical property of catchments interacting with climate drivers that can be explained, along with deviation from the behavior, without imposing an explicit curve or invoking catchment characteristics.

In principle, real catchments could exist anywhere within Budyko space. In our simulations, catchments with truncated sinusoidal distributions had the largest range of values within Budyko space, covering essentially all possible values (Figure 2-2a). This is partially due to the correlation structure resulting from random phase differences between $\bar{P}(t)_{a}$ and $\bar{E}_0(t)_{a}$. When $\bar{P}(t)_{a}$ and $\bar{E}_0(t)_{a}$ are in phase ($\varphi_P - \varphi_{E_0} \cong 0$ in Equation 2-21) they are positively correlated, leading to simulated $\frac{\bar{E}}{\bar{P}}$ closer to the energy- and water-limit lines. When they are out-of-phase ($\varphi_P - \varphi_{E_0} \cong \pi$), they are negatively correlated, leading to generally lower estimates of $\bar{E}$ for the same $\bar{P}$ and $\bar{E}_0$. This temporal correlation structure does not completely explain the distribution of simulated catchments in Budyko space, however, as the relative magnitudes of $\bar{P}(t)_{a}$ and $\bar{E}_0(t)_{a}$ are also important for driving $\bar{E}$ through Equations 2-14 and 2-18. For example, if $\bar{P}(t)_{a}$ and $\bar{E}_0(t)_{a}$ do not intersect, their temporal correlation is unimportant. Catchments with truncated normal and gamma distributions (Figure 2-2b,c), though they had similar median behavior, were confined to limited regions of Budyko space relative to the truncated sinusoidal distributions. In contrast to the sinusoidal distributions, the normal and gamma distributions have no inherent temporal correlation structure,
leading to uncorrelated $P$ and $E_0$ (i.e. each day’s climate is random), leading to more tightly constrained predictions of $\bar{E}$. Given the physical constraints of the Earth climate system (i.e. axial tilt, seasonality, etc.), we consider the truncated sinusoidal distributions to be the most physically valid of the distributions tested, since they have similar temporal structure to “real-world” observed climates. In fact, this type of distribution was used to model average daily $E_0$ in the MOPEX database [Schaake et al., 2006].

**Predictive Power of the Extended Budyko Hypothesis**

In addition to applying Equation 2-18 to simulated data, we also compared predictive estimates of $\bar{E}$ to empirical data from 426 catchments using the MOPEX dataset. Empirically derived estimates of $\bar{E}$ generally followed the “standard” Budyko curve and predictions of $\bar{E}$ from Equation 2-18 closely match the empirical estimates. For the majority of the MOPEX catchments, the agreement between $\bar{E}_p$ and $\bar{E}_e$ was good, with more than 80% of the catchments within prediction uncertainty intervals (Figure 2-4a). This suggests that with sufficiently accurate climatic data, Equation 2-18 can be used to estimate $\bar{E}$ for a wide range of climates. Equation 2-18 was not accurate for all catchments, however; $\bar{E}$ estimates in 76 catchments were outside of the prediction uncertainty interval. The majority of these catchments had lower $\bar{E}$ ($< 1.5$ mm, Figure 2-4a) and are located within mountainous regions (Figure 2-4b).

There are several potential reasons for the diminished accuracy of Equation 2-18 in more mountainous regions. First, the substantial spatial heterogeneities in $\bar{P}(t)_a$ and $\bar{E}_0(t)_a$ of mountainous regions may not be well described in the catchment-averaged values of $P$ and $E_0$ reported in the MOPEX database. This is particularly evident for the
mountainous region in the NOAA Evaporation Atlas maps from which the base daily PET in MOPEX is derived [Farnsworth et al., 1982]. Second, when a significant fraction of precipitation falls as snow, an “effective” $\bar{P}(t)_a$ is warranted. Snow accumulation typically acts to effectively “delay” precipitation, shifting it to the spring melt. This changes the “effective” $\bar{P}(t)_a$, reducing it for parts of the year with snowfall and increasing it during time of snowmelt. Additionally, alpine snowfall can be underestimated due to precipitation undercatch, further skewing empirical estimates of $\bar{P}(t)_a$ [Chubb et al., 2015]. Finally, in alpine regions, $E_0$, and hence, $\overline{E_0}(t)_a$, is underestimated for some time periods due to the sublimation of the snow pack [Hood et al., 1999]. In principle, all of these potential issues could be addressed either by using improved empirical data for $P$ and $E_0$ and modification of $\bar{P}(t)_a$ and $\overline{E_0}(t)_a$ to include snow melt and sublimation within Equation 2-18, or by using Equation 2-20 to account for spatial heterogeneity. These modifications would allow the extended Budyko hypothesis to be used to predict $\overline{E}$ in nearly any catchment.

**Summary and Conclusions**

In this study we have shown that explicit Budyko curves are not foundational to the understanding of the long term water-energy balance of catchments. Parametric Budyko curves are the result of applying this explicit Budyko curve concept to describe deviations of individual catchments from the “original” Budyko curves, which imputes unjustified physical meaning to the curve itself and the catchment parameter, $n$ or $w$. These parametric Budyko equations are inherently underdetermined and therefore lack predictive power. A simpler interpretation of these equations is as a coordinate transformation between Budyko space and “Budyko curve space”. We extended the
original Budyko hypothesis to describe $E$ in terms of the intra-annual properties of the climatic drivers, $P$ and $E_0$.

Using this extended Budyko hypothesis and a "supply-demand limited" evapotranspiration model, we developed a simple expression for $E$ that uses only climate drivers and produced both the general characteristic Budyko curve behavior observed for catchments overall, and also deviations from the general trend for individual catchments. "Budyko curve behavior" appears to be an emergent statistical property of catchments interacting with climate drivers that can be explained, along with deviation from the behavior, without imposing an explicit curve or invoking catchment characteristics. Our simple expression for $E$ was found to have good predictive power compared to empirical estimates of $E$ and requires no additional data burden over the original Budyko equations. It can thus be used to provide estimates of $E$ and $Q$ for ungauged catchments for current, past, and future climates, potentially making it an extremely useful application in catchment hydrology [Beck et al., 2016; Hrachowitz et al., 2013; Sivapalan et al., 2003; Wagener and Montanari, 2011].

In closing, we recommend that $E$ should be modeled directly rather than through the parametric Budyko equations. The calculation of $n$ or $w$ for the purpose of estimating $E$ is an unnecessary circular process that must always start at its eventual destination: an estimate of $E$. 
Table 2-1. Previously proposed functional forms for the Budyko hypothesis [Yang et al., 2008; S Zhou et al., 2015]. $\bar{P}$ is mean precipitation, $\bar{E}_0$ is mean potential evapotranspiration, and $\bar{E}$ is mean actual evapotranspiration.

<table>
<thead>
<tr>
<th>Functional Form</th>
<th>Reference</th>
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<tbody>
<tr>
<td>$\bar{E} = \bar{P} \left(1 - e^{-\frac{\bar{E}_0}{\bar{P}}}\right)$</td>
<td>[Schreiber, 1904]</td>
</tr>
<tr>
<td>$\bar{E} = \bar{E}_0 \tanh \left(\frac{\bar{P}}{\bar{E}_0}\right)$</td>
<td>[Ol’Dekop, 1911]</td>
</tr>
<tr>
<td>$E = \sqrt{\bar{P} \left(1 - e^{-\frac{\bar{E}_0}{\bar{P}}}\right) \bar{E}_0 \tanh \left(\frac{\bar{P}}{\bar{E}_0}\right)}$</td>
<td>[Bagrov, 1953; Budyko, 1974]</td>
</tr>
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Figure 2-1. Development of an expression for catchment $\bar{E}$ in terms of the intra-annual, time-dependent average values of $P$, $\bar{P}(t)_a$, and $E_0$, $\bar{E}_0(t)_a$ for two catchments with different correlation structure between $\bar{P}(t)_a$ and $\bar{E}_0(t)_a$. Panels a and d show generic functions of $\bar{P}(t)_a$ (blue) and $\bar{E}_0(t)_a$ (red) over the course of a year for catchments with out-of-phase (a) and in-phase (d) climate drivers. Panels b and e illustrate how the timing of $\bar{P}(t)_a$ and $\bar{E}_0(t)_a$ combine to drive intra-annual, time dependent average $E$, $\bar{E}(t)_a$, using the “supply-demand limited” evapotranspiration model (Equation 2-14); red portions of $\bar{E}(t)_a$ correspond to times when $\bar{E}_0(t)_a$ is limiting, blue portions of $\bar{E}(t)_a$ correspond to times when $\bar{P}(t)_a$ is limiting, and the annual average $\bar{E}$ is given as the green dotted line. Note that $\bar{E}$ is smaller for the catchment with negatively correlated climate drivers despite having identical $P$ and $\bar{E}_0$. Finally, panels c and f show that rearranging $\bar{E}(t)_a$ in time does not change the value of $\bar{E}$, allowing $\bar{E}$ to be defined in terms of the proportion of time that $\bar{E}_0(t)_a < \bar{P}(t)_a$, given as $t_p$ (vertical black dotted line).
Figure 2-2. Results of parameterizing Equation 2-18 using three intra-annual distributions for $\bar{P}(t)_{a}$ and $\bar{E}_0(t)_{a}$. (a) Simulated catchments with truncated sinusoidal distributions, (b) truncated normal distributions, (c) and gamma distributions for $\bar{P}(t)_{a}$ and $\bar{E}_0(t)_{a}$ plotted in Budyko space. Each black circle represents a single simulated catchment. Median behavior of simulated catchments is shown as the green curve. The “original” Budyko curves are plotted for comparison.
Figure 2-3. Empirical and predicted estimates of $\overline{E}$ for the 426 MOPEX catchments. (a) MOPEX catchments plotted in Budyko space. (b) $\overline{E}_e$ versus $\overline{E}_p$ with histograms inset on the respective axes.
Figure 2-4. Uncertainty in predictive estimates of $\bar{E}$ relative to empirically derived values for the 426 MOPEX catchments. (a) Quantifiable uncertainty in predictive estimates of $\bar{E}$. MOPEX catchments are ranked by $\bar{E}_p$, from highest to lowest (red line). Corresponding $\bar{E}_e$ values for each catchment are represented as black circles. The upper (lower) orange line represents the maximum (minimum) plausible value of $\bar{E}_p$ for each catchment given the quantifiable uncertainty in the estimation of $\bar{E}_0(\tau)\alpha$. (b) Locations of the stream gauges for the 426 MOPEX catchments used in this study. Black circles indicate catchments where $\bar{E}$ estimates from Equation 2-18 were within prediction uncertainty intervals; red and blue circles indicate over- and under-prediction, respectively.
CHAPTER 3
USING TRACERS TO QUANTIFY AND PREDICT HETEROGENEITY OF TRANSIENT STORAGE

Hydraulic Transport

Hydraulic transport is an important component of nutrient spiraling in streams, rivers, and wetlands [Newbold et al., 1981; SSW, 1990]. The processing of reactive solutes within streams depends upon both travel time and flow path; the former controls the time available for biogeochemical reactions to occur, while the latter controls the suitability of the environment for different reactions (e.g. differing redox potential of main channel versus sediments). Thus, understanding conservative solute transport is a critical prerequisite to understanding the cycling and ultimate fate of reactive solutes such as nutrients [Ensign and Doyle, 2005; Gooseff et al., 2004].

Modeling of solute transport within streams has typically been done using the one-dimensional advection, dispersion and storage (ADS) equation (Equation 3-1) [Bencala and Walters, 1983]. The ADS model conceptualizes a river reach as composed of two parts, advective zones (AZs), which are regions of uniform flow velocity which convey flow downstream, and storage zones (SZs), which are regions of zero flow velocity but that exchange water with adjacent AZs. The ADS model has been generalized to include multiple SZs, solute generation or removal, and inflows [Briggs et al., 2009; Harvey et al., 2005; Runkel, 1998]. Due to its relative simplicity, flexibility, and ability to capture the core hydraulic transport processes, the ADS has been used extensively in conjunction with tracer experiments to study solute dynamics (e.g. [González-Pinzón et al., 2015; Haggerty et al., 2009; Jin et al., 2009; Kelleher et al., 2013]). However, there are shortcomings to the ADS model when applied in certain contexts, largely due to its simplifying assumptions and one-dimensional nature. The
focus of this chapter is on quantifying the limitations of the ADS model’s treatment of stream SZs and suggesting how supplemental observations can make the application of the ADS model more robust.

Critically, there is no spatial information intrinsically assigned to either the AZ or SZ in the ADS model. Classically, SZs have been envisioned as occurring within hyporheic sediments [Cardenas, 2015], though in-channel SZs may also be significant (e.g. eddies, side-pools, vegetation beds) [Briggs et al., 2009; Ensign and Doyle, 2005; Gooseff et al., 2005; Hensley and Cohen, 2012; Stofleth et al., 2008]. While it is possible to infer the physical locations of a reach that are likely to act as the AZ (i.e. high flow velocity regions), it is usually not immediately obvious what locations or biophysical features will act as the SZ. In actuality, it is unlikely that transient storage occurs in discrete locations, but rather at a multitude of spatially variable locations, each with specific exchange characteristics with the AZ. Furthermore, the ADS model’s transient storage zones are unlikely to represent actual zero velocity zones in streams, but instead are used to represent flow paths slower than the main channel. Thus the membership of every location within a reach exists along a continuum between the AZ and SZ. For example, eddies may act more like SZs and less like AZs, while the thalweg acts more like AZs and less like SZs.

Fundamentally, the ADS’s SZ is a mathematical construct based on our conceptual understanding of hydraulic transport. Though the SZ is often conceptually ascribed physical locations and attributes (e.g. hyporheic sediments, eddies, side-pools, vegetation beds, etc.), in practice these conceptual assumptions are rarely verified. Our objective is to quantitatively attribute the SZ to actual biophysical features and thereby
test the explicit and implicit conceptual assumptions of what and where the SZ is when it is invoked through the use of the ADS to model solute transport processes in streams. By quantitatively understanding what biophysical features are associated with the SZ we further aim to develop the ability to predict its location a priori. We hypothesize that SZ is associated with measureable biophysical features that have traditionally been conceptually assigned it, locations with slow moving water within the stream reach.

Here we develop a method to measure and quantify the membership of locations within a stream reach as either AZ or SZ. We apply the experimental methodology to three different spring-fed rivers in Florida, USA. Using the results of these experiments, we develop a model to predict the probability of an in-stream position being associated with either that AZ or SZ using spatial and eco-geomorphological features as predictors. Next, the calibrated model was used to predict likely areas of transient storage using field measurements from cross sections from the experimental reaches. Results from these predictions are then compared to velocity fields observed at one of these cross sections. Finally, we explore implications of and applications for the predictive model.

**Methods**

**Methodology for Quantification of Transient Storage Membership**

Conceptually, the general methodology for sampling and quantifying the transient storage behavior of specific locations within a stream reach can be summarized as using a standard conservative tracer experiment to identify the behavior of the reach’s AZ and SZ and then determining which of these regions each of the roving sampler measurements is closer to. Specifically, conducting a tracer experiment on the reach of interest involves using either a single fixed measurement station at the end of the reach to collect a concentration breakthrough curve for the tracer and a known tracer injection
profile (e.g. instantaneous pulse), or two fixed measurement stations at the start and end of the reach to collect input and output concentration breakthrough curves. Fixed stations should be positioned in locations that approximate the AZ (i.e. areas of high flow conveyance).

As the tracer plume moves downstream through the reach, tracer concentration measurements are taken at various locations and times within the reach by roving samplers. The locations and timing of these measurements should be random, however in practice they would sampled haphazardly. Relevant spatial and/or eco-geomorphological features associated with each concentration measurement can also be collected to later determine if they are predictors of transient storage. Following the tracer experiment and roving sampling, the fixed station concentration breakthrough curves are used to calibrate the ADS model to the reach of interest. This reach-calibrated ADS model allows for the calculation of the expected concentrations of the AZ and SZ at any time or distance along the reach. Each of the tracer concentration measurements collected by the roving samplers are compared to the expected AZ and SZ concentrations at the corresponding position and time. Roving sampler measurements are classified as behaving as SZ if the absolute value of their deviation from the expected SZ concentration is smaller than the absolute value of their deviation from the expected AZ concentration and vice versa.

This methodology could be used with any conservative tracer and on any sized reach so long as the ADS model can adequately represent the river hydraulic transport processes. In our study we apply the methodology in three large spring-fed rivers and utilizing the conservative tracer Rhodamine WT, a fluorescent dye. While there are
some questions as to the conservative nature of Rhodamine WT [Runkel, 2015], the large discharge (i.e. > 2.8 m³/s) of the rivers of interest made alternative conservative solutes impractical.

Site Descriptions

The reaches investigated in this study were all within 1st magnitude (i.e. springs with average discharge > 2.8 m³/s), spring-fed rivers located in North Florida, specifically, Rainbow River, Silver River, and Alexander Springs Creek. Previous work [Hensley and Cohen, 2012] has suggested dense beds of submerged aquatic macrophytes to be the predominant SZs within these spring-fed systems. In addition to the mediating effect of the overlying vegetation beds, the relatively low turbulence from shallow bed slopes and low hydraulic conductivities of the sediments [Kurz et al., 2015] substantially limits hyporheic exchange.

Rainbow River reach

The Rainbow River is located in Marion County Florida. It is fed by a 1st magnitude group of vents and is a major tributary of the Withlacoochee River. Historically (1965–1974), the average discharge for this spring group is 21.6 m³/s. [Scott et al., 2004]. We selected a 1-km study reach from this river located in the lower half of the river before its confluence with the Withlacoochee River (Figure 3-1). This reach exhibited a large degree of spatial variation in bottom cover, from densely vegetated to completely bare. The reach also contained two significant side channels.

Silver River reach

The Silver River is fed by a composite of more than 30 contributing spring vents that form the headwaters of the Silver River [Scott et al., 2002; Scott et al., 2004], a major tributary of the Ocklawaha River. It is located about 9 km east of Ocala in Marion
County. Historically (1932–1974), the average discharge for this spring group is 23.2 m$^3$/s. [Scott et al., 2004]. The study reach for this river consisted of the majority of the river length, starting at the headspring and extending 8.2 km downstream (Figure 3-2). Most of this reach is heavily vegetated by submerged aquatic macrophytes. The upper portion of the reach is on average wider and shallower than the lower portion.

**Alexander Springs Creek reach**

Alexander Springs Creek is located in the Ocala National Forest, FL. This river is fed by a 1st magnitude group of vents located in Lake County within the boundaries of the Ocala National Forest. Historically (1931–2001), the average discharge for this spring group is 2.9 m$^3$/s. [Scott et al., 2004]. The study reach for this river started at the headspring and extended 5.4 km downstream (Figure 3-3). This reach is generally much shallower than those within the Rainbow and Silver rivers and thus has substantially more emergent vegetation throughout the channel.

**Data Collection**

Data collection was conducted in five separate field experimental efforts, one within the Rainbow River, three within the Silver River, and one within Alexander Springs Creek. In general, the methodological details between each effort were nearly identical, with the exception of the roving sampler measurements conducted in the Rainbow River. Specific methods, sampling differences, and data harmonization processes are discussed in the following subsections.

**Dye tracing**

In each of the five field experiments, we applied an approximately instantaneous pulse injection of Rhodamine WT at the upstream end of the study reach (Figure 3-4). Stationary fluorimeters (Turner Design C3, San Jose CA) measuring at one-minute
frequencies were positioned at the downstream end of the reach to record the tracer breakthrough curve. The mass of Rhodamine WT injected varied between each experiment, with 240 grams for Rainbow River, 3900 g for each of the Silver River experiments, and 635 g for Alexander Springs Creek.

Approximating an instantaneous pulse was a priority during the dye deployment to ensure that analytical solutions could be applied during the calibration of the ADS model to the tracer breakthrough curves (Equation 3-2 and the associated text). The deployment process to accomplish this varied between each experimental reach. For the Silver River and Alexander Springs Creek the upstream boundary of the reach was the headspring of the river, which allowed for tracing dye mass to be injected all at once as a point within the outflow of the spring vent. In the Silver River, this point injection was accomplished by rapidly pumping the dye mass 10 meters down to the spring vent with the assistance of scuba divers (Figure 3-4). For Alexander Springs Creek, the point injection was accomplished by releasing the mass of dye into the center of the spring boil from a canoe. The upstream boundary of the reach for the Rainbow River is an open channel rather than a point source. An instantaneous pulse injection was approximated for this reach by pouring the mass of dye in a line across the high-velocity portion of the channel.

**Roving sampling and eco-geomorphological feature characterization**

For each of the 5 experimental efforts, motorized roving sampler crafts haphazardly traversed and took measurements or samples from the dye plume as it was transported through the study reach. The roving sampling methodology for the Silver River and Alexander Springs Creek were identical. Three roving sampling craft were utilized. Each craft was equipped with a handheld GPS unit (Garmin,
Schaffhausen Switzerland) to record its location at 1 minute intervals. Discrete water samples were collected using a custom built apparatus consisting of weighted tubing connected to a hand pump (Figure 3-5). This apparatus was designed to collect representative samples from any depth within the reach. For each discrete sample, rover samplers recorded the time, depth, and classified the sample location as one of 5 categorical eco-geomorphological features:

- O – sample was taken from open water within the water column
- V – sample was taken within submerged aquatic macrophytes.
- E – sample was taken within emergent macrophytes.
- D – sample was taken within or behind woody debris
- B – sample was taken within a benthic depression.

Water samples were collected as frequently as possible and from as many locations as possible to provide a good overall coverage of the river. Samples were labeled and stored in the dark and refrigerated at 4 °C until they could be processed in the laboratory to obtain dye concentration.

The roving sampling methodology for the Rainbow River differed from the other two reaches in that instead of collecting water samples for subsequent laboratory processing, dye concentrations were measured directly in the field. This was accomplished by using field fluorimeters (Turner Design C3, San Jose CA) suspended from ropes beneath two roving sampler crafts. Ropes could be pulled in or let out in order to adjust the depth of where the sample was collected. To record depth, a pressure transducer (Solinst, Georgetown ON) was attached to each fluorimeter. The sampling frequency of both instruments was set at 12 seconds. Each sampling craft
was equipped with a handheld GPS unit (Garmin, Schaffhausen Switzerland) to continuously record its location.

**Sample processing**

Post-field processing was conducted for all the roving samples to obtain a harmonized data set consisting of the following information for each sample:

- Dye concentration (ppb)
- Distance from river centerline, a proxy for thalweg (m)
- Distance downstream from upstream reach boundary (m)
- Depth (m)
- Categorical eco-geomorphological feature classification (O, V, E, D, B)

Categorical eco-geomorphological feature classifications were excluded for the roving samples from the Rainbow River due to differences in sampling methodology.

For the discrete water samples obtained from the 4 experiments within the Silver River and Alexander Springs Creek, dye concentrations were obtained by measuring all of the water samples using a benchtop laboratory fluorimeter. First, a calibration curve was developed for Rhodamine WT. Using a 30 ppb stock solution, standard concentrations (30, 27, 21, 18, 15, 12, 9, 6, 3, 1.5, 0.3, 0.15, and 0 ppb) were produced, each with 7 replicates. Florescence of each of the 7 replicates was measured using an excitation filter of 530/25 nm and an emission filter of 590/35 nm with a detector sensitivity of 75. Replicate measurements for each concentration were averaged and a linear calibration model was fit to the averaged values ($R^2 = 0.997$). This calibration equation was then used to estimate dye concentrations of each of the discrete water samples collected based on their florescence measurements under the same excitation and emission settings.
Dye concentrations for each roving sample was paired with its corresponding GPS coordinate, depth, and categorical eco-geomorphological feature classification (except Rainbow River samples) by synchronizing the recorded time. GPS coordinates for each roving sample were converted into distances from river centerline and distances downstream from upstream reach boundary. This was accomplished by first defining a centerline for each reach within Google Earth and converting this centerline into a series of GPS coordinates. Both the centerline and roving samples GPS coordinates were translated to coordinates in representative 2-D plane that neglects the curvature of the Earth based on the average latitude and longitude of each reach. These 2-D coordinates (i.e. distance North-South and East-West) were transformed into the desired 2-D coordinates of distance from river centerline and distance downstream from upstream reach boundary.

The overall number of roving samples and their corresponding spatial and eco-geomorphological features for each of the 5 experimental efforts were:

- Alexander Springs Creek - 239 samples with dye concentration, distance from centerline, distance downstream, depth, and eco-geomorphological feature
- Silver River 1 – 299 samples with dye concentration, distance from centerline, distance downstream, depth, and eco-geomorphological feature
- Silver River 2 - 376 samples with dye concentration, distance from centerline, distance downstream, depth, and eco-geomorphological feature
- Silver River 3 - 401 samples with dye concentration, distance from centerline, distance downstream, depth, and eco-geomorphological feature
- Rainbow River - 1765 samples with dye concentration, distance from centerline, distance downstream, and depth.
Quantitative Analysis of Dye Traces and Roving Samples

The quantitative analysis of the data from the 5 field experiments consisted of two components: the calibration of the ADS model to the breakthrough curve data the classification of roving samples as behaving as either AZ or SZ. These analyses are described in the following subsections.

ADS model

The ADS model simulates one-dimensional flow and solute transport along river longitudinal distance, but assumes spatial homogeneity of solute concentration in the other two dimensions (width and depth). The model is based on the one-dimensional advection-dispersion equation, which relates changes in solute concentration at a point with respect to time to advection and dispersion. The ADS model adds the effect of having an area of zero velocity (i.e. SZ) that linearly exchanges water with the main channel (i.e. AZ). A set of coupled partial differential equations describes the two zones of the ADS model,

\[
\frac{\partial C}{\partial t} = -\frac{Q}{A} \frac{\partial C}{\partial x} + D \frac{\partial^2 C}{\partial x^2} + \alpha (C_s - C)
\]

\[
\frac{dC_s}{dt} = \alpha \frac{A}{A_s} (C - C_s)
\]  

(3-1)

where \(C\) is the AZ concentration, \(t\) is time, \(Q\) is discharge, \(A\) is the AZ cross-sectional area, where \(A_s\) is SZ cross-sectional area, \(D\) is the dispersion coefficient, \(\alpha\) is the storage exchange coefficient, and \(C_s\) is solute concentration in the SZ.

It is notoriously difficult to develop general analytical solutions for partial differential equations, which is why finite difference numerical methods have typically be applied to solve Equation 3-1 (e.g. [Runkel, 1998]). Numerical solutions, while advantageous in their generality of application, have a number of drawbacks such as
stability issues and the introduction of approximation errors [Causon and Mingham, 2010]; as such, analytical solutions are typically preferable when available. It is possible to analytically solve Equation 3-1 for an instantaneous pulse injection of solute into the reach, which yields [De Smedt, 2006; De Smedt et al., 2005; 2006; Huang et al., 2006],

\[
C(x, t) = e^{-\alpha t}C_0(x, t) + \alpha \int_0^t H(t, \tau)C_0(x, \tau) \, d\tau
\] (3-2)

with,

\[
H(t, \tau) = \left( e^{-\frac{\alpha}{\beta}(t-\tau)-\alpha \tau} \right) \frac{\tau I_1 \left( \frac{2\alpha}{\beta} \sqrt{\beta(t-\tau)} \right)}{\sqrt{\beta(t-\tau)}}
\]

\[
C_0(x, t) = \frac{M}{2A\sqrt{\pi Dt}} e^{-\frac{(x-Q_A t)^2}{4\beta t}}
\] (3-3)

where \( I_1(\ ) \) is the modified Bessel function of the first kind of order 1, \( \tau \) is a dummy integration time variable, and \( M \) is the mass of solute injected. While the analytical solution for the \( C \) has been published in the surface water literature [De Smedt, 2006; De Smedt et al., 2005; 2006; Huang et al., 2006], this is not the case for \( C_s \). To fill this gap and because it is required for the present study, we derived the analytical solution for \( C_s \),

\[
C_s(x, t) = e^{-\frac{\alpha}{\beta} t} \int_0^t \left[ e^{\frac{\alpha}{\beta} t} C_0(x, T) \right] dT
\]

\[
+ \alpha e^{-\frac{\alpha}{\beta} t} \int_0^t \left[ e^{\frac{\alpha}{\beta} T} \int_0^T H(T, \tau)C_0(x, \tau) \, d\tau \right] dT
\] (3-4)
Equation 3-4 uses the same definitions of terms as Equations 3-2 and 3-3, with the addition of a second dummy integration time variable, \( T \). The derivation of Equation 3-4 is located in Appendix B. It should be noted that following our derivation of Equation 3-4, we found equivalent forms of this equation within the groundwater literature \([Carnahan and Remer, 1984; Toride et al., 1993]\). However, due to this prior solution’s obscurity, the use of different parameter notation, and different methodology used in its derivation, we feel our rederivation is warranted to make it accessible to the stream hydrology community.

**Breakthrough curve calibration**

We used Bayesian statistical inference to calibrate Equation 3-2 to the measured breakthrough curves from each of the 5 field experiments, resulting in probability distributions for each of the model parameters \((A, A_s, D, \text{ and } \alpha)\), for each breakthrough curve. Bayesian inference is derived from Bayes theorem, which can be written as,

\[
p(\text{Model}|\text{Data}) \propto p(\text{Data}|\text{Model})p(\text{Model})
\]

where \( p(\text{Model}|\text{Data}) \) is the posterior probability distribution, which represents knowledge of the model parameters after taking into account observed data, \( p(\text{Data}|\text{Model}) \) is the likelihood probability distribution, which gives the probability of the observed data given the model and its parameters, and \( p(\text{Model}) \) is the prior probability distribution, which reflects knowledge about model parameters prior to accounting for the observed data.

When calibrating Equation 3-2 to a breakthrough curve containing \( N \) values of concentration and time (i.e., \( \{C_i\}, \{t_i\} \)), and assuming that measurement error is
normally distributed but excludes negative concentration values, Bayes theorem can be written as,

\[ p(A, A_s, D, \alpha | \{C_i\}, \{t_i\}) \propto \left( \prod_{i=1}^{N} R[\mathcal{C}_i|\mathcal{C}(x_0, t_i), \sigma^2] \right) p(A)p(A_s)p(D)p(\alpha)p(\sigma^2) \tag{3-6} \]

where \( R[\ ] \) is a rectified Gaussian distribution with mean equal Equation 3-2 and variance, \( \sigma^2 \), \( R[\mathcal{C}_i|\mathcal{C}(x_0, t_i), \sigma^2] \) is the probability of a single breakthrough curve concentration measurement, \( C_i \), given the corresponding \( t_i \) and ADS mode, \( x_0 \) is the distance downstream of the stationary fluorimeter, and \( p(\ldots) \) are the prior probability distributions for each parameter. All of the prior probability distributions were chosen to be rectified Gaussian distributions with mean equal to 0 and variance of \( 100^2 \). Prior distributions were selected to be the least informative given the known constraints for each parameter. Posterior probability distributions were sampled using a random walk Metropolis-Hasting Gibbs Sampling algorithm. The calibrated values of \( A, A_s, D, \) and \( \alpha \) used in subsequent analyses were assigned as the means as of the one-dimensional marginal probability distributions of each parameter.

**Transient storage classification**

Classification of roving samples as either behaving as either AZ or SZ was done by comparing the sample’s measured dye concentration with the expected dye concentrations of both zones. If the absolute value of sample’s deviation from the expected SZ concentration was smaller than the absolute value of their deviation from the expected AZ concentration, it was classified as behaving like the SZ, and vice versa. Expected dye concentrations for the AZ and SZ were calculated by inserting the reach-calibrated ADS parameters values (i.e. \( A, A_s, D, \) and \( \alpha \)), the roving sample’s
distance downstream, and the roving sample’s collection time into Equations 3-2 and 3-4, respectively. Mathematically, this classification methodology can be written as a function, $Z$, which gives a 1 to signify SZ behavior and a 0 to signify AZ behavior,

$$Z(C_i, x_i, t_i) = \begin{cases} 1, & |C(x_i, t_i) - C_i| > |C_s(x_i, t_i) - C_i| \\ 0, & |C(x_i, t_i) - C_i| \leq |C_s(x_i, t_i) - C_i| \end{cases}$$

(3-7)

where $C_i$ is the roving sample’s measured dye concentration, $x_i$ is the roving sample’s distance downstream, the roving sample’s collection time, $C(x_i, t_i)$ is the expected AZ concentration (i.e. Equation 3-2), and $C_s(x_i, t_i)$ is the expected SZ concentration (i.e. Equation 3-4).

**Probabilistic Transient Storage Model**

Following the transient storage classification, the roving sample dataset consisted of the following information for each sample:

- SZ membership (0 or 1)
- Distance from river centerline (m)
- Depth (m)
- Categorical eco-geomorphological feature classification (O, V, E, D, B)

Rainbow River samples lacked eco-geomorphological feature classification due to differences in field sampling methodology. The form of this dataset is that of a binary response variable (i.e. SZ membership) with 7 explanatory variables.

**Model description**

The binary response variable can be modeled as the outcome of a Bernoulli trial. A Bernoulli trial has two outcomes, 1 or 0, with a probability, $P$, that 1 will be the outcome of the trial, and a probability, $1 - P$, that 0 will be the outcome of the trial. To model $P$ in
terms of the 7 explanatory variables and interactions between them, we use a logistic regression,

\[
P(\{\eta_k\}) = \frac{1}{1 + e^{-y}}
\]

\[
y = \alpha_0 + \sum_{k=1}^{8} \alpha_k \eta_k
\]

(3-8)

where \(\eta_1\) is the distance from centerline (m), \(\eta_2\) is the depth (m), \(\eta_3\) sample location is in open water (0 or 1), \(\eta_4\) sample location is in a benthic depression (0 or 1), \(\eta_5\) sample location is within woody debris, \(\eta_6\) sample location is within emergent vegetation, \(\eta_7\) sample location is within submerged vegetation, \(\eta_8\) is the interaction between depth and distance \((m^2)\), \(\alpha_0\) is constant whose value determines whether \(P\) differs from 0.5 in the absence of explanatory variables, and \(\alpha_1\) to \(\alpha_8\) are the coefficients associated with each explanatory variable or interactions.

**Model calibration**

We used Bayesian statistical inference to calibrate Equation 3-8 to the 3080 roving sample SZ membership classifications from all of the 5 field experiments, resulting in probability distributions for each of the model parameters, \(\{\alpha_k\}\). Bayes theorem is written as,

\[
p(\{\alpha_k\}|\{S_i\}, \{\{\eta_k\}_i\}) \propto \left(\prod_{i=1}^{3080} P(\{\{\eta_k\}_i\})^S_i [1 - P(\{\{\eta_k\}_i\})]^{1-S_i}\right) \left(\prod_{k=0}^{8} p(\alpha_k)\right)
\]

(3-9)

where \(\{S_i\}\) are the SZ membership classifications (i.e. 0 or 1) and \(p(\alpha_k)\) are the prior probability distributions for each parameter. All of the prior probability distributions were chosen to be Gaussian distributions with mean equal to 0 and variance equal to 100^2. Prior distributions were selected to be the least informative given the known constraints
for each parameter. Posterior probability distributions were sampled using a random walk Metropolis-Hasting Gibbs Sampling algorithm.

Following the initial calibration of Equation 3-8, each of the one-dimensional marginal probability distributions for the model parameters, \{\alpha_k\}, was inspected to see if their 95% credible interval (CI) contained zero. Only parameters whose 95% CI did not contain zero were considered statistically significant. Non-statistically significant parameters were dropped from Equation 3-8 and the model was recalibrated. The calibrated values of the model parameters, \{\alpha_k\}, used in subsequent analyses were assigned as the means as of the the one-dimensional marginal probability distributions of each parameter from the second calibration.

**Predicting transient storage in experimental reach cross sections**

Finally, spring cross-sections were created from transects measurements for each of the three experimental reaches (Figures 3-1 to 3-3). Transect measurements included depth, height of submerged aquatic macrophytes, and presence of emergent vegetation. Using the roving sample-calibrated Equation 3-8 developed in the previous subsection, the probability of SZ was mapped onto each of the cross sections.

As an additional comparison, the velocity field of the Silver River cross section was quantified by measuring point flow velocities at various depths across that transect. Velocity was measured using an electromagnetic flow meter (EFM) (MF Pro Flow Meter, OTT Hydromet Inc., Loveland, CO). The EFM was found to provide reasonable velocity data even in dense vegetation, where other methods are unable to do so. Based on the average value at each measurement point, we created velocity contours and surfaces for each transect by ordinary kriging using statistical software (Surfer 11, Golden Software, Golden, CO).
The velocity field cross section map was compared to the cross section map of the probability of SZ. This allowed for a qualitative evaluation of the predictive ability of the calibrated Equation 3-8. In the ADS model the SZ has zero velocity, therefore it would be expected that the areas Equation 3-8 predicts as having a high probability of behaving as the SZ should have low velocities, while areas predicted as having low SZ probability should have high velocities.

Results

Quantitative Analysis of Dye Traces and Roving Samples

Breakthrough curve calibration

The calibrated values of $A$, $A_s$, $D$, and $\alpha$ the five experiments are given in Table 3-1. The ADS model simulated breakthrough curves corresponding to each set of parameters for both the AZ and SZ and their relations to the measured breakthrough curves are given in Figure 3-6. The parameters vary substantially between the different reaches reflecting the differences in channel geometry and hydraulic transport properties. In general both the AZ and SZ cross sectional areas were larger in the Silver River as compared to the other two.

Transient storage classification

Figures 3-7, 3-8, and 3-9 illustrate the two-dimensional positions and classifications (behaving as either AZ or SZ) for a subset of the roving samples in Alexander Springs Creek, the Silver River, and the Rainbow River, respectively. The visually evident pattern is that SZ points (red) occur at the edge more often that AZ points (blue), which more often occur in the center of the channel. It is important to note that these are three dimensional samples projected onto a two dimensional map and so the importance of depth is obscured.
Probabilistic Transient Storage Model

Model calibration

Out of the nine parameters in the probabilistic transient storage model, \( \{ \alpha_k \} \), six were found to be statistically significant. They are listed here with their associated meaning or explanatory variable: \( \alpha_0 \) (base rate probability), \( \alpha_1 \) (distance from centerline), \( \alpha_2 \) (depth), \( \alpha_6 \) (emergent vegetation), \( \alpha_7 \) (submerged vegetation), \( \alpha_8 \) (distance from centerline and depth interaction). Plots of the posterior probability distributions for these six parameters can be found in Figure 3-10, while their numerical values are summarized in Table 3-2. The three parameters that were found to be statistically indistinguishable from zero were \( \alpha_3 \), \( \alpha_4 \), and \( \alpha_5 \), which correspond to the eco-geomorphological features of open water, benthic depressions, and woody debris, respectively.

Figure 3-11 illustrates the output of the calibrated probabilistic transient storage model. The non-dimensional variable "y" is the linear combination of the spatial and eco-geomorphological features, as given in Equation 3-8. Negative values of y result in a less than 50% probability a given location will be in the SZ, while positive values of y results in a greater than 50% probability. All 3080 of the roving samples used in the calibration are plotted in Figure 3-11 in two different ways. First, the blue dots give the samples classification as either SZ (i.e. a value of 1) or AZ (i.e. a value of 0). For each of these blue dots, a corresponding black dot gives the calibrated probability of the underlying Bernoulli trial that produced the 1 or 0. It is the probability of this underlying process that the calibrated probabilistic transient storage model is predicting.
Predicting transient storage in experimental reach cross sections

The cross sections created from the transect measurements from each of the study reaches are given in panel (a) of Figures 3-12, 3-13, and 3-14. Notably, morphology and eco-geomorphological features vary substantially among the cross sections. The Rainbow River cross section has the least amount of vegetation and a relatively large hydraulic radius, as compared to Alexander Springs Creek which is shallow and wide, with abundant submerged and emergent macrophytes. The Silver River cross section has substantial vegetation, but the channel morphology still allows for a large hydraulic radius.

Panel (b) of Figures 3-12, 3-13, and 3-14 illustrates the locations within the cross sections that are more likely to behave as storage or advective zones based on the spatial and eco-geomorphological features presented in the corresponding panel (a). Finally, the predicted storage/advective zone behavior and measured velocity field for the Silver River cross section is given in Figure 3-15, illustrating their close correspondence.

Discussion

Quantitative Analysis of Dye Traces and Roving Samples

Breakthrough curve calibration

Visually, all of the calibrated fits of the AZ of the ADS model in Figure 3-6 appear to be reasonable or “behavioral” representations of the measured breakthrough curves. There are larger discrepancies between the calibrated model and data in the tail of the breakthrough curve compared to the peak, however, given relatively coarse classification method used (Equation 3-7) and the relatively large difference between
the AZ and SZ concentrations in the tails (Figure 3-6) it is unlikely to impact the results of the membership classification.

From the parameters in Table 3-1 it is clear that the Silver River differs from the other two reaches in that it has a much larger dispersion coefficient and SZ cross-sectional area. Also from Table 3-1, we can see that the size of the cross sectional area of the AZ and SZ can change substantially over time, as was the case for the Silver River, with the AZ ranging between 117.8 m² and 75.7 m², and the SZ ranging between 46.1 m² and 23.7 m². We attribute this to differences in discharge from the spring and in the downstream hydraulic control. Since all of the roving sample data was combined into the calibration of a single model, having a wider range of flow conditions likely strengthens the generality of the probabilistic transient storage model in predicting SZ behavior.

**Transient storage classification**

While useful for illustrative and conceptual purposes, caution must be exercised when interpreting Figures 3-7, 3-8, and 3-9 as they represent only a subset of the data, do not reflect depth effects. However, one pattern that can be assessed visually is that roving samples further from the river centerline appear to be more likely to be classified as SZ, while samples closer to the centerline appear to be more likely to be classified as AZ. At the same time it should be noted that examples of roving samples classified as either AZ and SZ can be found almost anywhere in the channel. This suggests that the locations and geometry of the SZ are variable and may not be immediately obvious or simply derived from a causal survey of geomorphic features.
Probabilistic Transient Storage Model

Model calibration

The parameters of Equation 3-8 that were found to be statistically significant shed light on what spatial and eco-geomorphological features govern transient storage in spring runs and how each features impacts it. Figure 3-10 and Table 3-2 show that the parameter $\alpha_0$ is significant and negative in value. This parameter is not associated with a specific feature in the model, and as such, we may interpret that, in the absence of information about any spatial and eco-geomorphological features within the spring run, any given location has less than a 50% probability of behaving like the SZ. This intuitively makes sense as we would expect that more likely than not most locations in a river are flowing. The next significant parameter, $\alpha_1$, is positive and is associated with distance from the centerline. This means that the probability of a location acting as the SZ increases with distance from centerline. The parameter $\alpha_2$ is negative and associated with depth, meaning that the probability of a location acting as the SZ decreased with depth. Parameters $\alpha_6$ and $\alpha_7$ are associated with emergent and submerged vegetation, respectively, and are both positive. This is interpreted as the probability of a location acting as the SZ is increased if it located within either emergent or submerged vegetation. Finally, parameter $\alpha_8$, which is associated with the interaction between depth and distance from centerline is also positive. This means that a location’s probability of acting like the SZ increases with depth and at a faster rate the further it is from the centerline. The action of $\alpha_8$ in counteracts the decrease in SZ probability with depth caused by $\alpha_2$, for distances further from the center. Intuitively this makes sense as for most natural river channels the depth and distance from the
centerline will be negatively correlated. This interaction term suggests that areas further from the river centerline, even if they are deep are still more likely to act as the SZ. This is in agreement with our conceptual understanding of river channels, with the edges of the river having lower flow conveyance than the center.

**Predicting transient storage in experimental reach cross sections**

All three of the cross sections given in Figures 3-12 to 3-14 give rise to plausible maps of locations illustrating probabilities of storage vs. advective zones. The predicted areas of high probability of SZ behavior occur in regions of the channel typically known to support transient storage (i.e. channel edges, vegetation). Conversely, predicted areas of low probability of SZ behavior occur in regions of the channel typically known to support advection (i.e. the center of the channel). Moreover, areas of high measured velocity are associated with areas low probability of SZ behavior while areas of high velocity have high probability of SZ behavior (Figure 3-15). This close agreement lends support that the predictive model could be applied more generally, however additional velocity validation is likely needed.

**Applications for the predictive model**

An obvious application for this method and model is to improve the coupling between stream ecosystem models and hydraulic solute transport models. Hydrodynamics and solute transport can exert large controls on ecosystems, but in many cases when applied to stream ecosystem models they are simplified. For example, the early methods to determine stream ecosystem metabolism for dissolved \( \text{O}_2 \) concentrations implicitly implied plug flow [Odum, 1956]. Simplification of the hydraulics can induce sizable errors when calculating ecosystem function from solutes [Hensley and Cohen, 2016]. A specific example of where this model could be utilized is
the improving the coupling of ecosystem metabolism models to the hydraulic environment. As previously stated, one method of ecosystem metabolism assessing is from time series of dissolved O₂ concentrations [Odum, 1956]. In order to estimate the quantities of interest, such as primary production and respiration, other variables that influence dissolved O₂ concentrations must be constrained, for example, reaeration rates of water column. The reaeration rate is highly dependent on the flow velocity, with larger velocities causing the water column to exchange gases with the atmosphere more quickly. Using the ADS model to estimate AZ zone velocities in conjunction with the probabilistic transient storage developed in this study, the relative proportion of the stream’s water surface acting as SZ with zero flow velocity could be estimated. Given that reaeration’s dependency on flow velocity is nonlinear [Wilcock, 1988], estimating the overall effective reaeration rate would be more accurate if calculated from the proportionally weighted average reaeration rates of the SZ and AZ rather than assuming an average uniform flow velocity over the entire water surface’s area.

Summary and Conclusions

In this study we developed and tested a method and model to measure, quantify, and predict the storage behavior of locations within a stream using easily measured spatial and eco-geomorphological features as predictors. Our calibrated predictive model was able to produce plausible predictions of storage zone locations from measured transects. Additionally, its predictions closely mirrored a measured velocity field in one the study reaches. Our methodology extends the utility of the relatively simple 1-D hydraulic transport ADS model to allow for 2-D and possibly 3-D prediction of solute transport within a river reach. Further subdivision of reaches used in this analysis will allow for a better approximation of the membership probability of each
roving sample. The probabilistic transient storage regression model developed can be used to estimate what regions of a river act as transient storage zones, which, when coupled with ecosystem metabolic models, may allow for improved predictions of the cycling and fate of reactive solutes such as nutrients.
Figure 3-1. Rainbow River reach used in this study. The white line within the channel represents the centerline of the river, a proxy for the thalweg. The red line perpendicular to the centerline is the location of the measured transect from this reach (Figure 3-13).

Figure 3-2. Silver River reach used in this study. The white line within the channel represents the centerline of the river, a proxy for the thalweg. The red line perpendicular to the centerline is the location of the measured transect from this reach (Figures 3-14 and 3-15).
Figure 3-3. Alexander Springs Creek reach used in this study. The white line within the channel represents the centerline of the river, a proxy for the thalweg. The red line perpendicular to the centerline is the location of the measured transect from this reach (Figure 3-12).
Figure 3-4. UF scientific divers performing an approximate instantaneous pulse injection of the conservative tracer solute Rhodamine WT dye into the outflow of the spring vent. The dye mass is being rapidly pumped 10 meters down from the surface. Photo courtesy of author.
Figure 3-5. Custom built apparatus for collecting water samples from any depth within the study reach. The apparatus consists of weighted tubing connected to a hand pump. Clockwise from top: hand pump device, sampling tube and weight deployed for sample collection, “rover” boat sample collection. Photos courtesy of author.
Table 3-1. Calibrated ADS model parameters for each of the 5 experimental efforts.

<table>
<thead>
<tr>
<th>ADS Parameters</th>
<th>Rainbow</th>
<th>Silver 1</th>
<th>Silver 2</th>
<th>Silver 3</th>
<th>Alexander</th>
<th>Units</th>
</tr>
</thead>
<tbody>
<tr>
<td>$A$</td>
<td>55.8</td>
<td>101.3</td>
<td>117.8</td>
<td>75.7</td>
<td>31.3</td>
<td>m$^2$</td>
</tr>
<tr>
<td>$A_s$</td>
<td>7.2</td>
<td>36.9</td>
<td>46.1</td>
<td>23.7</td>
<td>5.2</td>
<td>m$^2$</td>
</tr>
<tr>
<td>$D$</td>
<td>1.9</td>
<td>11.7</td>
<td>15.4</td>
<td>13.2</td>
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<tr>
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<td>3.09e-05</td>
<td>2.24e-05</td>
<td>1.28e-05</td>
<td>2.67e-05</td>
<td>1/s</td>
</tr>
</tbody>
</table>

Figure 3-6. Simulated breakthrough curves from the calibrated ADS model for each of the 5 experimental efforts of this study. In all subfigures, red lines correspond to the advective zone solution, blue lines correspond to the storage zone solution, blue dots are the measured Rhodamine WT breakthrough curves that the ADS model is calibrated to, solid lines are the solutions using the mean parameter values for $A$, $A_s$, $D$, and $\alpha$, while dotted lines represent the 95% credible intervals. Panels (a-c) correspond to the 3 experimental efforts...
conducted within the Silver River. Panel (d) corresponds to the Rainbow River experiment. Panel (e) corresponds to the Alexander Springs Creek experiment.

Figure 3-7. ADS model zone classification of subset of roving samples for Alexander Springs Creek. The white line within the channel represents the centerline of the river. Red points are those that are classified as behaving like the storage zone. Blue points are those that as behaving like the advective zone.

Figure 3-8. ADS model zone classification of subset of roving samples for the Silver River. The white line within the channel represents the centerline of the river. Red points are those that are classified as behaving like the storage zone. Blue points are those that as behaving like the advective zone.
Figure 3-9. ADS model zone classification of subset of roving samples for the Rainbow River. The white line within the channel represents the centerline of the river. Red points are those that are classified as behaving like the storage zone. Blue points are those that as behaving like the advective zone.

Figure 3-10. Probability distributions for each of the statistically significant model parameters of the probabilistic transient storage model. Blue dotted vertical lines signify the mean of the distribution. Red dotted lines mark the ends of
the 95% credible interval of the distribution. Panels (a-c) correspond to the parameters $\alpha_0$ to $\alpha_2$, respectively. Panels (d-e) correspond to the parameters $\alpha_6$ to $\alpha_8$, respectively.

Table 3-2. Calibrated statistically significant parameters of the probabilistic transient storage model.

<table>
<thead>
<tr>
<th>Statistically Significant Parameters</th>
<th>Lower 95% CI Bound</th>
<th>Mean</th>
<th>Upper 95% CI Bound</th>
</tr>
</thead>
<tbody>
<tr>
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<td>-0.4790</td>
<td>-0.3271</td>
<td>-0.1788</td>
</tr>
<tr>
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<td>0.0145</td>
<td>0.0239</td>
</tr>
<tr>
<td>$\alpha_2$</td>
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<td>-0.2538</td>
<td>-0.0098</td>
</tr>
<tr>
<td>$\alpha_6$</td>
<td>0.0065</td>
<td>0.2914</td>
<td>0.5753</td>
</tr>
<tr>
<td>$\alpha_7$</td>
<td>0.0384</td>
<td>0.2665</td>
<td>0.4919</td>
</tr>
<tr>
<td>$\alpha_8$</td>
<td>0.0032</td>
<td>0.0114</td>
<td>0.0206</td>
</tr>
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</table>
Figure 3-11. Plot of the calibrated probabilistic transient storage model, Equation 3-8 (red line). Both the storage zone classification (blue dots) and the storage zone probability (black dots) are plotted for all of the roving samples (N=3080).
Figure 3-12. Cross section created from transects measurements in Alexander Springs Creek (Figure 3-3). Panel (a) gives the locations of open water column (dark blue), submerged aquatic macrophytes (dark green) and emergent macrophytes (light green). Panel (b) shows what locations within the cross section that are more likely to behave as the storage zone (red) or more likely to behave as the advective zone (blue) given the morphology presented in panel (a).
Figure 3-13. Cross section created from transects measurements in the Rainbow River (Figure 3-1). Panel (a) gives the locations of open water column (dark blue) and submerged aquatic macrophytes (dark green). Panel (b) shows what locations within the cross section that are more likely to behave as the storage zone (red) or more likely to behave as the advective zone (blue) given the morphology presented in panel (a).
Figure 3-14. Cross section created from transects measurements in the Silver River (Figure 3-2). Panel (a) gives the locations of open water column (dark blue) and submerged aquatic macrophytes (dark green). Panel (b) shows what locations within the cross section that are more likely to behave as the storage zone (red) or more likely to behave as the advective zone (blue) given the morphology presented in panel (a).
Figure 3-15. Comparison of predicted storage/adveective zone behavior cross section map (top) to the measured velocity field cross section map (bottom) for the Silver River.
CHAPTER 4
HYDRODYNAMIC CONTROLS ON PRIMARY PRODUCERS COMMUNITIES IN SPRING-FED RIVERS

Primary Producers and Hydrodynamics

In many of Florida’s spring-fed rivers, benthic macro- and periphytic algae are increasing and, in some cases, replacing rooted vascular plants (VP), which are critical to ecosystem function. While much focus has been on nutrient increases to explain this change, in-channel hydrodynamics also control VP and algal abundance and their interactions. Understanding relationships between hydrology and primary producers is essential for developing ecologically relevant flow regulations. We investigated the relationship between flow velocity and primary producer abundance in spring-fed rivers using observational data from 16 springs to determine critical velocity thresholds for periphyton, macroalgae, and VP. We also used flow suppression experiments to quantify periphyton growth rates and test for hysteretic behavior of its establishment. Results suggest a critical velocity of 0.22 m/s (95% CI: 0.13-0.28 m/s) for periphyton, but no thresholds for macroalgae or VP. Experimental and theoretical results support these findings and suggest periphyton establishment is not hysteretic.

Hydrodynamics play an important role in structuring primary producer communities in lotic (flowing-water) ecosystems [Biggs, 1996; Biggs and Stokseth, 1996; Franklin et al., 2008; Jowett and Biggs, 2010]. Higher flow velocities can increase nutrient delivery rate by thinning the diffusive boundary layer over primary producer surfaces, increasing their productivity [Biggs, 1996; Biggs and Stokseth, 1996; Larned et al., 2004; Nepf, 2012a; b; Saravia et al., 1998]. However, if velocities are too high, primary producers can be dislodged from the substrate or be prevented from colonizing [Franklin et al., 2008; Ghosh and Gaur, 1998; Ryder et al., 2006; Wellnitz and Rader,
2003]. Lotic primary producers include rooted vascular plants (VP), macroalgae, and periphyton [O’Hare, 2015], and for all communities, biomass is generally negatively correlated with velocity [Biggs, 1996; Biggs and Stokseth, 1996]. As such, changes in velocity driven by natural or human-induced flow alterations have the potential to drive substantial variation in the primary producer community structure (PPCS) of lotic ecosystems.

Spring-fed rivers (springs) are highly productive, clear-water ecosystems fed by groundwater discharge [Scott et al., 2004]. Compared to surface water-fed systems, springs have extremely stable discharge, temperature, and chemical composition, making them ideal settings for controlled experiments [Heffernan et al., 2010b; Odum, 1957b]. Florida (USA) has one of the highest concentrations of springs and spring-fed rivers in the world [FSTF, 2000], and these unique ecosystems represent a vital ecological, cultural, and economic resource [Bonn and Bell, 2003; Borisova et al., 2014; Dunbar et al., 1989; Huth and Morgan, 2011; Laist and Reynolds III, 2005]. Florida springs are generally dominated by VP (primarily Vallisneria americana and Sagittaria kurziana), although benthic and periphytic algae are increasing in a majority of Florida springs [Stevenson et al., 2004], substantially shifting PPCS and associated ecological and recreational functions [Foss et al., 2012]. Notably, these shifts have occurred contemporaneously with observed increases in nitrogen concentration and declines in the discharge of many springs [FSTF, 2000].

The root cause (or causes) of observed shifts in PPCS continue to be investigated, and multiple plausible hypotheses have been advanced [Heffernan et al., 2010a; Hensley and Cohen, 2017; Liebowitz et al., 2014]. One potential driver of shifts
in PPCS is hydraulic control of algal abundance, specifically the ability of flow velocity to limit or prevent algal colonization, establishment, and accrual of biomass. In this work, we hypothesized that if flow velocity exerts a consistent control on the abundance of primary producers, the effect will be evident in field observations of velocity and algal cover across multiple spring-fed rivers. We tested this by applying a critical threshold velocity model to observational datasets of VP, macroalgae, periphyton, and velocity from 16 Florida springs. Additionally, we manipulated flow velocity in one spring-fed system (Silver River, FL) to experimentally verify this observed threshold velocity for periphyton, as well as to quantify periphyton growth dynamics and test for hysteretic behavior. Finally, we applied a mechanistic model to describe a plausible physical mechanism for the critical velocity thresholds derived here.

Data and Methods

Observational and Experimental Datasets

Observational datasets from five separate studies involving 16 springs were used to identify critical velocity thresholds, if present, for VP, macroalgae, and periphyton abundance. Specific data formats varied among datasets, however, all studies included primary producer abundance and flow velocity measurements, which were harmonized as described in the following section and Appendix C. The five studies were: 1) the Gulf Coast Springs Survey, containing periphyton, macroalgae, and VP data from three spring-fed rivers from 2003 to 2011 [Frazer et al., 2006; Hoyer et al., 2004]; 2) the Gum Slough Filamentous Algae Survey, containing macroalgae data from one spring-fed river from 2010 to 2013 [King, 2014]; 3) the Synoptic Biological Springs Study, containing periphyton, macroalgae, and VP data from 14 spring-fed rivers from 2015; 4) the Collaborative Research Initiative on Sustainability and Protection of Springs
(CRISPS) Submerged Aquatic Vegetation (SAV) Groundtruthing Survey, containing periphyton and VP data from one spring-fed river from 2014 to 2016; and 5) the CRISPS Hydraulics and Hydrodynamics Periphyton Survey, containing periphyton data from one spring-fed river from 2017. Additional details about each dataset are given in Appendix C.

Experimental data were derived using in-situ flow manipulation to reduce velocity in a section of the bed of the Silver River, observing the rate of periphyton growth or colonization on VP in areas with suppressed velocity, and then restoring flow and measuring periphyton removal. Periphyton growth, colonization, and removal rates were also measured in adjacent control sections without flow manipulation. The flow control structure diverted flow above and around its footprint, effectively reducing velocity behind the structure to zero, without blocking light (Figures C-1 to C-2 and Object C-1 in Appendix C). Structures were deployed at 19 sites in the Silver River across gradients of velocity and VP/algal cover. During each deployment, periphytic algal cover on VP was measured at treatment and control sites using digital photography (n = 6 images per site, per sampling event, maximum sampling interval of two days). After one week, flow was restored, and periphyton cover was measured for several days (with maximum sampling interval of two days) using the same procedure. Algal abundance was quantified by randomizing images and visually assigning each an algal abundance of “very low”, “low”, “medium”, “high”, or “very high”. This post-field ranking methodology mitigates potential observer bias or error present when using other defined-threshold categorization schemes, such as Braun-Blanquet classification [Wikum and
Estimating Critical Velocity Thresholds from Observational Data

We applied a simple critical threshold velocity model that tests whether two distinct abundance distributions exist for a given primary producer above and below a critical velocity threshold (Figure 1a). Any measure of primary producer abundance could be used for this test; here we use algal percent cover (A) based on the availability of these data across all studies. The distribution of A can then be written as,

\[ A \sim \begin{cases} \beta[\mu_1, \sigma_1^2], & v < v_c \\ \beta[\mu_2, \sigma_2^2], & v > v_c \end{cases} \]

where \( \beta[\mu_1, \sigma_1^2] \) is a Beta distribution with mean \( \mu_1 \) and variance \( \sigma_1^2 \) for flow velocities, \( v \), below the critical threshold velocity, \( v_c \). Similarly, \( \beta[\mu_2, \sigma_2^2] \) is a Beta distribution with mean \( \mu_2 \) and variance \( \sigma_2^2 \) for \( v \) above \( v_c \). We used the Beta distribution for A since it has finite support between 0 and 1, which corresponds to the 0% to 100% range for A.

Using the Heaviside step function, \( \Phi(\ ) \), we can rewrite Equation 4-1 as a single distribution with its parameters \( \mu(v) \) and \( \sigma^2(v) \) as functions of \( v \),

\[
\begin{align*}
A(v) & \sim \beta[\mu(v), \sigma^2(v)] \\
\mu(v) & = \mu_1 \Phi(v) + (\mu_2 - \mu_1) \Phi(v - v_c) \\
\sigma^2(v) & = \sigma_1^2 \Phi(v) + (\sigma_2^2 - \sigma_1^2) \Phi(v - v_c)
\end{align*}
\]

Equation 4-2 is illustrated conceptually in Figure 4-1a. A form of Equation 4-2 was used for all observational datasets that quantified algal abundance in terms of cover, while an analogous form was used for datasets that measured algal biomass (Appendix C).

We used Bayesian statistical inference to calibrate Equation 4-2 for each of the observational datasets, resulting in probability distributions for each of the model parameters \( (v_c, \mu_1, \sigma_1^2, \mu_2, \text{ and } \sigma_2^2) \), for each dataset. When calibrating Equation 4-2 to
$N$ values of algal abundance and flow velocity observations (i.e., $\{A_i\}, \{v_i\}$), Bayes theorem can be written as,

$$p(v_c, \mu_1, \sigma_1^2, \mu_2, \sigma_2^2|\{A_i\}, \{v_i\}) \propto$$

$$\left( \prod_{i=1}^{N} \beta[A_i|\mu(v_i), \sigma^2(v_i)] \right) p(v_c)p(\mu_1)p(\sigma_1^2)p(\mu_2)p(\sigma_2^2)$$

(4-3)

where $\beta[A_i|\mu(v_i), \sigma^2(v_i)]$ is the probability of a single abundance observation, $A_i$, given the corresponding $v_i$ and Equation 4-2; and $p(\ldots)$ are the prior probability distributions for each parameter. Explicit functional forms of the posterior distributions for each dataset are given in Appendix C. Posterior probability distributions were sampled using a random walk Metropolis-Hasting Gibbs Sampling algorithm. One-dimensional marginal probability distributions for $v_c$ for each observational dataset were obtained from samples of corresponding multivariate posterior distributions. Overall estimates of $v_c$ for each primary producer class (i.e., periphyton, macroalgae, and VP) were obtained by creating mixture distributions from all $v_c$ marginal distributions for each class.

**Quantifying Periphyton Growth Dynamics and Hysteresis from Experimental Data**

We applied a logistic growth model to describe the growth dynamics of periphyton released from hydraulic control. The model assumes that the mean behavior of periphyton cover as a function of time, $A(t)$, is logistic, and that variance around this mean follows a Beta distribution. Mathematically, this can be expressed as,

$$A(t) \sim \beta[\mu(t), \sigma^2]$$

$$\mu(t) = \frac{KA_0e^{rt}}{K + A_0(e^{rt} - 1)}$$

(4-4)

where $A_0$ is the initial algal coverage, $K$ is the carrying capacity, and $r$ is the intrinsic growth rate. Equation 4-4 is illustrated conceptually in Figure 1b. We again used
Bayesian statistical inference to calibrate Equation 4-4 to algal abundance time series. Since algal abundance was quantified categorically (Observational And Experimental Datasets section), relative thresholds between categories were defined as explicit parameters ($\varphi_1$, $\varphi_2$, $\varphi_3$, and $\varphi_4$), which corresponded to the divisions between the five algal abundance categories (“very low” to “very high”). For this calibration, Bayes theorem is written as,

$$p(A_0, K, r, \sigma^2, \varphi_1, \varphi_2, \varphi_3, \varphi_4 | N_1, \{t_{1,i}\}, N_2, \{t_{2,j}\}, N_3, \{t_{3,k}\}, N_4, \{t_{4,w}\}, N_5, \{t_{5,q}\}) \propto$$

$$\left( \prod_{i=1}^{N_1} I_{\varphi_1}[\mu(t_{1,i}), \sigma^2] \right) \left( \prod_{j=1}^{N_2} I_{\varphi_2}[\mu(t_{2,j}), \sigma^2] - I_{\varphi_1}[\mu(t_{2,j}), \sigma^2] \right)$$

$$\left( \prod_{k=1}^{N_3} I_{\varphi_3}[\mu(t_{3,k}), \sigma^2] - I_{\varphi_2}[\mu(t_{3,k}), \sigma^2] \right) \left( \prod_{w=1}^{N_4} I_{\varphi_4}[\mu(t_{4,w}), \sigma^2] - I_{\varphi_3}[\mu(t_{4,w}), \sigma^2] \right)$$

$$\left( \prod_{q=1}^{N_5} 1 - I_{\varphi_4}[\mu(t_{5,q}), \sigma^2] \right) p(A_0)p(K)p(r)p(\sigma^2)p(\varphi_1)p(\varphi_2)p(\varphi_3)p(\varphi_4)$$

(4-5)

where $I_x[\mu, \sigma^2]$ is the regularized incomplete Beta function (Appendix C); $N_1$, $N_2$, $N_3$, $N_4$, and $N_5$ are the number of algal abundance observations of “very low” “low”, “medium”, “high”, and “very high”, respectively; $\{t_{1,i}\}$, $\{t_{2,j}\}$, $\{t_{3,k}\}$, $\{t_{4,w}\}$, and $\{t_{5,q}\}$ are the corresponding timings of the algal abundance observations; and $p(\ldots)$ are the prior probability distributions for each parameter. Explicit functional forms of each posterior distribution are given in Appendix C.

Calibrated posterior probability distributions were used to quantify characteristics of periphyton growth, including the intrinsic doubling time, $T_d$,

$$T_d = \frac{\ln(2)}{r}$$

(4-6)

and growth potential, $G_p$. 

115
\[ G_p = K - A_0 \]  

We used growth potential as a quantitative measure of how much periphyton abundance was suppressed when under hydraulic control, with high (unrealized) growth potential indicating greater growth suppression. Overall estimates of \( T_d \) and \( K \) were obtained by creating mixture distributions from the marginal distributions of \( T_d \) and \( K \) for each deployment. Additionally, \( G_p \) estimates for each deployment were paired with corresponding velocity measurements to verify periphyton critical velocity thresholds derived from observational data.

To test for hysteresis in periphyton abundance, we compared algal abundance distributions before flow modification and several days after flow was restored (periphyton abundance quickly declined and stabilized after \(~1\) day; Object C-2 in Appendix C). Figure 4-1b conceptually illustrates our approach. Periphyton abundance distributions can be written as,

\[ A_b \sim \beta[\mu_b, \sigma_b^2] \quad A_a \sim \beta[\mu_a, \sigma_a^2] \]

where \( b \) corresponds to before flow modification and \( a \) corresponds to after flow modification. Statistical difference was assessed by comparing the distributions of \( \mu_b - \mu_a \) and \( \sigma_b^2 - \sigma_a^2 \) for each deployment. If the 95% credible intervals of \( \mu_b - \mu_a \) or \( \sigma_b^2 - \sigma_a^2 \) contained zero, \( A_b \) and \( A_a \) were considered statistically indistinguishable, and no hysteretic effect was supported; if they did not contain zero, there was statistical evidence for a hysteretic effect. Explicit functional forms of all posterior distributions are given in Appendix C.
Threshold Velocity for Rooted Vascular Plant Canopy Motion

One plausible physical mechanism for the existence of critical velocity thresholds for periphyton is a corresponding velocity threshold for VP canopy continuous motion. Since periphyton grow on VP surfaces, it is susceptible to mechanical removal from abrasion as VP blades slide past each other. The frequency of contact-induced abrasive events increases dramatically when the VP canopy is in continuous motion [Doaré et al., 2004]. Flexible VP canopy motion is known to be sustained by the generation of traveling vortices by Kelvin-Helmholtz instabilities, which can induce traveling waves within VP known as monami [Okamoto and Nezu, 2009; Okamoto et al., 2016; Patil and Singh, 2010] (Object C-3 in Appendix C). Monami occur when the instantaneous drag force exerted by the vortices exceeds the buoyancy and rigidity of the VP [Nepf, 2012a] and has a well-defined physical threshold. Using conceptual frameworks, formulae, and values from Ghisalberti and Nepf [2002], Ghisalberti and Nepf [2006], Nepf [1999], Nepf [2012b], and Ortiz et al. [2015], we derived an approximation (Appendix C) of the minimum average mixing layer (i.e., turbulent layer above the VP canopy) velocity required for monami generation, \( v_m \),

\[
v_m \cong \frac{1}{\Omega} v_a = \frac{1}{\Omega} \left[ \frac{2}{3} \right] v_i = \left[ \frac{1.4}{3} \right] \sqrt{\frac{E \tau^3}{3 \rho_w C_S \delta_e \left( h - \frac{\delta_e}{2} \right)^2}} + \frac{2 \Delta \rho \tau g (\delta_e + 2h)}{3 \rho_w C_S \delta_e} \tag{4-9}
\]

where \( v_a \) is the traveling velocity of the vortices, \( \Omega \) is the ratio \( \frac{v_a}{v_m} \), which ranges between 1 and 1.8, \( v_i \) is the maximum instantaneous velocity a vortex, related to \( v_a \) by \( v_a = \frac{2}{3} v_i \),

\[
\delta_e = \frac{0.23 \Delta S^2}{C_D W} \quad \text{and is the depth into which the vortices can penetrate the canopy,}
\]

\[
C_S = 1.11 + 0.02 \left( \frac{W}{\delta_e} + \frac{\delta_e}{W} \right) \quad \text{and is the drag coefficient of an individual VP blade,}
\]

\[
C_D \quad \text{is the bulk}
\]
drag coefficient of the whole VP canopy, $\Delta \rho = (\rho_w - \rho_s)$, $\rho_w$ is the density of water, $\rho_s$ is the density of VP tissue, $E$ is the Young’s modulus of VP tissue, $\Delta S$ is the characteristic distance between VP blades, $W$ is the characteristic VP blade width, $h$ is the characteristic VP height, $\tau$ is the characteristic VP blade thickness, and $g$ is the acceleration due to gravity. Equation 4-9 was parameterized using VP morphology data from the two CRISPS studies described above and [Hauxwell et al., 2007; Lei and Nepf, 2016; Nepf, 2012b; Tanino and Nepf, 2008], with resulting parameters, $C_D = 1$, $\rho_s = 850$ kg/m$^3$, $E = 0.883$ GPa, $\Delta S = 15.3$ mm, $W = 12.0$ mm, $h = 787$ mm, and $\tau = 0.7$ mm. Estimates of $v_m$ were then compared to critical velocity threshold estimations for periphyton abundance from observational and experimental data.

**Results**

Observational critical velocity threshold analyses are summarized in Fig 2. Representative model calibrations for each primary producer class (periphyton, macroalgae, and VP) are given in Figs 2a-c, and Figs. 2d-f summarize $v_c$ estimates across all datasets for each class. Periphyton showed a clear velocity threshold, as exemplified both by the sharp decline in median primary producer abundance (red line in Figure 2a) as well as by the relatively narrow 95% credible interval (0.13-0.28 m/s) around the overall median periphyton $v_c$ (0.22 m/s) across studies (Figure 2d). In contrast, there was no clear velocity threshold for macroalgae or VP (Figs. 2b-c), and $v_c$ for these classes had 95% credible intervals that encompassed nearly the entire velocity range in the datasets (0.02-0.63 m/s for macroalgae and 0.02-0.61 m/s for VP).

Figure 3 shows an example of the digital images and logistic growth model calibrated to periphyton abundance data from one deployment of the flow suppression
experiment. These images illustrate that periphyton abundance at the control sites remained essentially unchanged throughout the deployment, while it increased dramatically at treatment sites. Results from all flow suppression experiments are summarized in Figure 4. Figure 4-4a shows $G_p$ as a function of velocity for all deployments and illustrates a distinct transition between lower and higher values of $G_p$ near 0.2 m/s, similar to the finding of median $v_c = 0.22$ m/s for periphyton abundance in the observational study. Figures 4-4b-c summarize results for periphyton $T_d$ and $K$, which were estimated at 0.64 days (95% CI: 0.14 to 2.3 days) and 82% cover (95% CI: 45-98%), respectively.

Hysteresis analysis revealed that only 3 of 19 deployments showed statistically distinguishable periphyton distributions before and after the flow manipulation; two had significantly more periphyton after the manipulation, and one had significantly less. Finally, we estimated a mean monami generation velocity threshold, $v_m$, of 0.23 m/s, with a range between 0.13 and 0.33 m/s for sparse and dense VP canopies, respectively.

**Discussion and Conclusions**

Understanding how flow regime structures PPCS in lotic ecosystems is critical for attributing causal mechanisms of ecological change and setting flow management or restoration goals. In this study, we synthesized and analyzed paired observations of abundance and velocity from 16 spring-fed rivers for three primary producer classes, finding that periphyton abundance had a distinct, critical velocity threshold, while benthic macroalgae and VP did not. This finding is illustrated by Figure 2d, which shows that $v_c$ estimates from all observational datasets were well-constrained and similar in
magnitude. This consistency across 16 springs, using a variety of data collection methods, suggests that 0.22 m/s (or the narrow range of velocities around it) does indeed represent a significant hydraulic-driven control on periphyton abundance. In contrast, macroalgae and VP abundance did not appear to have well-defined velocity-driven controls, as their median $v_c$ estimates varied substantially between datasets and had large uncertainty bounds (Figs 2e-f). These differences in velocity control behavior likely arise from biophysical differences in anchoring mechanisms and substrate types. The periphyton studied here typically require VP as a substrate [Notestein et al., 2003]. This places their anchoring point higher in the water column subjecting them to higher velocities and shear stresses relative to benthic macroalgae and VP, which anchor to the river bottom. Additionally, periphyton’s VP substrate is flexible and capable of substantial motion and abrasive interactions, which can cause mechanical removal of the periphyton.

The lack of evidence of a well-defined $v_c$ for macroalgae and VP contrasts with several previous studies. For example, Hoyer et al. [2004] observed that macroalgae and VP biomass in three springs were both substantially reduced at velocities $> 0.25$ m/s. There are several potential reasons for this discrepancy. First, our study used percent cover data, while Hoyer et al. [2004] used biomass, and the two are not always well correlated (Appendix C). It is also possible that variables other than velocity were driving low VP biomass above 0.25 m/s in the Hoyer et al. [2004] study; specifically, they found a lack of suitable benthic substrate for VP rooting above 0.25 m/s. Additionally, observations from a single spring by King [2014] found macroalgal cover to decrease substantially above 0.22 m/s. We used the same dataset as King [2014], and
our median macroalgae $v_c$ estimate, 0.23 m/s, closely matched this value and was relatively well-constrained (95% CI 0.20-0.35 m/s) compared to the other two macroalgae studies. Closer inspection of the King [2014] dataset revealed that observations were of macroalgae colonizing VP and thus effectively acting as periphyton. This velocity closely matches the values of $v_c$ (0.22 m/s) and $v_m$ (0.21 m/s) that we found for periphyton, which also colonizes VP; this point is discussed further below.

We augmented these observational findings using an *in-situ* flow manipulation experiment to verify critical threshold velocity behavior for periphyton and characterize its growth dynamics when released from hydraulic-driven control. Agreement between observational and experimental findings is illustrated in Figure 4a, which clearly shows a transition from low to high $G_p$ at velocities above $\sim$0.2 m/s, indicating strong growth suppression at higher velocities. This threshold-type behavior corresponds to our mean observational periphyton $v_c$ estimate of 0.22 m/s. In combination with findings in Figs. 4b and 4c, i.e. rapid periphyton growth (mean $T_d = 0.64$ days) and high carrying capacity (median $K = 82$ % cover), these results indicate that without hydraulic-driven control, periphyton rapidly accumulate and reach to near-complete coverage of their host substrate. This behavior has important implications for spring ecosystems, where periphyton directly competes with VP for light [O’Hare, 2015; Zhang et al., 2015]. Without sufficient hydraulic-driven control of periphyton, VP can be outcompeted and lost from the ecosystem [O’Hare, 2015], with broad and cascading effects across trophic levels [Choudhury et al., 2015; Duarte, 1995; UFWI, 2017]. In springs exhibiting reduced flow, this process may play a major role in restructuring the PPCS. However,
results from our hysteresis analysis suggest that management activities to reintroduce velocities > $v_c$ in systems where periphyton has accumulated to nuisance levels can return the system to a previous state with low periphyton abundance.

Finally, we proposed the onset of continuous VP canopy motion and associated abrasive contacts within the canopy as a physical mechanism explaining critical threshold velocity behavior of algae growing on VP and estimated this velocity ($v_m$) from theory. It is striking how similar the value of $v_m$, 0.23 m/s, is to our observationally determined periphyton $v_c$, experimentally determined periphyton $v_c$, and the $v_c$ estimate for macroalgae growing on VP (0.22, ~0.20, and 0.23 m/s, respectively). It is likely that when macroalgae colonizes VP, it is subject to the same mechanical removal, and would hence have a $v_c$ close to that for periphyton. In short, the similarity between the suite of observational and experimental $v_c$ estimates for algae growing on VP, and to the theoretically derived threshold for monami creation, supports the hypothesis that the initiation of continuous VP canopy motion generates the critical threshold velocity behavior in algal abundance. Overall, this nexus of theory, observation, and experimental findings suggest that hydrodynamic controls are critical for structuring flowing water ecosystems by shifting the competitive balance between primary producers.
Figure 4-1. Conceptual summary of the methods used in the observational and experimental components of Chapter 4. (a) Conceptual summary of the critical velocity threshold model. One primary producer abundance distribution (in this case algal percent cover) exists below the critical velocity (black), while a different distribution exists above this velocity (red). (b) Conceptual summary of the periphyton growth dynamics model and test for hysteresis. Flow is interrupted at time zero, after which periphyton abundance increases logistically from its initial value, $A_0$, to the carrying capacity, $K$. When flow is restored, periphyton abundance is reduced. Comparison of periphyton abundance distributions before and after flow modification indicates potential hysteretic behavior.
Figure 4-2. Summary of observational critical velocity threshold results. Panels a, b, and c show representative critical threshold velocity model calibrations for periphyton (CRISPS Hydraulics and Hydrodynamics Periphyton Survey), macroalgae (Gulf Coast Springs Survey), and VP (Synoptic Biological Springs Study), respectively. The solid red lines represent the median primary producer abundance, while the dotted black lines represent 95% credible intervals. Solid black horizontal lines give the thresholds between the visual classification values. Panels d, e, and f give the medians with 95% credible intervals for $v_c$ across all observational datasets (black) and the overall mixture distribution (red) for periphyton, macroalgae, and VP, respectively.
Figure 4-3. Representative results of periphyton accrual during flow suppression experiments. Solid black lines signify calibrated mean values for the relative thresholds parameters ($\varphi_1$, $\varphi_2$, $\varphi_3$, and $\varphi_4$), and blue dots represent the observed periphyton abundance timeseries, with digital images from the treatment and control site corresponding to each measurement. Median and 95% credible intervals of periphyton abundance are depicted by the solid red and dashed black lines, respectively.
Figure 4-4. Results of flow manipulation experiments (19 deployments). (a) Growth potential, $G_p$, as a function of flow velocity, with the solid black circles representing the median values and horizontal and vertical lines representing the 95% credible intervals for flow velocity and $G_p$, respectively. (b) Median values with 95% credible intervals for the intrinsic doubling time, $T_d$, for each deployment (black) and the overall mixture distribution (red). (c) Median values with 95% credible intervals for the carrying capacity, $K$, for each deployment (black) and the overall mixture distribution (red).
Overview

Multiscale modeling is a process to understand a system’s behavior at one scale using information or models from different scales [Famiglietti and Wood, 1994a; Horstemeyer, 2009]. In this chapter, my objective was to quantitatively link landscape-scale discharge generating processes to primary producer scale dynamics. To do so, I combined the results from the landscape- (Chapter 2), river reach- (Chapter 3), and primary producer-scale (Chapter 4) analyses into a multiscale modeling framework to investigate drivers of primary producer community shifts in the Silver River. This linkage allowed me to test the hypothesis that primary producer community shifts observed in the Silver River have been driven, at least in part, by a reduction in the hydraulic control of algal abundance, which has been induced by declines in spring discharge caused by climatic changes within the springshed.

Conceptually, there are three linkages that must be established within this multiscale modeling framework to test the stated hypothesis (Figure 1-3):

- The relationship between algal abundance and above roote aquatic vascular plant (VP) canopy flow velocity.
- The relationship between above VP canopy flow velocity and spring discharge.
- The relationship between spring discharge and rainfall and potential evapotranspiration distributions.

Of these linkages, the first was completely developed in Chapter 4, and the methodology for the third was developed in Chapter 2, though the method was not applied to the Silver River. The second linkage was not developed in
preceding chapters, however the hydraulic tracer experiments of Chapter 3 can be utilized to explicitly develop this linkage for the Silver River. In this chapter, I complete the development of the second and third linkages use the linked models to state and test the multiscale hypothesis.

Methods

Site Description

The Silver River is a 1st magnitude spring-fed river located about 9 km east of Ocala in Marion County, FL. This river was described in Chapter 3, and further general details can be found there. In this study, the reach of interest was the upper portion of the river, starting at the headspring and extending 2.8 km downstream (Figure 5-1). Most of this reach is heavily vegetated by submerged aquatic macrophytes, and is on average wider and shallower than the lower portion. This reach was chosen to study for several reasons. First, in this reach algae abundance has been observed to increase over time, at least anecdotally, motivating research and management actions [UFWI]. This area is the most heavily-trafficked area of the river (e.g., daily trips by glass-bottom boats), and therefore has many observations of algal proliferation. Additionally, a USGS gauge station (02239501) in the middle of this reach, 1.2 km from the headspring. The location of this gauge station allows for stage changes at this location to be used as representative of stage changes across the reach.

Linking Spring Discharge to Above Canopy Flow Velocity

Developing an area-discharge curve

In this section I use dye tracing data to create a relationship between the Silver River discharge and its cross sectional area that is conveying flow. In
Chapter 3, the general principles of hydraulic tracer experiments were described, along with the details of three dye trace experiments on the Silver River. During each of these three dye trace experiments, 3900 g of Rhodamine WT was applied in an approximately instantaneous pulse injection at the headspring (Figure 3-4), and a stationary fluorimeter, (Turner Design C3, San Jose CA) measuring at one-minute frequencies was positioned at the downstream end of the reach to record the tracer breakthrough curve. Critically, these breakthrough curves are distinct from those used in Chapter 3 as the only represent the hydraulic properties of the upper reach (Figure 5-1). One additional dye trace was conducted on the Silver River, using the same methodology, bringing the total number of dye traces on the upper reach to four (Figure 5-2).

Crucially, the four dye trace experiments were conducted during times of different discharge in the Silver River. The average residence time, $\tau_r$, for each of the dye traces was calculated directly from the breakthrough curves by calculating the first moment of the data,

$$\tau_r = \frac{\sum_i C_i}{\sum_i C_i t_i}$$

(5-1)

where $C_i$ is the dye concentration measurement at each corresponding time, $t_i$. Using $\tau_r$, and the length of the reach, $x_r$, the average velocity, $v_r$, can be calculated for each dye trace,

$$v_r = \frac{x_r}{\tau_r}$$

(5-2)

Similarly, the cross section area of river, $A_r$ for each dye trace can be calculated using,
\[ A_r = \frac{Q}{v_r} \] 

where is the discharge associated with each dye trace. Plotting \( Q \) vs. \( A_r \) (Figure 5-3), yields a near linear relationship \( (R^2 = 0.97) \). This means that the cross sectional area of the upper reach of the Silver River can be approximated to scale linearly with \( Q \), at least over the range of discharges under which dye traces were conducted.

**Developing an effective depth-discharge curve**

Here, I combine the area-discharge curve developed in the previous section with the USGS measured stage discharge curve create an effective depth-discharge curve. While the stage-discharge curve of the Silver River has changed over time [UFWI, 2017], the relationship remained stable over the period of the four dye trace experiments. Over the entire range of discharge values, this relationship can be reasonably approximated by a linear function (Figure 5-4). If both the area-discharge curve and stage-discharge curve are approximately linear, this means that width of the river does not change with increasing discharge, but the depth of the river increases approximately linearly.

The depth-discharge curve, \( H(Q) \), can be found by combining the area-discharge and stage-discharge curves, yielding,

\[
H(Q) = m_s Q + b_A \left( \frac{m_s}{m_A} \right)
\]

where \( m_s \) is the slope of the stage-discharge curve, \( m_A \) is the slope of the area-discharge curve, and \( b_A \) is the intercept of the area-discharge curve.
Velocity profiles for vegetated channel

In Chapter 4, the critical threshold velocities found for algae observationally, experimentally, and theoretically were all for the average velocity above the submerged macrophyte canopy. The velocities obtained from the moment analysis of the dye trace breakthrough curves, $v_r$, are the average velocity of all flow paths and therefore are not representative of above canopy velocities. It is possible that a significant portion of a channel cross sectional area contains submerged macrophytes (e.g. Figure 3-14). In Chapter 3, I showed statistically, through the probabilistic transient storage model, and observationally, through point velocity measurements, that macrophyte canopies are associated with low flow velocity. If a sizable portion of the channel cross sectional area has low flow velocities (i.e. inside macrophyte canopies), this implies that the remaining portion (i.e. the above canopy area) must have much higher velocities to obtain the mid-range overall average velocities. To predict the average above canopy flow velocity we can use theory of flow through aquatic vegetation.

The average velocity, $v$, as a function of depth, $z$, both in and above a submerged macrophyte canopy can be described by [Nepf, 2012a],

$$v(z) = \begin{cases} v_1 + (v_h - v_1)e^{-Kv(h-z)}, & z < h \\ \frac{v_*}{K}\ln\left(\frac{z - z_m}{z_0}\right), & z \geq h \end{cases} \tag{5-4}$$

where,
\[ v_1 = \sqrt{\frac{2g \sin \theta}{C_D a}} \]
\[ v_h = \frac{v_*}{\kappa} \ln \left( \frac{h - z_m}{z_0} \right) \] (5-5)

and \( z_m = h - \frac{0.1}{C_D a}, z_0 = \frac{0.04}{a}, K_v = \frac{C_D a}{2(0.172)}, \) \( v_* = \sqrt{g \sin \theta (H - h)}, \) \( \kappa = 0.4, \) \( a = \frac{W}{\Delta S^2} H \)

is flow depth, \( \sin \theta \) is the channel slope, \( g \) is the acceleration due to gravity, \( \Delta S \)

is the characteristic distance between VP blades, \( W \) is the characteristic VP blade width, \( C_D \) is the bulk drag coefficient of the whole VP canopy, and \( h \) is the characteristic VP height. The average above canopy flow velocity, \( v_m \), as function of \( H \) can be calculated from Equation 5-4 as,

\[ v_m(H) = \frac{1}{(H - h)} \int_h^H \frac{v_*}{\kappa} \ln \left( \frac{z - z_m}{z_0} \right) dz \] (5-6)

which becomes,

\[ v_m(H) = \frac{1}{(H - h)} \left[ (H - z_m) \ln \left( \frac{H - z_m}{z_0} \right) - H - (h - z_m) \ln \left( \frac{h - z_m}{z_0} \right) + h \right] \] (5-7)

Equations 5-4 and 5-7 were parameterized with the same values in Chapter 4 which are representative of the VP in the Silver River, \( C_D = 1, \Delta S = 15.3 \) mm, \( W = 12.0 \) mm, and \( h = 787 \) mm. The average slope for the reach was computed as \( \sin \theta = 3 \times 10^{-5} \). To validate the parameterized Equation 5-4, I compared the to predicted velocity profiles to measured velocity profiles from the study reach.

By inserting Equation 5-3 into Equation 5-7, \( v_m(H(Q)) \), the average above canopy flow velocity is expressed as a function of discharge. In Chapter 4, I showed that the critical threshold velocity for algae is \( \sim 0.22 \) m/s. Using \( v_m(H(Q)) \), I calculated the critical threshold discharge corresponding to the critical threshold velocity, and thus defining relationship between above VP
canopy flow velocity and spring discharge. The critical threshold discharge was compared to the time series of the Silver River discharge.

**Linking Climatic Shifts to Spring Discharge**

**Prediction of long-term discharge**

Here, I apply the methodology developed in Chapter 2 to the Silver River springshed. Daily weather data (i.e. rainfall depths and max and min temperatures) from 1932 to 2017, were obtained for the Ocala weather station within the Florida Climate Center database. Using the methods described in Chapter 2 and Table A-2, daily estimates for potential evapotranspiration were calculated from the temperature data for the entire period of record. Corresponding daily spring discharge data from 1932 to 2017, were obtained from the USGS.

The exact methodology used for catchments in Chapter 2 was applied to Silver River springshed, resulting in an estimate of $\bar{E}$ for the springshed. An estimate of $\bar{Q}$ was calculated by multiplying springshed recharge, $\bar{P} - \bar{E}$, by a spring shed area of 2700 km². This value was obtained as the mean of 3100 km² from *UFWI* [2017] and 2300 km² from *Munch et al.* [2006]. The estimate value of $\bar{Q}$ was compared with the mean value of the entire record of the daily discharge data.

**Prediction of temporal varying recharge**

Next, I calculated $\bar{P}$, $\bar{E}_0$, $\bar{P} - \bar{E}$ using the same methodology as in Chapter 2 except using a 23-year moving window, rather than the entire period of record. Additionally, the day of the year that the central tendency of $\bar{P}$ and $\bar{E}_0$ occurred on was calculated using a 23 year moving window.
was chosen as this has been determined to be the approximate lag time of the Silver River discharge for long term changes in recharge.

The Budyko framework developed in Chapter 2 is likely not suitable to apply directly to only a 23-year period of record, as this might not be a long enough time frame for the precipitation dynamics to converge to a stable representative distribution (e.g. as given in Figure 2-1). The framework thus produces recharge estimates that are too large, since the precipitation distribution behave stocatics slaly rather than a smooth distribution such as given in Figure 2-1. To correct for this over-prediction, the average of all 23-year moving window $\bar{P} - \bar{E}$ estimates was normalized to have the same average value as the recharge estimate using the entire period of record, requiring a 28% correction. The normalized $\bar{P} - \bar{E}$ was divided by $\bar{P}$ to produce the fraction of rain that is converted to recharge and was then compared to the 23-year moving of observed fraction of rainfall converted to spring discharge.

**Results**

**Linking Spring Discharge to Above Canopy Flow Velocity**

**Discharge-dependent above canopy flow velocities**

Validation of the parameterized Equation 5-4 show good agreement between the predicted and measured profiles (Figure 5-5 and 5-6). Figure 5-7 illustrates $v_m(H(Q))$ plotted for a range of discharges and also shows the values of the critical threshold velocities identified in Chapter 4. Critical threshold discharge values correspond to locations where the critical threshold velocities cross $v_m(H(Q))$. The critical threshold discharge corresponding to the critical threshold velocity of $\sim$0.22 m/s was found to be $\sim$15.5 m$^3$/s. The comparison of
the critical threshold discharge to the Silver River discharge time series is given in Figure 5-8. During the year 2000, the Silver River transitioned from almost exclusively being above the critical threshold discharge to frequently falling below that value.

**Linking Climatic Shifts to Spring Discharge**

**Prediction of long-term discharge**

The long-term rainfall and potential evapotranspiration distributions for the Silver River springshed are given in Figure 5-9. In general, rainfall is higher than potential evaporation, particularly in the summer and winter. During the fall and spring, average rainfall drops below the evaporative demand. The estimated value of $\bar{Q}$ calculated from the climatic distributions was found to be 20.4 m$^3$/s, in close agreement with mean value of the entire record of the daily discharge data, 20.9 m$^3$/s.

**Prediction of temporal varying recharge**

Results from temporally varying $\bar{P}$ and $\bar{E}_0$ are given in Figure 5-10. $\bar{P}$ has declined substantially over the past 50 years, only recently starting to show an upward trend. $\bar{E}_0$ increased from 1960 to 1970, decreased from 1970 to 2000, and has been steadily increasing since that time. The magnitude of shifts observed in $\bar{P}$ were approximately 0.5 mm/day, while they were on the order of 0.1 mm/day for $\bar{E}_0$. Notably, $\bar{P}$ became less than $\bar{E}_0$ around the year 2000, by definition shifting the springshed from a humid climate to an arid one. In recent years, $\bar{P}$ has become slightly larger than $\bar{E}_0$. Temporal variation in $\bar{P}$ and $\bar{E}_0$ are shown in Figure 5-11. From 1960 to 1990, the timing of the center of mass of $P$ has shifted about 10 days earlier. Since 1990, $\bar{P}$ has been shifting back to later in
the year. During this time, the timing of $\overline{E_0}$ has remained relatively stable, with a shift of 1 day later in the year. Results from the comparison of the temporally varying predicted fraction of rain becoming recharge to the temporally varying observed fraction of rain becoming spring discharge are given in Figure 5-12.

Discussion

Linking Spring Discharge to Above Canopy Flow Velocity

Discharge-dependent above canopy flow velocities

The close agreement of the predicted and measured velocity profiles in Figures 5-5 and 5-6 suggest that both the velocity profile model and parameterization are valid representations of the physical system, providing confidence in the subsequent models. It is perhaps unsurprising that there would be a critical threshold discharge associated with the Chapter 4 critical velocity thresholds, since velocity and discharge are often closely related. However, this is not always the case, particularly when there is significant hydraulic control in the form of another water body. The upper reach of the Silver River is relatively isolated from its tail water boundary compared to the lower reach, which is significantly controlled by the tail water head (UFWI 2017).

It is also not surprising that the critical threshold discharge value, $\sim 15.5 \text{ m}^3/\text{s}$, was historically absent from or rarely seen in the early discharge record. Algal proliferation is a relatively recent phenomena, and if the driver is a reduction in hydraulic control, it would be expected that in historic discharge would almost always exceed the critical threshold. Under the current flow regime, there appear to be significant periods of time when algae can proliferate, but
there are almost equally significant times when algae should be removed, as is likely the case currently given the relatively high discharge (Figure 5-8).

**Linking Climatic Shifts to Spring Discharge**

**Prediction of long-term discharge**

The close agreement of the estimated value of $\bar{Q}$ calculated from the climatic distributions, 20.4 m$^3$/s, to the mean value of the entire record of the daily discharge data, 20.9 m$^3$/s, suggests that the methodology developed in Chapter 2 is valid to apply to springshed, if the period is sufficiently long. One of the key assumptions of the Budyko framework is that the changes in storage are zero over the long term. However, in large groundwater systems such as the Floridan Aquifer and its associated springs it is not obvious that this assumption should hold true. Critically, this calculation of discharge depends linearly on the area of the springshed. Springsheds are dynamic boundaries defined by groundwater heads rather than elevation for surface catchments.

**Prediction of temporal varying recharge**

Figures 5-10, 5-11, and 5-12 are particularly interesting in the context of attributing causes of observed declines in spring discharge. From Figure 5-10 it is obvious that rainfall has decreased at a much higher rate than potential evaporation, and therefore recharge must have declined in this time period. Ultimately, spring discharge is limited by recharge into the springshed. If recharge declines, eventually spring discharge will decline. Other processes may buffer this process or amplify it, but ultimately the control on discharge is the recharge. Therefore, the large decline in rainfall would suggest a significant decline in discharge. However, due to the corresponding decline in potential
evapotranspiration, recharge did not decrease as much as would be expected from the decrease in rainfall. The apparent cyclical nature of the patterns in both $\bar{P}$ and $\bar{E_0}$ suggest a large scale climatic phenomena impacting both of these processes.

In Figure 5-12, it is evident that fraction of rain becoming spring discharge does not track well with the fraction of rain becoming recharge. In fact they almost appear to be negatively correlated. This suggests other physical mechanisms, such as deep aquifer storage, must be taken into account to fully understand the connection between aquifer recharge and spring discharge.

**Summary and Conclusions**

In this chapter, I synthesized the models, methodologies and results from Chapters 2, 3, and 4 into a multiscale modeling framework to investigate the hypothesis that primary producer community shifts observed in the Silver River have been driven by a reduction in the hydraulic control of algal abundance, which was induced by declines in spring discharge, which in turn was caused by climatic changes within the springshed. Using dye trace data from the reach scale, I was able to create a relationship between discharge and the local velocities experienced by the primary producer community. This relationship allowed me to determine a critical threshold discharge. I compared this threshold to the discharge time series of the Silver River and found that in recent times discharge levels drop below this level regularly, when historically they had not. The time frame in which this transition occurred coincides with the appearance of increased algal abundance the algal proliferation by reduction in the hydraulic control hypothesis. I also investigated causes of the observed discharge declines.
by analyzing climatic driver of aquifer recharge at the spring shed scale. From the analysis presented, it is obvious the rainfall and subsequently recharge has decreased sustainably over the past 50 years, and therefore must be one of the primary reasons driving declines in spring discharge. However, time-varying average recharge and spring discharge are not well correlated, suggesting the need for additional investigation.

Figure 5-1. Silver River reach used in this study. The white line within the channel represents the centerline of the river. Due North is vertical in the image.
Figure 5-2. Breakthrough curves for the four dye traces conducted on the upper reach with their associated discharges.
Figure 5-3. Plot of $Q$ vs. $A_r$. The relationship between the cross sectional area of the the Silver River upper reach has a near linear relationship with discharge.

Figure 5-4. Stage-discharge curve for the Silver River for years 2000-2018. Over the entire range of current discharge values, the relationship can be approximated by a linear function.
Figure 5-5. Comparison of a predicted Silver River velocity profile (black) to measured velocity profile (red) for a depth of 2 meters. Solid red lines represent the mean, while dotted lines represent plus and minus one standard deviation.
Figure 5-6. Comparison of a predicted Silver River velocity profile (black) to measured velocity profile (red) for a depth of 1.2 meters. Solid red lines represent the mean, while dotted lines represent plus and minus one standard deviation.
Figure 5-7. $v_m(H(Q))$ vs. $Q$ for a range of discharges (solid blue curve). Critical threshold velocities identified in Chapter 4 are shown as horizontal lines. The solid red line corresponds to the overall mean critical threshold or 0.22 m/s, with the dotted red lines corresponding to the 95% credible intervals. The green solid line corresponds to the experimental determine threshold from the Silver River, and the black solid line corresponds to the threshold identified for filamentous algae growing on VP.
Figure 5-8. Comparison of the critical threshold discharge (red), 15.5 m$^3$/s, to the Silver River discharge time series (blue). Dotted red lines correspond to the 95% credible interval. During the year 2000, discharge transitioned from typically being about the threshold discharge to typically being below the threshold discharge.
Figure 5-9. Long-term rainfall (blue) and potential evapotranspiration (red) distributions for the Silver River springshed.
Figure 5-10. Temporally varying $\bar{P}$ (blue) and $\bar{E}_0$ (red) for the Silver River springshed.
Figure 5-11. Timing of the temporally varying $\bar{P}$ (blue) and $\bar{E}_0$ (red) for the Silver River springshed.
Figure 5-12. Comparison of temporally varying predicted fraction of rain becoming recharge, $\frac{P - E}{P}$, (green) to temporally varying observed fraction of rain becoming spring discharge (blue), for the Silver River springshed.
The declining health of many of Florida’s springs and spring-fed rivers is of significant concern to many Floridians, which has resulted in large efforts for restore these iconic and unique Florida ecosystems. Understanding the fundamental drivers and processes of these ecosystems is a necessary component of taking management actions for restoration. Substantial research effort has been directed at uncovering the causes of the observed degradation, resulting in a much greater understanding of these systems and how to better manage them. However, there are still many questions about the drivers of flow declines and changes in primary producer structure. To answer some of these questions, this study took a multiscale modeling approach to trace causal threads from the landscape scale to the scale of individual organism. Through the course of this work I was able to draw causal link between spring discharge and primary producer structure while also providing general contributions to landscape hydrology, reach scale hydrology and solute transport, and the hydrodynamics of aquatic vegetation.

The work described in Chapter 2 extends the landscape hydrology methodology of the Budyko framework by increasing its predictive power to estimate evapotranspiration and discharge from a catchment without increasing the data burden. Additionally, it provides a physical mechanism and explanation for why the semi-empirical “Budyko curve” behavior is observed in catchments around the world. Notably, the framework developed in this chapter excludes any land surface effects on the partitioning of rainfall into evapotranspiration and stream discharge as they appear to be second order effects. Future extensions
of this work could quantify the relative importance of various landscape processes on the discharge generation process. In particular focusing on human-altered landscapes and the incorporating the effects of precipitation in the form of snow.

In Chapter 3, I presented work linking the concept of reach-scale transient storage to measureable biophysical features, through the use hydraulic tracer experiments. My findings show that locations and geometry transient storage may not be immediately obvious or simply derived from a causal survey of geomorphic features but their probability of occurrence can be predicted a priori. As I discussed within the chapter, future research could focus on the use of transient storage zone predictive models coupled with stream ecosystem models to better simulate their interactions with their hydraulic environment. Two promising areas where this coupling could be applied are nutrient uptake models (e.g. nitrate) ecosystem respiration models (e.g. primary production and respiration).

The work presented in Chapter 4 connected reach scale hydraulic processes to primary producer community structure and dynamics. I demonstrated observationally and experimentally that algae growing periphytically (i.e. on submerged macrophytes) have a critical threshold behavior, with lower abundances occurring with the above canopy flow velocity exceeds ~0.22 m/s. This provides a well-defined potential management target for the control of algae in many springs. However, increasing reach scale flow velocities is likely only practical through the increase of spring discharge. The theoretical model I developed to explain the observed critical threshold behavior also
predicts a threshold value of ~0.22 m/s, when parameterized with typical values for spring run macrophytes. Possible extensions of this work would be to observationally and experimentally verify the theoretical monami mechanism I proposed. This could likely be easily verified (or disproven) with observational measurements in the spring runs or tested within a laboratory flume.

The multiscale modeling framework I presented in Chapter 5 connected methodologies and results from each of the other somewhat disparate chapters to investigate causes of algal proliferation in the Silver River. In this work I developed a critical threshold discharge for algal abundance in the upper Silver River associated with the critical threshold velocity described in Chapter 4. It is clear that in recent decades, the discharge of the Silver River has regularly dropped below this threshold, suggesting that observed algal proliferation likely is related. Possible extensions of this work would be regular field monitoring of algal abundance, particularly when the Silver River discharge is near this critical threshold.

While the analysis on changes in climatic drivers in the Silver River springshed suggest that overall recharge has declined significantly due to changes in the distributions of rainfall and potential evapotranspiration, it was unable to explain all of the observed behavior and decline seen in the spring discharge. To further explore the drivers of the discharge declines in the Silver River, I propose a multiple hypothesis testing methodology in which several hypotheses are modeled independently and then coupled together into a single model. For this processes to be successful, it will be important to diagnose “fingerprint” signatures of each hypothesis on measurable quantities, such as
spring discharge volumes or water table elevations in the aquifer. Comparison of these hypothesis “fingerprint” signatures to measurements over the period of available data will likely allow for the rejection of some hypothesis and for the quantification of the likelihood of the remaining hypothesized mechanisms driving observed declines in spring discharge.

Another complementary research effort would be the application of dynamic system theory and data driven modeling spring ecosystems. A spring ecosystem model of sufficient complexity would be able to test all of the proposed hypotheses and measure their likely effects. Additionally, by applying the tools of dynamic system analysis (i.e. finding fixed points, bifurcations, phase space reconstruction with empirical data), it may be possible to assess what the possible behaviors the primary producer community structure of a spring run ecosystem could have, restricting the number of plausible hypotheses. Additionally, there is a wealth of historic data, studies, and models on spring ecosystems that could inform this process.

This dissertation was motivated by the hypothesis that shifts in primary producer communities are being caused by a reduction in the hydraulic control of algal abundance, and that this shift could be causally linked through multiple spatially and temporal scales to changes in landscape hydrologic processes. The work presented strongly supports that the hypothesis that the hydraulic control of algal abundance, and tentatively supports causal linkage to changes in landscape hydrology. Further research will be required to strengthen that claim.
APPENDIX A
SUPPORTING INFORMATION FOR CHAPTER 2

Overview

I have included several items to support Chapter 2. They are as follows:

- Figure A-1 demonstrates how the parametric Budyko equations describe a family of curves within Budyko space.
- Table A-1 lists all of the studies that have developed relationships for the catchment-specific parameter, \( n \) or \( w \), in terms of biophysical features, as well as their explicit equations, known to the author.
- Table A-2 lists the explicit equations to calculate potential evaporation for the three methods used in Chapter 2.
- Text A-1, Figure A-2, and Table A-3 present a complete derivation of the analytical solutions for \( n \) and \( w \) in terms of \( E \), \( P \), and \( E_0 \) (i.e. Equations 2-11 and 2-12 in Chapter 2).
- Text A-2 and Figures A-3 to A-6 provide descriptions and demonstrations of the mathematical behavior of the analytical solutions for \( n \) and \( w \).

Text A-1

Here we develop analytical solutions for the two parametric forms of the Budyko equation. The steps for these derivations are:

- Produce a general form for both parametric forms of the Budyko equation.
- Determine the Mellin transform for the general form.
- Manipulate the Mellin transformed general form into known functions.
- Take the inverse Mellin transform of the general form to find a general solution.
- Substitute the specific functional forms of each parametric Budyko equation into the general solution to produce explicit expressions for \( n \) and \( w \).

Producing a General Form for Both Parametric Forms of the Budyko Equation

We start with the first parametric Budyko Equation,
\[
\frac{\bar{E}}{\bar{P}} = \frac{\frac{\bar{E}}{\bar{P}}}{1 + \left(\frac{\bar{E}}{\bar{P}}\right)^n}^{\frac{1}{n}} \quad (A-1)
\]

where \( n \) is the catchment specific parameter. Equation A-1 can be rearranged to,

\[
\left(\frac{\bar{E}}{\bar{P}}\right)^n - \left(\frac{\bar{E}}{\bar{P}}\right)^n = 1 \quad (A-2)
\]

Equation S2 is can be algebraically manipulated to the following,

\[
\left(\frac{\bar{E}}{\bar{P}}\right)^n - \left(\frac{\bar{E}}{\bar{P}}\right)^n = \left(e^{\ln\left(\frac{\bar{E}}{\bar{P}}\right)}\right)^n - \left(e^{\ln\left(\frac{\bar{E}}{\bar{P}}\right)}\right)^n = e^{n\ln\left(\frac{\bar{E}}{\bar{P}}\right)} - e^{n\ln\left(\frac{\bar{E}}{\bar{P}}\right)} = 1 \quad (A-3)
\]

Which leads to,

\[
(e^n)^{\ln\left(\frac{\bar{E}}{\bar{P}}\right)} - (e^n)^{\ln\left(\frac{\bar{E}}{\bar{P}}\right)} = 1 \quad (A-4)
\]

Using the same methodology given above, an alternative form of Equation A-1,

\[
\frac{\bar{E}}{\bar{E}_0} = \frac{\bar{P}}{\bar{E}_0} \left[1 + \left(\frac{\bar{P}}{\bar{E}_0}\right)^n\right]^{\frac{1}{n}} \quad (A-5)
\]

can be made into,

\[
(e^n)^{\ln\left(\frac{\bar{E}}{\bar{E}_0}\right)} - (e^n)^{\ln\left(\frac{\bar{E}}{\bar{E}_0}\right)} = 1 \quad (A-6)
\]

Next we take the other form of the parametric Budyko Equation,

\[
\frac{\bar{E}}{\bar{P}} = 1 + \frac{\bar{E}_0}{\bar{P}} - \left(1 + \left(\frac{\bar{E}_0}{\bar{P}}\right)^w\right)^{\frac{1}{w}} \quad (A-7)
\]

where \( w \) is the catchment specific parameter. Equation A-7 can be rearranged to,

\[
\left(\frac{\bar{E}_0 + \bar{P} - \bar{E}}{\bar{P}}\right)^w - \left(\frac{\bar{E}_0}{\bar{P}}\right)^w = 1 \quad (A-8)
\]

Equation A-8 is algebraically manipulated to the following,
\[
\left( \frac{E_0 + \bar{P} - \bar{E}}{\bar{P}} \right)^w - \left( \frac{E_0}{\bar{P}} \right)^w = \left( e^{\ln \left( \frac{E_0 + \bar{P} - \bar{E}}{\bar{P}} \right)} \right)^w - \left( e^{\ln \left( \frac{E_0}{\bar{P}} \right)} \right)^w
\]
(A-9)

\[
e^{w \ln \left( \frac{E_0 + \bar{P} - \bar{E}}{\bar{P}} \right)} - e^{w \ln \left( \frac{E_0}{\bar{P}} \right)} = 1
\]

which leads to,

\[
(e^w)^{\ln \left( \frac{E_0 + \bar{P} - \bar{E}}{\bar{P}} \right)} - (e^w)^{\ln \left( \frac{E_0}{\bar{P}} \right)} = 1
\]
(A-10)

Using the same methodology given above, an alternative form of Equation A-7,

\[
\frac{\bar{E}}{E_0} = 1 + \frac{\bar{P}}{E_0} - \left( 1 + \left( \frac{\bar{P}}{E_0} \right)^w \right)^{\frac{1}{w}}
\]
(A-11)

can be made into,

\[
(e^w)^{\ln \left( \frac{E_0 + \bar{P} - \bar{E}}{E_0} \right)} - (e^w)^{\ln \left( \frac{\bar{P}}{E_0} \right)} = 1
\]
(A-12)

Equations A-4, A-6, A-10, and A-12 are all specific examples of a general form,

\[
y^C + zy^D = 1
\]
(A-13)

where $C$ and $D$ are constants, $z$ is an arbitrary numeric variable, and $y$ is a function of $z$. For later steps in this derivation we require $C > D > 0$. This condition holds true for Equations A-4 and A-10 for arid climates (i.e. $E_0 > \bar{P}$), and Equations A-6 and A-12 for humid climates (i.e. $E_0 < \bar{P}$; Table A-3). We use the general form, Equation A-13, and the condition, $C > D > 0$, to derive a general solution which will allow for specific solutions of $n$ and $w$.

**The Mellin Transform for $y(z)$**

The Mellin transform for $y(z)$, of Equation A-13, is,

\[
Y(s) = \int_0^\infty z^{s-1}y(z)dz
\]
(A-14)

156
where $s$ is a complex number. The Mellin transform is closely related to the Laplace transform. Whether the improper integral in Equation A-14 converges or diverges depends on the behavior of $y(z)$. For Equation A-13 to hold true, $y(0) = 1$. Taking the first derivative of Equation A-13 gives,

$$
\frac{dy}{dz} = \frac{-y^D}{Cy^{C-1} + zDy^{D-1}} \tag{A-15}
$$

Since $C > D > 0$, Equation A-15 is always negative, meaning that $y(z)$ is a monotonically decreasing function for $0 \leq z < \infty$. Additionally, $y(z) = 0$ is not a valid solution to Equation A-13. Therefore, $1 \geq y(z) > 0$ for $0 \leq z < \infty$. As $z \to \infty$, $y(z)$ will become very small. This allows us to rearrange Equation A-13 to get an approximate functional form for $y(z)$ for large values of $z$,

$$
y^D = \frac{1 - y^C}{z} \approx \frac{1}{z} \tag{A-16}
$$

therefore,

$$
y(z) \approx z^{-\frac{1}{D}} \tag{A-17}
$$

Inserting Equation A-17 into the integrand of Equation A-14 results in,

$$
z^{s-1}y(z) \approx z^{s-\frac{1}{D}-1} \tag{A-18}
$$

The integrand is in the general form, $z^{-p}$, so we can use the “p-test” for convergence of improper integrals to determine if Equation S14 will converge as $z \to \infty$. For large $z$, Equation A-14 is a Type 1 improper integral. The “p-test” states that if $p > 1$, the integral converges, while if $p \leq 1$, the integral will be divergent. We can use the exponent in Equation A-18 and the “p-test” to determine what values of $s$ will allow Equation A-14 to converge. Specifically, we solve the inequality,
\[ s - \frac{1}{D} - 1 < -1 \]  
\[ (A-19) \]

which gives,

\[ s < \frac{1}{D} \]  
\[ (A-20) \]

This means Equation A-14 converges and the Mellin transform exists if the real part of \( s < \frac{1}{D} \).

**Mellin Transformed \( y(z) \) in Terms of Known Functions**

Now that we know the conditions under which Equation A-14 is valid, we can evaluate it explicitly. To do this, we switch the integration from \( z \) to \( y \), using Equation S13. This involves expressing \( z \) in terms of \( y \),

\[ z = y^D - y^{C-D} \]  
\[ (A-21) \]

expressing \( dz \) in terms of \( y \) and \( dy \),

\[ dz = -[Dy^{-D-1} + (C - D)y^{C-D-1}]dy \]  
\[ (A-22) \]

and expressing the limits of integration in terms of \( y \),

\[ \text{when } z = 0, \quad y = 1 \]  
\[ \text{when } z \to \infty, \quad y \to 0 \]  
\[ (A-23) \]

We can now rewrite Equation S14 in terms of a \( y \) integration,

\[ Y(s) = -\int_{0}^{1} y(y^{-D} - y^{C-D})^{s-1}[Dy^{-D-1} + (C - D)y^{C-D-1}]dy \]  
\[ (A-24) \]

which can be rearranged to,

\[ Y(s) = D \int_{0}^{1} y^{-Ds}(1 - y^{C})^{s-1}dy + (C - D) \int_{0}^{1} y^{-Ds+C}(1 - y^{C})^{s-1}dy \]  
\[ (A-25) \]

If we make the substitution \( y^{C} = u \), we have,
\[ dy = \frac{1}{c} y^{-c+1} du = \frac{1}{c} u^{\frac{1}{c} - 1} du \]  \hspace{1cm} (A-26)

and the limits of integration remain the same,

\[ \text{when } y = 0, \quad u = 0 \]
\[ \text{when } y = 1, \quad u = 1 \]  \hspace{1cm} (A-27)

and Equation A-25 becomes,

\[ Y(s) = \frac{D}{C} \int_{0}^{1} u^{\frac{1-Ds}{c}} (1-u)^{s-1} du + \frac{C-D}{C} \int_{0}^{1} u^{\frac{1-Ds}{c}+1-1} (1-u)^{s-1} du \]  \hspace{1cm} (A-28)

The integrals in Equation A-28 are the same form as the integral definition of the Beta function, allowing us to express \( Y(s) \) as a sum of Beta functions,

\[ Y(s) = \left[ \frac{D}{C} B \left( \frac{1-Ds}{C}, s \right) \right] \left[ \frac{C-D}{C} B \left( \frac{1-Ds}{C} + 1, s \right) \right] \]  \hspace{1cm} (A-29)

where \( B(\ , \ ) \) is the Beta function. The Beta function in turn can also be defined in terms of the Gamma function (i.e. \( B(q, L) = \frac{\Gamma(q) \Gamma(L)}{\Gamma(q+L)} \)), allowing us to rewrite Equation A-29 as,

\[ Y(s) = \left[ \frac{D}{C} \frac{\Gamma \left( \frac{1-Ds}{C} \right) \Gamma(s)}{\Gamma \left( \frac{1-Ds}{C} + s \right)} \right] \left[ \frac{C-D}{C} \frac{\Gamma \left( \frac{1-Ds}{C} + 1 \right) \Gamma(s)}{\Gamma \left( \frac{1-Ds}{C} + 1 + s \right)} \right] \]  \hspace{1cm} (A-30)

where \( \Gamma(\ ) \) is the Gamma function. The Gamma function has the property,

\( \Gamma(q + 1) = q \Gamma(q) \), which allows us to simplify Equation A-30 to,

\[ Y(s) = \left[ \frac{\Gamma(s)}{C} \right] \left[ \frac{D \Gamma \left( \frac{1-Ds}{C} + s \right) \Gamma \left( \frac{1-Ds}{C} \right)}{\Gamma \left( \frac{1-Ds}{C} + 1 + s \right)} + \frac{(C-D) \Gamma \left( \frac{1-Ds}{C} + 1 \right) \Gamma \left( \frac{1-Ds}{C} \right)}{\Gamma \left( \frac{1-Ds}{C} + 1 + s \right)} \]  \hspace{1cm} (A-31)

which further becomes,

\[ Y(s) = \left[ \frac{\Gamma(s)}{C} \right] \left[ \frac{sD \Gamma \left( \frac{1-Ds}{C} \right) + C \left( \frac{1-Ds}{C} \right) \Gamma \left( \frac{1-Ds}{C} \right) \Gamma \left( \frac{1-Ds}{C} + 1 + s \right)}{\Gamma \left( \frac{1-Ds}{C} + 1 + s \right)} \right] \]  \hspace{1cm} (A-32)
which becomes,

\[
Y(s) = \left[ \Gamma(s) \Gamma \left( \frac{1 - Ds}{C} \right) \right] \left[ \frac{1 - Ds + Ds}{\Gamma \left( \frac{1 - Ds}{C} + 1 + s \right)} \right]
\]  

(A-33)

which becomes,

\[
Y(s) = \frac{\Gamma(s) \Gamma \left( \frac{1 - Ds}{C} \right)}{C \Gamma \left( \frac{1 - Ds}{C} + 1 + s \right)}
\]  

(A-34)

The Inverse Mellin Transform and Solution for \(y(z)\)

We now can use Equation A-34 to take the inverse Mellin transform and solve for \(y(z)\) explicitly. The inverse Mellin transform is defined as,

\[
y(z) = \frac{1}{2\pi i} \int_{k - \infty i}^{k + \infty i} Y(s) z^{-s} ds
\]  

(A-35)

where \(i = \sqrt{-1}\) and the integral from \(k - \infty i\) to \(k + \infty i\) is interpreted as a line integral along a vertical line in the complex plane. For our specific function the inverse Mellin transform is,

\[
y(z) = \frac{1}{2\pi i} \int_{k - \infty i}^{k + \infty i} z^{-s} \Gamma(s) \Gamma \left( \frac{1 - Ds}{C} \right) ds \text{ where } 0 < k < \frac{1}{D}
\]  

(A-36)

The constraint \(0 < k < \frac{1}{D}\) is due to the constraints on \(s\) that were established previously so that Equation A-14 would converge. What this means is the vertical line in the complex plane over which the line integral is taken must fall between 0 and \(\frac{1}{D}\) on the real axis (Figure A-2). We evaluate the integral in Equation A-36 to find an explicit form of \(y(z)\) using the following methodology:

- We define an appropriate contour in the complex plane to perform a contour integration of \(Y(s)z^{-s}\).
• We use residue integration to evaluate the value of this contour integral.

• We show that the only part of this contour that does not vanish is the line integral defined in Equation A-36, meaning the inverse Mellin transform, and therefore $y(z)$, is equal to the value of the contour integral evaluated in the previous residue integration step.

First, we choose a semicircle contour in the complex plane, with the straight portion as a vertical line crossing the real axis at $k$, and the circular portion connecting the ends of this line across the left side of the complex plane (Figure A-2). This contour is consistent with the constraints on $s$ that were established previously so Equation A-14 would converge. We can now define the integral of $Y(s)z^{-s}$ over this contour,

$$\Lambda(z) = \oint Y(s)z^{-s} ds$$

(A-37)

$\Lambda(z)$ can also be expressed as the sum of two line integrals, one over the vertical line portion of the contour, and one over the circular arc portion of the contour,

$$\Lambda(z) = \int_{k-Ri}^{k+Ri} Y(s)z^{-s} ds + \int_{arc} Y(s)z^{-s} ds$$

(A-38)

where $R$ is the radius of the semicircle contour. If we allow $R \to \infty$, we get the following,

$$\Lambda(z) = \int_{k-\infty i}^{k+\infty i} Y(s)z^{-s} ds + \int_{arc} Y(s)z^{-s} ds$$

(A-39)

We can now evaluate $\Lambda(z)$ over the infinitely large contour using residue integration. Residue integration relates the value of a contour integral to the sum of the residues of the function being integrated. Residues occur when the function of interest has singularities within the contour. If we inspect $Y(s)z^{-s}$ (i.e. the integrand in Equation S36) inside the semicircle contour we defined, the only
component which has singularities is $\Gamma(s)$. $\Gamma(s)$ is undefined at and has simple poles at $s = -r$ where $r = 0, 1, 2, 3, \ldots \infty$. The residues of the gamma function for each value of $r$ are,

$$\text{Res}(\Gamma(s), -r) = \frac{(-1)^r}{r!}$$

(A-40)

Using the residue theorem we can evaluate $\Lambda(z)$

$$\Lambda(z) = \oint Y(s)z^{-s}ds = 2\pi i \sum \text{Res}(Y(s)z^{-s}, -r)$$

$$= 2\pi i \sum_{r=0}^{\infty} z^r \frac{(-1)^r \Gamma \left(\frac{1 + Dr}{C} \right)}{r! \Gamma \left(\frac{1 + Dr}{C} + 1 - r \right)}$$

(A-41)

which contains the sum over the infinite number of residues of $Y(s)z^{-s}$ within the semicircular contour. Substituting this solution into Equation A-39 gives,

$$\Lambda(z) = \int_{k-i\infty}^{k+i\infty} Y(s)z^{-s}ds + \int_{arc} Y(s)z^{-s}ds = 2\pi i \sum_{r=0}^{\infty} z^r \frac{(-1)^r \Gamma \left(\frac{1 + Dr}{C} \right)}{r! \Gamma \left(\frac{1 + Dr}{C} + 1 - r \right)}$$

(A-42)

We have just evaluated the line integral of $Y(s)z^{-s}$ for the entire contour; now we investigate the contribution of the line integral over just the circular arc portion of the contour. Using the estimation lemma, we can write the following inequality for the line integral over the arc,

$$\left| \int_{arc} Y(s)z^{-s}ds \right| \leq ML$$

(A-43)

where $L$ is the length of the arc and $M$ is the maximum value of $|Y(s)z^{-s}|$ along the length of the arc. The complex number $s$ can be written as the sum of its real and imaginary parts, $s = a + bi$. The length of the arc is defined as the product of the central angle and radius of the circle,
\[ L = \pi R = \pi \sqrt{a^2 + b^2} \]  
\[ \text{(A-44)} \]

We can write \(|Y(s)z^{-s}|\) as,
\[ |Y(s)z^{-s}| = \frac{|z^{-s}| |\Gamma(s)| \left| \Gamma\left(\frac{1-DS}{C}\right) \right|}{C |\Gamma\left(\frac{1-DS}{C} + 1 + s\right)|} \]
\[ \text{(A-45)} \]

Since we are interested in the value of \(|Y(s)z^{-s}|\) as \(R \to \infty\), we can approximate the absolute values of the gamma functions using Stirling’s approximation, which is valid for large values of \(s\),
\[ |\Gamma(s)| = |\Gamma(a + bi)| \approx \sqrt{2\pi e^{-\frac{\pi|b|}{2}}} |b|^a e^{-\frac{\pi}{2}b} \]
\[ \text{(A-46)} \]

Applying Stirling’s approximation to Equation A-45 yields,
\[ |Y(s)z^{-s}| \approx \frac{|z^{-a-b}\left(\sqrt{2\pi e^{-\frac{\pi|b|}{2}}} |b|^a e^{-\frac{\pi}{2}b}\right)^{\left(c+1-D\right)\left(\frac{1-a}{2}\right)}}{C \left(1 - \frac{D}{C}\right)^{\left(c+1-D\right)\left(\frac{1-a}{2}\right)}} \]
\[ \text{(A-47)} \]

Which becomes
\[ \frac{\sqrt{2\pi z^{-a-b}e^{-\frac{\pi b}{2}}}}{CD - Dz} z^{-a} e^{-\frac{\pi Db}{2}} \left(D\frac{1-a}{c}\right)^{\left(c+1-D\right)\left(\frac{1-a}{2}\right)}} \]
\[ \text{(A-48)} \]

and,
\[ \frac{\sqrt{2\pi}}{CD - Dz} z^{-a} e^{-\frac{\pi Db}{2}} \left(D\frac{1-a}{c}\right)^{\left(c+1-D\right)\left(\frac{1-a}{2}\right)}} \]
\[ \text{(A-49)} \]

resulting in,
If we inspect Equation A-50, we see that $|Y(s)z^{-s}|$ decreases as $|b|$ increases and $|Y(s)z^{-s}|$ increases as $a$ increases. Therefore, $M$ occurs at the start and end point of the arc, where $a = k$. When $a = k$, letting $R \to \infty$ is equivalent to letting $|b| \to \infty$, allowing us to evaluate $ML$,

$$ML = \lim_{|b| \to \infty} \pi\sqrt{k^2 + b^2} \left[ \frac{2\pi}{\sqrt{CD - D^2}} \right] \left[ \frac{D}{C} \frac{(1-D)}{c} \right] \left[ \frac{e^{-\pi Db}}{C} \right] b^{-\frac{3}{2}} = 0 \quad (A-51)$$

We now know that the contribution the circular arc portion of the contour vanishes,

$$0 \leq \left| \int_{arc} Y(s)z^{-s} \, ds \right| \leq ML = 0 \quad (A-52)$$

which means,

$$\int_{arc} Y(s)z^{-s} \, ds = \left| \int_{arc} Y(s)z^{-s} \, ds \right| = 0 \quad (A-53)$$

And therefore,

$$y(z) = \frac{1}{2\pi i} \text{A}(z) = \frac{1}{2\pi i} \int_{k - \infty i}^{k + \infty i} Y(s)z^{-s} \, ds = \sum_{r=0}^{\infty} \frac{z^r (-1)^r \Gamma \left( \frac{1 + Dr}{C} \right)}{r! \Gamma \left( \frac{1 + Dr}{C} + 1 - r \right)} \quad (A-54)$$

which is the solution to the general form, Equation A-13.
Specific Functional Forms of Each Parametric Budyko Equation

By comparing the specific forms of the parametric Budyko equations (i.e. Equations A-4, A-6, A-10, and A-12) to the general form, Equation A-13, we see that \( z = -1 \) for all of them. We substitute \( z = -1 \) into Equation A-54 to produce,

\[
y(-1) = \sum_{r=0}^{\infty} \frac{(-1)^{2r}}{r!} \Gamma \left( \frac{1 + Dr}{C} + 1 - r \right) = \frac{1}{C} \sum_{r=0}^{\infty} \Gamma(r+1) \Gamma \left( \frac{1 + Dr}{C} + 1 - r \right)
\]

Substitution of the appropriate \( y \) (i.e. \( e^n \) or \( e^w \)), \( C \), and \( D \) (Table A-3) into Equation A-55 yields the analytical solutions for the two parametric forms of the Budyko equation. Specifically these are:

\( n \) for arid climates, \( \overline{E_0} > \overline{P} \),

\[
n = \ln \left[ \frac{1}{\ln \left( \frac{\overline{E_0}}{\overline{E}} \right)} \sum_{r=0}^{\infty} \frac{\Gamma\left( \frac{1 + \ln \left( \frac{\overline{E_0}}{\overline{E}} \right) r}{\ln \left( \frac{\overline{E_0}}{\overline{E}} \right)} \right)}{\Gamma(r+1) \Gamma \left( \frac{1 + \ln \left( \frac{\overline{E_0}}{\overline{E}} \right) r}{\ln \left( \frac{\overline{E_0}}{\overline{E}} \right)} + 1 - r \right)} \right]
\]

\( n \) for humid climates, \( \overline{E_0} < \overline{P} \),

\[
n = \ln \left[ \frac{1}{\ln \left( \frac{\overline{P}}{\overline{E}} \right)} \sum_{r=0}^{\infty} \frac{\Gamma\left( \frac{1 + \ln \left( \frac{\overline{P}}{\overline{E}} \right) r}{\ln \left( \frac{\overline{P}}{\overline{E}} \right)} \right)}{\Gamma(r+1) \Gamma \left( \frac{1 + \ln \left( \frac{\overline{P}}{\overline{E}} \right) r}{\ln \left( \frac{\overline{P}}{\overline{E}} \right)} + 1 - r \right)} \right]
\]

\( w \) for arid climates, \( \overline{E_0} > \overline{P} \),
\[ w = \ln \left[ \frac{1}{\ln \left( \frac{E_0 + \bar{P} - \bar{E}}{\bar{P}} \right)} \sum_{r=0}^{\infty} \frac{\Gamma \left( 1 + \ln \left( \frac{\bar{P}}{E_0} \right) r \right)}{\ln \left( \frac{E_0 + \bar{P} - \bar{E}}{\bar{P}} \right)} \right] \]

\[ w = \ln \left[ \frac{1}{\ln \left( \frac{\bar{P}}{E_0} \right)} \sum_{r=0}^{\infty} \frac{\Gamma \left( 1 + \ln \left( \frac{\bar{P}}{E_0} \right) r \right)}{\ln \left( \frac{E_0 + \bar{P} - \bar{E}}{E_0} \right)} \right] \]  

\[ w \text{ for humid climates, } \bar{E}_0 < \bar{P}, \]

For critical point catchments (i.e. where \( \bar{E}_0 = \bar{P} \)) the explicit solutions can be found by solving Equations A-4 (or A-6) and A-10 (or A-12) for \( n \) and \( w \), respectively. For Equation A-4 we have,

\[ (e^n)^{\ln \left( \frac{E_0}{E} \right)} - (e^n)^{(1)} = 1 \]  

which becomes,

\[ (e^n)^{\ln \left( \frac{E_0}{E} \right)} - 1 = 1 \]  

and,

\[ n = \frac{\ln(2)}{\ln \left( \frac{E_0}{E} \right)} = \frac{\ln(2)}{\ln \left( \frac{\bar{P}}{E} \right)} \]

Similarly, for Equation A-10 we have,

\[ (e^w)^{\ln \left( \frac{2 - \bar{E}}{\bar{P}} \right)} - (e^w)^{(1)} = 1 \]

which becomes,
\[(e^w)\ln\left(\frac{2 - \overline{E}}{\overline{P}}\right) - 1 = 1 \quad (A-64)\]

and,
\[w = \frac{\ln(2)}{\ln(2 - \overline{E})} = \frac{\ln(2)}{\ln(2 - \overline{P})} \quad (A-65)\]

**Text A-2**

Here we investigate the general mathematical properties of the analytical solutions for \(n\) and \(w\). First, we look at the behavior of Equations A-62 and A-65 as \(\overline{E} \to 0\) and \(\overline{E} \to \overline{E}_0\) or \(\overline{P}\). Mathematically, the values of \(n\) are constrained between 0 and \(\infty\), while the values of \(w\) are constrained between 1 and \(\infty\). Therefore, the upper and lower limits of Equations A-62 and A-65 should be equal to these respective constraints. The lower limit for Equations A-62,
\[\lim_{\overline{E} \to 0} n = \frac{\ln(2)}{\infty} = 0 \quad (A-66)\]

and the upper limit,
\[\lim_{\overline{E} \to \overline{E}_0} n = \lim_{\overline{E} \to \overline{P}} n = \frac{\ln(2)}{0} = \infty \quad (A-67)\]

both are equal to the lower and upper constraint for \(n\). Similarly, the lower limit for Equation S65,
\[\lim_{\overline{E} \to 0} w = \frac{\ln(2)}{\ln(2 - 0)} = 1 \quad (A-68)\]

and the upper limit,
\[\lim_{\overline{E} \to \overline{E}_0} w = \lim_{\overline{E} \to \overline{P}} w = \frac{\ln(2)}{\ln(2 - 1)} = \frac{\ln(2)}{0} = \infty \quad (A-69)\]

both are equal to the lower and upper constraint for \(w\).
Next, we investigate the validity of Equations A-56 to A-59. These equations contain convergent infinite series whose value asymptotically approaches $e^n$ or $e^w$ as $r \to \infty$. The behavior of the series’ terms (i.e. monotone decreasing or alternating and absolute value decreasing) depends on the specific values of $\bar{E}$, $\bar{P}$, and $\bar{E}_0$. We would like to verify that Equations A-56 to A-59 indeed produce the correct values of $n$ and $w$ given $\bar{E}$, $\bar{P}$, and $\bar{E}_0$. To do so, we first compute the “correct” value of $n$ and $w$. This is done by numerically solving for the zeros of Equation A-1 and A-7 for given $\bar{E}$, $\bar{P}$, and $\bar{E}_0$, specifically,

$$\frac{\bar{E}}{\bar{P}} - \frac{\bar{E}_0}{\bar{P}} \left[ 1 + \left( \frac{\bar{E}_0}{\bar{P}} \right)^{n_{\text{numeric}}} \right]^{n_{\text{numeric}}} = 0 \quad (A-70)$$

and,

$$\frac{\bar{E}}{\bar{P}} - 1 - \frac{\bar{E}_0}{\bar{P}} + \left( 1 + \left( \frac{\bar{E}_0}{\bar{P}} \right)^{w_{\text{numeric}}} \right)^{w_{\text{numeric}}} = 0 \quad (A-71)$$

We then compute approximations of Equations A-56 to A-59 using finite series with increasing numbers of terms. As the number of terms in the finite series increase, the approximations asymptotically converge to the numerically calculated “correct” values of $n$ and $w$ (Figures A-3 to A-6). This convergence gives strong numeric evidence that Equations A-56 to A-59 are valid analytical solutions for $n$ and $w$. 

168
Figure A-1. The parametric Budyko equation (i.e. Equation A-1 or Equation 2-4 in Chapter 2) plotted in Budyko space as a function of $\frac{E_0}{P}$ for different values of the catchment-specific parameter, $n$. Budyko space has coordinates of $\left(\frac{E_0}{P}, \frac{E}{P}\right)$. As the value of $n$ increases, more of the rainfall that falls in a catchment returns to the atmosphere via evapotranspiration. As $n$ approaches $\infty$, actual evapotranspiration approaches 100% of rainfall in arid, water-limited catchments (i.e., where $\frac{E_0}{P} > 1$), while actual evapotranspiration approaches potential evapotranspiration in humid, energy-limited catchments (i.e., where $\frac{E_0}{P} < 1$).
Table A-1. Existing relationships for the catchment-specific parameter in terms of biophysical features. Variables in each of the expressions are defined within the table. Complicated statistical expressions not amenable to tabulation are listed as a general function, $F(\cdot)$, of the statistically significant variables, with details available in the cited work.

<table>
<thead>
<tr>
<th>Functional Forms</th>
<th>Parameters</th>
<th>Methodology</th>
<th>Reference</th>
</tr>
</thead>
<tbody>
<tr>
<td>$w = 1 + 0.852\left(\frac{K_s}{C}\right)^{0.3046} \left(\frac{S_{ext}}{S_{sat}}\right)^{0.4476} e^{-0.644 \tan \beta}$ and $w = 2.947 - 0.55\left(\frac{K_s}{C}\right) + 0.882\left(\frac{S_{ext}}{S_{sat}}\right) - 2.096 \tan \beta$</td>
<td>$K_s$, saturated hydraulic conductivity $C$, mean precipitation intensity in 24 hours $S_{ext}$, plant extractable water capacity $S_{sat}$, mean annual potential evapotranspiration $\tan \beta$, average slope</td>
<td>Optimization of $w$ values to measured catchment $\bar{E}$, followed by stepwise regression analysis</td>
<td>[Yang et al., 2007]</td>
</tr>
<tr>
<td>$n = 5.755\left(\frac{K_s}{C}\right)^{0.3046} M^{0.208} e^{-1.428 \tan \beta}$ and $n = 2.721\left(\frac{K_s}{C}\right)^{0.3046} M^{-0.002} e^{4.551 \tan \beta}$</td>
<td>$K_s$, saturated hydraulic conductivity $C$, mean precipitation intensity in 24 hours $M$, vegetation coverage $\tan \beta$, average slope</td>
<td>Optimization of $n$ values to measured catchment $\bar{E}$, followed by stepwise regression analysis</td>
<td>[Yang et al., 2009]</td>
</tr>
<tr>
<td>$n = 0.21\left(\frac{K_s}{C}\right) + 0.60$</td>
<td>$x$, fractional plant-available water holding capacity $Z_r$, effective rooting depth $\alpha$, mean depth per storm event $PF C$, percentage of forest coverage $P F E$, number of months that peak precipitation follows peak potential evapotranspiration</td>
<td>Optimization of $n$ values to a soil moisture model at single aridity index value followed by linear regression</td>
<td>[Donohue et al., 2012]</td>
</tr>
<tr>
<td>$w = F(P F C, P F E, R r, A S D, C V_r)$</td>
<td>$R r$, relief ratio $A S D$, average storm depth $C V_r$, coefficient of variation of precipitation</td>
<td>Optimization of $w$ values to measured catchment $\bar{E}$, followed by multivariate adaptive regression splines (MARS)</td>
<td>[Shao et al., 2012]</td>
</tr>
<tr>
<td>$w = 2.36(M) + 1.16$</td>
<td>$M$, vegetation coverage</td>
<td>Optimization of $w$ values to measured catchment $\bar{E}$, followed by linear regression</td>
<td>[Li et al., 2013]</td>
</tr>
<tr>
<td>$w = (-0.0932)l a t + (0.1308)0.10097) N D V I$ $+ (0.00093)1 A$ $+ (-0.000018)\text{ele} v$ $+ 5.05722$ and $w = (-0.01842)l a t + (0.14618)0.10097$ $+ (2.81063)N D V I$ $+ 0.65387$</td>
<td>$l a t$, absolute latitude of basin center $l o n g$, basin center longitude $s l p$, slope gradient $C T I$, compound topographic index $N D V I$, normalized difference vegetation index</td>
<td>Optimization of $w$ values to measured catchment $\bar{E}$, followed by stepwise multiple linear regression (MLR)</td>
<td>[Xu et al., 2013]</td>
</tr>
<tr>
<td>$w = (-0.03288)l a t + (-0.09311)\text{ele} v$ $+ (1.12312)N D V I$ $+ (-0.00205)l o n g$ $+ (-0.0002)\text{ele} v$ $+ 3.50412$</td>
<td>$A$, drainage area $e l e v$, elevation</td>
<td></td>
<td></td>
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<tr>
<td>Functional Forms</td>
<td>Parameters</td>
<td>Methodology</td>
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<td>---------------------------------------------------------------------------------</td>
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<td>-------------------------------------------------</td>
<td>--------------------</td>
</tr>
<tr>
<td>$w = F(lat, slp, NDVI, long, elev)$</td>
<td>$\text{lat}$, absolute latitude of basin center</td>
<td>Optimization of $w$ values to measured catchment $\bar{E}$, followed by stepwise multiple linear regression (MLR) to select input variables to train a neural network</td>
<td>[Xu et al., 2013]</td>
</tr>
<tr>
<td></td>
<td>$\text{long}$, basin center longitude</td>
<td>NDVI, normalized difference vegetation index</td>
<td></td>
</tr>
<tr>
<td></td>
<td>$\text{slp}$, slope gradient</td>
<td>$\text{elev}$, elevation</td>
<td></td>
</tr>
<tr>
<td></td>
<td>$\text{lat}$, absolute latitude of basin center</td>
<td>Optimization of $w$ values to measured catchment $\bar{E}$, followed by stepwise multiple linear regression (MLR) to select input variables to train a neural network</td>
<td>[Xu et al., 2013]</td>
</tr>
<tr>
<td>$n = 0.7078 \left( \frac{kZ_r}{\bar{\alpha}} \right)^{\text{snows}}$</td>
<td>$k$, fractional plant-available water holding capacity</td>
<td>Optimization of $n$ values to a soil moisture model followed by curve fitting</td>
<td>[Cong et al., 2015]</td>
</tr>
<tr>
<td></td>
<td>$Z_r$, effective rooting depth</td>
<td>$\bar{\alpha}$, mean depth per storm event</td>
<td></td>
</tr>
<tr>
<td></td>
<td>$a$, mean depth per storm event</td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td>$AWC$, available soil water holding capacity</td>
<td>Optimization of $w$ values to measured catchment $\bar{E}$, followed by stepwise forward regression to build a generalized additive model</td>
<td>[Abatzoglou and Ficklin, 2017]</td>
</tr>
<tr>
<td>$w = F\left( \frac{A}{P}, rCMS, slope, SF \right)$</td>
<td>$A$, average storm depth</td>
<td>$rCMS$, relative cumulative moisture surplus</td>
<td></td>
</tr>
<tr>
<td></td>
<td>$P$, precipitation</td>
<td>$slope$, mean watershed slope</td>
<td></td>
</tr>
<tr>
<td></td>
<td>$SF$, fraction of annual precipitation falling as snow</td>
<td>Optimization of $w$ values to measured catchment $\bar{E}$, followed by stepwise forward regression to build a generalized additive model</td>
<td>[Abatzoglou and Ficklin, 2017]</td>
</tr>
<tr>
<td>$n = (2.10)CI + (-0.157)SIM + (-0.284)PDSI + (-1.203)SI + (-45.4)Rr + 1.299$</td>
<td>$CI$, precipitation concentration index</td>
<td>$SIM$, Milly's index of seasonality</td>
<td></td>
</tr>
<tr>
<td></td>
<td>$PDSI$, Palmer drought severity index</td>
<td>$SI$, seasonality index of precipitation</td>
<td></td>
</tr>
<tr>
<td></td>
<td>$Rr$, relief ratio</td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td>$M$, vegetation coverage</td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td>ASD, average storm depth</td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td>$CV$, coefficient of variation of precipitation</td>
<td>Optimization of $n$ values to measured catchment $\bar{E}$, followed by multivariate adaptive regression splines (MARS)</td>
<td>[Xing et al., 2018a]</td>
</tr>
<tr>
<td>$n = F(M, ASD, CV, SI, PDSI, IA, CA)$</td>
<td>$SI$, seasonality index of precipitation</td>
<td>$PDSI$, Palmer drought severity index</td>
<td></td>
</tr>
<tr>
<td></td>
<td>$IA$, effective irrigated area ratio</td>
<td>$CA$, cultivated land area ratio</td>
<td></td>
</tr>
</tbody>
</table>
Table A-2. Selected $E_0$ estimation methods. The units of $E_0$ for each method are mm/day. Variables in the expressions are defined as: $T_{\text{max}}$, maximum daily temperature (°C); $T_{\text{min}}$, minimum daily temperature (°C); $T_{\text{av}} = \frac{T_{\text{max}} + T_{\text{min}}}{2}$, average daily temperature (°C); $T_{\text{month}}$, average monthly temperature for each month, j (°C); $L_{\text{Lat}}$, catchment latitude in degrees; $J$, number of the day in the year (i.e. 1 for January 1\text{st} and 365 for December 31\text{st}); $N = \frac{24}{\pi} \arccos \left[ \tan \left( \frac{\pi}{180} L_{\text{Lat}} \right) \tan(\delta) \right]$, number of daylight hours; $\delta = (0.409) \sin \left( \frac{2\pi}{365} J - 1.39 \right)$, solar declination in radians.

<table>
<thead>
<tr>
<th>Method</th>
<th>Expression</th>
<th>Reference</th>
</tr>
</thead>
<tbody>
<tr>
<td>Thornthwaite</td>
<td>$E_0 = \left( \frac{N}{360} \right) (16) \left[ \frac{10T_{\text{av}}}{I} \right]^a$</td>
<td>[Tabari et al., 2011; Thornthwaite, 1948]</td>
</tr>
<tr>
<td>(daily)</td>
<td>$I = \sum_{j=1}^{12} \left( \frac{T_{\text{month}}}{5} \right)^{1.514}$, $T_{\text{month}} &gt; 0$</td>
<td></td>
</tr>
<tr>
<td></td>
<td>$a = (6.75 \times 10^{-7})I^3 + (-7.71 \times 10^{-5})I^2 + (1.7912 \times 10^{-2})I$</td>
<td></td>
</tr>
<tr>
<td></td>
<td>$+ (0.49239)$</td>
<td></td>
</tr>
<tr>
<td>Hamon 1</td>
<td>$E_0 = (25.4)(0.55) \left( \frac{N}{12} \right)^2 Pt$</td>
<td>[Chang et al., 2016; Hamon, 1961]</td>
</tr>
<tr>
<td></td>
<td>$\text{where,}$ $Pt = \left( \frac{4.95}{100} \right) e^{\left( 0.062T_{\text{av}} \right)}$</td>
<td></td>
</tr>
<tr>
<td>Hamon 2</td>
<td>$E_0 = (25.4)(0.0065) \left( \frac{N}{12} \right) \left( \frac{216.7es_a}{T_{\text{av}} + 273.3} \right)$</td>
<td>[Hamon, 1963; Lu et al., 2005]</td>
</tr>
<tr>
<td></td>
<td>$\text{where,}$ $es_a = \frac{6.108}{2} \left( e^{\left( \frac{17.27T_{\text{max}}}{T_{\text{max}} + 237.3} \right)} + e^{\left( \frac{17.27T_{\text{min}}}{T_{\text{min}} + 237.3} \right)} \right)$</td>
<td></td>
</tr>
</tbody>
</table>
Figure A-2. Illustration of the semicircular contour in the complex plane, used to evaluate Equation A-36. The contour is composed of a vertical line crossing the real axis at $s = k$ and an arc connecting the two ends of the vertical line. The radius of this semicircle is given as $R$. We let $R \to \infty$ so the vertical line portion of the contour will encompass the entire imaginary axis.
Table A-3. Illustration of why the condition, $C > D > 0$, holds true for Equations A-4 and A-10 for arid climates and Equations S6 and S12 for humid climates. From Left to Right: The first column gives the equation and associated climate. The second column gives mathematical constraints that must be true given an arid or humid climate. The third column gives specific mathematical constraints derived from the climatic constraints. The last column gives the condition, $C > D > 0$, for each associated equation and climate, given the climatic and derived constraints.

<table>
<thead>
<tr>
<th>Equation and Climate</th>
<th>Climatic Constraints</th>
<th>Derived Constraints</th>
<th>Resulting Condition, $C &gt; D &gt; 0$</th>
</tr>
</thead>
<tbody>
<tr>
<td>Equation S4, arid</td>
<td>$E_0 &gt; \bar{P}$ and $\bar{P} &gt; \bar{E}$</td>
<td>$\frac{1}{\bar{E}} &gt; \frac{1}{\bar{p}}$ and $\frac{E_0}{\bar{P}} &gt; 1$</td>
<td>$\ln \left( \frac{E_0}{\bar{E}} \right) &gt; \ln \left( \frac{E_0}{\bar{P}} \right) &gt; 0$</td>
</tr>
<tr>
<td>Equation S6, humid</td>
<td>$E_0 &lt; \bar{P}$ and $E_0 &gt; \bar{E}$</td>
<td>$\frac{1}{\bar{E}} &gt; \frac{1}{E_0}$ and $\frac{\bar{P}}{E_0} &gt; 1$</td>
<td>$\ln \left( \frac{\bar{P}}{\bar{E}} \right) &gt; \ln \left( \frac{\bar{P}}{E_0} \right) &gt; 0$</td>
</tr>
<tr>
<td>Equation S10, arid</td>
<td>$E_0 &gt; \bar{P}$ and $\bar{P} &gt; \bar{E}$</td>
<td>$\bar{P} - \bar{E} &gt; 0$ and $\frac{E_0}{\bar{P}} &gt; 1$</td>
<td>$\ln \left( \frac{E_0 + \bar{P} - \bar{E}}{\bar{P}} \right) &gt; \ln \left( \frac{E_0}{\bar{P}} \right) &gt; 0$</td>
</tr>
<tr>
<td>Equation S12, humid</td>
<td>$E_0 &lt; \bar{P}$ and $E_0 &gt; \bar{E}$</td>
<td>$\bar{E}_0 - \bar{E} &gt; 0$ and $\frac{\bar{P}}{E_0} &gt; 1$</td>
<td>$\ln \left( \frac{\bar{P} + E_0 - \bar{E}}{E_0} \right) &gt; \ln \left( \frac{\bar{P}}{E_0} \right) &gt; 0$</td>
</tr>
</tbody>
</table>
Figure A-3. Comparison of numerically calculated values of $n$ to finite series approximations of Equation A-56 for an arid catchment. The finite series approximations of Equation A-56 asymptotically converge to $n_{\text{numeric}}$ with increasing numbers of terms.

Figure A-4. Comparison of numerically calculated values of $n$ to finite series approximations of Equation A-57 for a humid catchment. The finite series approximations of Equation A-57 asymptotically converge to $n_{\text{numeric}}$ with increasing numbers of terms.
Figure A-5. Comparison of numerically calculated values of \( w \) to finite series approximations of Equation A-58 for an arid catchment. The finite series approximations of Equation A-58 asymptotically converge to \( w_{\text{numeric}} \) with increasing numbers of terms.

Figure A-6. Comparison of numerically calculated values of \( w \) to finite series approximations of Equation A-59 for a humid catchment. The finite series approximations of Equation A-59 asymptotically converge to \( w_{\text{numeric}} \) with increasing numbers of terms.
APPENDIX B
SUPPORTING INFORMATION FOR CHAPTER 3

Overview

Using the solution for the advective zone developed by several other researchers, we can obtain the solution to the transient storage zone.

Method

The ADS model is the following,

\[ \frac{\partial C}{\partial t} = -\frac{Q}{A} \frac{\partial C}{\partial x} + D \frac{\partial^2 C}{\partial x^2} + \alpha (C_s - C) \]

\[ \frac{dC_s}{dt} = \alpha \frac{A}{A_s} (C - C_s) \] \hspace{1cm} (B-1)

The solution to the advective zone concentration for an impulse solute application has been found to be,

\[ C(x, t) = e^{-\alpha t} C_0(x, t) + \alpha \int_0^t H(t, \tau) C_0(x, \tau) d\tau \] \hspace{1cm} (B-2)

where

\[ \beta = \frac{A_s}{A} \]

\[ (t, \tau) = (e^{-\frac{\alpha}{\beta} (t - \tau) - \alpha \tau}) \frac{\tau I_1 \left( \frac{2\alpha}{\beta} \sqrt{\beta (t - \tau)} \tau \right)}{\sqrt{\beta (t - \tau) \tau}} \] \hspace{1cm} (B-3)

\[ C_0(x, t) = \frac{M}{2A\sqrt{\pi Dt}} e^{-\frac{(x - \frac{Q}{A} t)^2}{4Dt}} \]

Using the second part of Equation B-1, we can see it is a first order linear differential equation,

\[ \frac{dC_s}{dt} = -\frac{\alpha}{\beta} C_s + \frac{\alpha}{\beta} C \] \hspace{1cm} (B-4)

with the general form,
\[
\frac{dy}{dt} = g(t)y + h(t) \quad (B-5)
\]

Equation B-5 has a general solution of the form,

\[
y(t) = \frac{y(t_0)u(t_0)}{u(t)} + \frac{1}{u(t)} \int_{t_0}^{t} u(s) h(s) ds
\]

\[
u(t) = e^{-\int g(t) dt} \quad (B-6)
\]

**Result**

Substituting the specific functions from Equation B-4 leads to the transient storage zone solution,

\[
C_s(x, t) = e^{-\frac{\alpha}{\beta} t} \int_{0}^{t} \left[ e^{\left(\frac{\alpha}{\beta} - \alpha\right) T} C_0(x, T) \right] dT
\]

\[
+ \alpha e^{-\frac{\alpha}{\beta} t} \int_{0}^{t} \left[ e^{\frac{\alpha}{\beta} \tau} \int_{0}^{\tau} H(T, \tau) C_0(x, \tau) d\tau \right] dT \quad (B-7)
\]
APPENDIX C
SUPPORTING INFORMATION FOR CHAPTER 4

Overview

I have included several items to support the main text of the manuscript. They are listed here in the order they are referred to in Chapter 4:

- Text C-1 discusses the details of each of the observational datasets used in the main text, including field site locations and data collection methodologies.
- Text C-2 describes the models used in the analysis of the critical threshold velocity from each observational dataset.
- Table C-1 gives a summary of the visual classification scales that were used in the observational datasets.
- Figure C-1 illustrates the performance of the flow control structures in reducing velocity.
- Figure C-2 shows images of the flow control structures prior to deployment.
- Object C-1 (file uploaded separately) is a video showing a flow control structure during deployment in the field. The caption is included in this Appendix.
- Text C-3 describes the model used in the analysis of the periphyton growth dynamics from experimental data and test for hysteresis.
- Object C-2 (file uploaded separately) is a video showing monami within a rooted vascular plant canopy within the Silver River. The caption is included in this Appendix.
- Object C-3 (file uploaded separately) is a video illustrating that when flow velocity is restored, periphyton abundance quickly declines. The caption is included in this Appendix.
- Text C-4 describes the derivation and parameterization of Equation 4-10 in Chapter 4, the threshold velocity for rooted vascular plants (VP) canopy motion.
- Figure C-3 provides a conceptual diagram for monami interaction with the VP canopy.
- Figure C-4 provides a visualization of the model of rooted VP as a cantilever beam used to derive Equation 4-10 in Chapter 4.
Figures C-5 to C-7 demonstrate that biomass and cover estimates for periphyton, macroalgae, and VP are not always well correlated.

Text C-1

This section provides a summary and details for each of the observational datasets used in the critical velocity threshold analysis of this manuscript.

Gulf Coast Springs Survey

General description of dataset

This dataset consists of measurements of the VP, periphyton, and macroalgae abundance distributions and flow velocities, for three different springs along the Gulf Coast of Florida. The springs included in this dataset are: Chassahowitzka, Homosassa, and Weeki Wachee. The data is from the year 2003-2011.

Data collection and processing methodology

Fill in data collection procedures.

Data format

This dataset contains paired abundance and flow velocity data for three primary producer classes, periphyton, VP, and macroalgae. Periphyton data consists of paired biomass abundance in units of mg chlorophyll per g of dry VP substrate and current velocities in units of m/s. VP and macroalgae data consist of paired Braun-Blanquet classification scores and current velocities in units of m/s.

Site locations

Chassahowitzka River, FL, USA; headspring latitude and longitude, 28.715541, -82.575957. Homosassa River, FL, USA; headspring latitude and longitude, 28.801441, -82.576920. Weeki Wachee River, FL, USA; headspring latitude and longitude, 28.517353, -82.573382.
Funding sources

The collection effort for this dataset was funded by the Grant ##.

Gum Slough Filamentous Algae Survey

General description of dataset

This dataset consists of measurements of the macroalgae (primarily Lyngbya wolleii) abundance distributions and flow velocities from three transects along the length of Gum Slough. Transects ran perpendicular to the flow direction of the river (i.e. from one bank to the other) and were sampled every 2 meters. One transect was excluded from the analysis of this manuscript as one transect was substantially different from the other two and not representative of the rest of the river. Specifically, the first transect was measured at or adjacent to the headspring of the river, which typically behave more like still water pools and often more directly impacted by human activity. The data spans the years 2010-2013.

Data collection and processing methodology

Macroalgae abundance was measured along each transect visually by estimating percent cover in 5% increments using a 0.25 m² quadrat. These data were translated onto the Braun-Blanquet classification scale. Flow velocity measurements were taken using a portable velocity meter (Model 2000; Marsh-McBirney Inc., Frederick, Maryland). For each macroalgae abundance measurement location, velocity was measured at 10 cm increments throughout the water column. The maximum flow velocity was taken to be most representative of the above canopy velocity. These velocity measurements paired to corresponding macroalgae abundance measurements. For additional details see [King, 2014].
Data format

The data consist of paired macroalgae Braun-Blanquet classification scores and above canopy flow velocity estimates in units of m/s.

Site locations

Gum Slough, FL, USA; headspring latitude and longitude, 28.958812, -82.231555.

Funding sources

The collection effort for this dataset was funded by a University of Florida Alumni Fellowship.

Synoptic Biological Springs Study

General description of dataset

This dataset consists of measurements of the VP, periphyton, and macroalgae abundance distributions and flow velocities, 14 different springs across Florida. The springs included in this dataset are: Alexander, Gum Slough, Ichetucknee, Juniper, Manatee, Rainbow, Rock, Silver, Silver Glen, Blue (Volusia County), Wacissa, Wakulla, Weeki Wachee, and Wekiva. The data is from the year 2015.

Data collection and processing methodology

Data format

This dataset contains paired abundance and flow velocity data for three primary producer classes, periphyton, VP, and macroalgae. All three sets of data consists of paired Braun-Blanquet classification scores and current velocities in units of m/s.

Site locations

Alexander Springs Creek, FL, USA; headspring latitude and longitude, 29.081330, -81.575776. Gum Slough, FL, USA; headspring latitude and longitude, 28.958812, -82.231555. Ichetucknee River, FL, USA; headspring latitude and longitude, 29.984159, -82.761762. Juniper Creek, FL, USA; headspring latitude and longitude, 29.183796, -81.712453. Manatee Spring Run, FL, USA; headspring latitude and longitude, 29.489600, -82.976850. Rainbow River, FL, USA; headspring latitude and longitude, 29.102515, -82.437493. Silver River, FL, USA; headspring latitude and longitude, 29.216236, -82.052674. Silver Glen Spring Run, FL, USA; headspring latitude and longitude, 29.245851, -81.643437. Blue Spring Run, FL, USA; headspring latitude and longitude, 28.947469, -81.339524. Wacissa River, FL, USA; headspring latitude and longitude, 30.339234, -83.991166. Wakulla River, FL, USA; headspring latitude and longitude, 30.235323, -84.303033. Weeki Wachee River, FL, USA; headspring latitude and longitude, 28.517353, -82.573382. Wekiva River, FL, USA; headspring latitude and longitude, 28.517353, -82.573382.

Funding sources

The collection effort for this dataset was conducted by Amec Foster Wheeler for the St. Johns River Water Management District (SJRWMD), funded by the SJRWMD contract 28146.
CRISPS SAV Groundtruthing Survey

General description of dataset

This dataset consists of measurements of the VP species, height, density, and periphyton abundance distributions and flow velocities above and within the VP beds, from three transects along the length of the Silver River and one downstream below the confluence with the Ocklawaha River. An accompanying 3D velocity dataset of the above canopy water column over each transect and entire main channel of Silver River was also captured within one week of the transect vegetation measurements, typically the same day. Top of canopy elevations along the transects and entire mainstem were also captured with M9 sonar systems corrected to the water surface elevation and gages surveyed in at each transect. The data was collected seasonally and spans the years 2014-2016.

Data collection and processing methodology

VP abundance was measured at either seven or nine marked stations along each transect visually by scuba divers using a 1 m² quadrat and the Braun-Blanquet classification scale. Additionally, for the majority of VP measurements, the divers recorded notes about the visual abundance of periphytic algal cover on the VP, giving rankings of “low”, “medium”, “high”, and “very high”. These ranks are constrained in that they are sequential (i.e., low < medium < high < very high) and are bounded between 0% and 100% cover. This allowed for them to be interpreted as a classification scale with unknown thresholds between categories (Text S2). Corresponding numeric values of 1-4 were assigned from to “low” to “very high” for each classification score. Three flow velocity measurements along the sides and center of the channel were taken 20 cm above the top of the VP canopy and mid canopy at each transect. These three
velocity measurements were averaged and paired to corresponding VP and periphyton abundance measurements.

**Data format**

This dataset contains paired abundance and flow velocity data for two primary producer classes, VP and periphyton. The VP data consists of paired Braun-Blanquet classification scores and above canopy flow velocities in units of m/s. The periphyton data consists of paired periphytic algal abundance classification scores and above VP canopy flow velocities in units of m/s.

**Site locations**

Silver River, FL, USA; headspring latitude and longitude, 29.216236, -82.052674.

**Funding sources**

The collection effort for this dataset was operated by Karst Environmental Services Inc. and funded by SJRWMD contract 27704.

**CRISPS Hydraulics and Hydrodynamics Periphyton Survey**

**General description of dataset**

This dataset consists of measurements of the periphyton abundance distributions and flow velocities for each of the treatment and control sites within the periphyton growth dynamics flow suppression experiment prior to the deployment of the flow control structures. This dataset is a subset of the larger dataset collected for the flow suppression experiment and provided the initial conditions for growth dynamics model and test for hysteresis. As these observations were taken before any experimental manipulation, they can be considered a separate observational dataset analogous to the others used in the observational critical threshold velocity estimations. The data is from the year 2017.
Data collection and processing methodology

Periphyton cover was measured by free divers using digital photography. The camera used for data collection was an Olympus Stylus TG-4 Tough (Olympus Corporation of the Americas, Center Valley, PA, USA). An ISO speed of 800 was used for all images. A minimum of six images were taken for each treatment and control site. These images were taken at slightly different heights, horizontal translations, and angles in order to capture a complete representation of the algal distribution. Each image was given a periphytic algal abundance classification score by randomizing the images and visually assigning each an algal abundance value of “very low”, “low”, “medium”, “high”, and “very high”. The constraint on these categories is that they are sequential (i.e., very low < low < medium < high < very high) and must be bounded between 0% and 100% cover. This allows the observer to only have to give relative ranks to abundances, which are likely more accurate that assigning definitive cover estimates. Corresponding numeric values of 1-5 were assigned from to “very low” to “very high” for each classification score.

Flow velocity measurements were taken using an OTT MF Pro electromagnetic water flow meter (OTT Hydromet, Loveland, CO, USA). Velocity profiles were taken for each treatment and control site. Profiles consisted of 9 depths, starting from the river bottom in ~15 cm increments and extending past the top of VP canopy, each with 6 velocity measurements. An example of these profiles is given in Figure S1. The mean above-canopy velocity was estimated by averaging the velocities of the shallowest three depths of the profiles. This was repeated for each of the 6 sets of velocity measurements, resulting in 6 mean above-canopy velocities for each treatment and control site.
Finally, to produce the dataset used in the observational critical threshold velocity estimation, each of the 6 periphytic algal abundance classification scores were randomly paired with one of the 6 mean above canopy velocities for each site.

**Data format**

The data consist of paired periphytic algal abundance classification scores and above VP canopy flow velocities in units of m/s.

**Site locations**

Silver River, FL, USA; headspring latitude and longitude, 29.216236, -82.052674.

**Funding sources**

The collection effort for this dataset was funded by the St. Johns Water Management District through the Collaborative Research Initiative on Sustainability and Protection of Springs (CRISPS) project (Contract 27789) and the University of Florida Graduate Fellowship

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**Text C-2**

In this section we develop and describe the models used in the analysis of the critical velocity threshold from each observational dataset. As described in Text C-1, all of the observational datasets consisted of a measure of primary producer cover paired with flow velocities, except for the periphyton abundance from the Gulf Coast Springs Survey, which consisted of biomass estimates rather than estimates of cover.

**Explicit Posterior Distributions for Primary Producer Cover Datasets**

For all of the datasets with cover estimates we can use Equation 4-2 from the main text to model their distributions. Here we show Equation 4-2 in this explicit form,
\[
A(v) \sim \beta[\mu(v), \sigma^2(v)] = \frac{\Gamma(a + b)A^{a-1}(1 - A)^{b-1}}{\Gamma(a)\Gamma(b)} \\
a = \frac{-\mu(v)[\sigma^2(v) + \mu(v)^2 - \mu(v)]}{\sigma^2(v)} \\
b = \frac{[1 - \mu(v)][\sigma^2(v) + \mu(v)^2 - \mu(v)]}{\sigma^2(v)} \\
\mu(v) = \mu_1 \Phi(v) + (\mu_2 - \mu_1)\Phi(v - v_c) \\
\sigma^2(v) = \sigma_1^2\Phi(v) + (\sigma_2^2 - \sigma_1^2)\Phi(v - v_c)
\]

where \(\Gamma(\ )\) is the Gamma function and \(a\) and \(b\) are the traditional beta distribution parameters that are defined in terms of more familiar parameters, mean, \(\mu\), and variance, \(\sigma^2\), as described in Section 2.2 of the main text.

For each of the datasets with cover estimates, those estimates are not explicit percent cover values, but instead have been translated onto visual classification scales. We must account for this translation in order to calibrate Equation 2 to the data. Specifically, the likelihood probability distribution model (Equation 4 in main text) must be modified.

The two types of classification scales used are the Braun-Blanquet scale and the relative abundance scale. The Braun-Blanquet scale assigns values between 1 and 5 for percent cover estimate that fall between defined thresholds (Table S1). The relative abundance scale is just a more generalized version of the Braun-Blanquet scale. This scale assigns values of “very low”, “low”, “medium”, “high”, or “very high”, separated by unknown thresholds, \(\varphi_1, \varphi_2, \varphi_3,\) and \(\varphi_4\) (Table S1). These relative abundance values constrained that they be sequential (i.e., very low < low < medium, etc.) and bounded between 0 and 100 % cover.

As an example, using the Braun-Blanquet scale, the likelihood for a primary producer abundance observation of Braun-Blanquet value 2 and flow velocity \(v_i\), given the model described by Equation 4-2 of the main text, is,
\[ p(2, v_i | v_c, \mu_1, \sigma_1^2, \mu_2, \sigma_2^2) = \int_{0.05}^{0.25} \beta(\mu(v_i), \sigma^2(v_i)) dA \] (C-2)

The right side of Equation C-2 can be rewritten in terms of the regularized incomplete beta function, \( I_x[\mu, \sigma^2] = \int_0^x \beta(\mu, \sigma^2) dA \), yielding,

\[ p(2, v_i | v_c, \mu_1, \sigma_1^2, \mu_2, \sigma_2^2) = I_{0.25}[\mu(v_i), \sigma^2(v_i)] - I_{0.05}[\mu(v_i), \sigma^2(v_i)] \] (C-3)

Similarly, if we use the relative abundance scale, the likelihood for a primary producer abundance observation of relative abundance of “low” and flow velocity \( v_i \), is,

\[ p(“low”, v_i | v_c, \mu_1, \sigma_1^2, \mu_2, \sigma_2^2) = \int_{\varphi_1}^{\varphi_2} \beta(\mu(v_i), \sigma^2(v_i)) dA \] (C-4)

and in terms of \( I_x[\mu, \sigma^2] \),

\[ p(“low”, v_i | v_c, \mu_1, \sigma_1^2, \mu_2, \sigma_2^2) = I_{\varphi_2}[\mu(v_i), \sigma^2(v_i)] - I_{\varphi_1}[\mu(v_i), \sigma^2(v_i)] \] (C-5)

We can now rewrite the posterior distribution (Equation 4-4 from Chapter 4), for all the datasets using the Braun-Blanquet scale,

\[
p\left(v_c, \mu_1, \sigma_1^2, \mu_2, \sigma_2^2 | N_1, \{v_{1,i}\}, N_2, \{v_{2,j}\}, N_3, \{v_{3,k}\}, N_4, \{v_{4,w}\}, N_5, \{v_{5,q}\}\right) \propto \left( \prod_{i=1}^{N_1} I_{0.05}[\mu(v_{1,i}), \sigma^2(v_{1,i})] \right) \left( \prod_{j=1}^{N_2} I_{0.25}[\mu(v_{2,j}), \sigma^2(v_{2,j})] - I_{0.05}[\mu(v_{2,j}), \sigma^2(v_{2,j})] \right) \left( \prod_{k=1}^{N_3} I_{0.5}[\mu(v_{3,k}), \sigma^2(v_{3,k})] - I_{0.25}[\mu(v_{3,k}), \sigma^2(v_{3,k})] \right) \left( \prod_{w=1}^{N_4} I_{0.75}[\mu(v_{4,w}), \sigma^2(v_{4,w})] - I_{0.5}[\mu(v_{4,w}), \sigma^2(v_{4,w})] \right) \] (C-6)

189
To finalize the model, we must assign explicit forms for the prior distributions, $p(v_c)$, $p(\mu_1)$, etc. Prior distributions were selected to be the least informative given the known constraints for each parameter. Uniform distributions, $U[s, f]$, were selected for $v_c$, $\mu_1$, and $\mu_2$, where,

$$U[s, f] = \begin{cases} 
\frac{1}{f - s}, & s \leq v_c, \mu_1, \mu_2 \leq f \\
0, & \text{otherwise}
\end{cases}$$

Specifically, $p(v_c) = U[0, v_{\text{max}}]$, where $v_{\text{max}}$ is the largest flow velocity measurement in the dataset, and $p(\mu_1) = p(\mu_2) = U[0,1]$. Lognormal distributions, $LogN[\eta, \lambda]$, were selected for $\sigma_1^2$ and $\sigma_2^2$. The lognormal distribution was chosen due to its semi-infinite support of $(0, \infty)$ which matches the possible values for $\sigma_1^2$ and $\sigma_2^2$. The explicit form of $LogN[\eta, \lambda]$ for $\sigma_1^2$ is,

$$LogN[\eta, \lambda] = \frac{1}{\sigma_1^2 \lambda \sqrt{2\pi}} e^{-\frac{(ln\sigma_1^2 - \eta)^2}{2\lambda^2}}$$

Specifically, $p(\sigma_1^2) = p(\sigma_2^2) = LogN[0, 1000]$, which produces a very wide and flat distribution (except very close to zero), reflecting the lack of prior lack of knowledge of the values of $\sigma_1^2$ and $\sigma_2^2$.

We are now able to write the explicit form of the posterior distribution for all datasets using the Braun-Blanquet scale,

$$p(v_c, \mu_1, \sigma_1^2, \mu_2, \sigma_2^2 | N_1, \{v_{1,i}\}, N_2, \{v_{2,j}\}, N_3, \{v_{3,k}\}, N_4, \{v_{4,w}\}, N_5, \{v_{5,q}\}) \propto$$

$$\left( \prod_{q=1}^{N_5} 1 - I_{0.75}[\mu(v_{5,q}), \sigma^2(v_{5,q})] \right) p(v_c)p(\mu_1)p(\sigma_1^2)p(\mu_2)p(\sigma_2^2)$$
\[
\begin{align*}
&\left( \prod_{i=1}^{N_1} I_{0.05}[\mu(v_{1,i}), \sigma^2(v_{1,i})] \right) \\
&\left( \prod_{j=1}^{N_2} I_{0.25}[\mu(v_{2,j}), \sigma^2(v_{2,j})] - I_{0.05}[\mu(v_{2,j}), \sigma^2(v_{2,j})] \right) \\
&\left( \prod_{k=1}^{N_3} I_{0.5}[\mu(v_{3,k}), \sigma^2(v_{3,k})] - I_{0.25}[\mu(v_{3,k}), \sigma^2(v_{3,k})] \right) \\
&\left( \prod_{w=1}^{N_4} I_{0.75}[\mu(v_{4,w}), \sigma^2(v_{4,w})] - I_{0.5}[\mu(v_{4,w}), \sigma^2(v_{4,w})] \right) \\
&\left( \prod_{q=1}^{N_5} 1 - I_{0.75}[\mu(v_{5,q}), \sigma^2(v_{5,q})] \right) U[0, v_{max}] U[0,1] U[0,1] \\
&\left( \frac{1}{\sigma_1^2(1000)\sqrt{2\pi}} e^{-\frac{(ln\sigma_1^2)^2}{2(1000)^2}} \right) \left( \frac{1}{\sigma_2^2(1000)\sqrt{2\pi}} e^{-\frac{(ln\sigma_2^2)^2}{2(1000)^2}} \right)
\end{align*}
\]

Equation C-9 was used for the analysis of the critical velocity threshold for following datasets: 1) Gulf Coast Springs Survey – VP and macroalgae. 2) Gum Slough Filamentous Algae Survey – macroalgae. 3) Synoptic Springs Study – VP, macroalgae, and periphyton. 4) CRISPS Study – VP.

The posterior distributions, for all the datasets using the relative abundance scale, are very similar to those using the Braun-Blanquet scale, with the exception that we must add unknown thresholds, $\varphi_1$, $\varphi_2$, etc., as parameters. Taking into account the sequential nature of these parameters, (i.e. $\varphi_1 < \varphi_2 < \ldots$) the prior distributions can be defined in terms of uniform distributions, specifically, $p(\varphi_1) = U[0, \varphi_2], p(\varphi_2) = U[\varphi_1, \varphi_3], p(\varphi_3) = U[\varphi_2, \varphi_4]$, and $p(\varphi_4) = U[\varphi_3, 1]$. Using the same explicit forms for the
prior distributions for \( v_c, \mu_1, \sigma_1^2, \mu_2, \) and \( \sigma_2^2 \) as in Equation S2-9, we can write explicit form of the posterior distribution for all datasets using the relative abundance scale with 4 thresholds,

\[
p(v_c, \mu_1, \sigma_1^2, \mu_2, \sigma_2^2, \varphi_1, \varphi_2, \varphi_3, \varphi_4 | N_1, \{v_{1,i}\}, N_2, \{v_{2,j}\}, N_3, \{v_{3,k}\}, N_4, \{v_{4,w}\}, N_5, \{v_{5,q}\})
\]

\[
\propto \prod_{i=1}^{N_1} I_{\varphi_1}[\mu(v_{1,i}), \sigma^2(v_{1,i})] \\
\prod_{j=1}^{N_2} I_{\varphi_2}[\mu(v_{2,j}), \sigma^2(v_{2,j})] - I_{\varphi_1}[\mu(v_{2,j}), \sigma^2(v_{2,j})] \\
\prod_{k=1}^{N_3} I_{\varphi_3}[\mu(v_{3,k}), \sigma^2(v_{3,k})] - I_{\varphi_2}[\mu(v_{3,k}), \sigma^2(v_{3,k})] \\
\prod_{w=1}^{N_4} I_{\varphi_4}[\mu(v_{4,w}), \sigma^2(v_{4,w})] - I_{\varphi_3}[\mu(v_{4,w}), \sigma^2(v_{4,w})] \\
\prod_{q=1}^{N_5} 1 - I_{\varphi_4}[\mu(v_{5,q}), \sigma^2(v_{5,q})] \cdot U[0, v_{\text{max}}] U[0, 1] U[0, 1] \\
\left( \frac{1}{\sigma_1^2(1000)\sqrt{2\pi}} e^{-\frac{(ln \sigma_1^2)^2}{2(1000)^2}} \right) \left( \frac{1}{\sigma_2^2(1000)\sqrt{2\pi}} e^{-\frac{(ln \sigma_2^2)^2}{2(1000)^2}} \right) \cdot U[0, \varphi_2] U[\varphi_1, \varphi_3] U[\varphi_2, \varphi_4] U[\varphi_3, 1]
\]

and the explicit form of the posterior distribution for all datasets using the relative abundance scale with 3 thresholds,

\[
p(v_c, \mu_1, \sigma_1^2, \mu_2, \sigma_2^2, \varphi_1, \varphi_2, \varphi_3 | N_1, \{v_{1,i}\}, N_2, \{v_{2,j}\}, N_3, \{v_{3,k}\}, N_4, \{v_{3,w}\}) \propto \prod_{i=1}^{N_1} I_{\varphi_1}[\mu(v_{1,i}), \sigma^2(v_{1,i})]
\]

(C-11)
Equation C-10 was used for the analysis of the critical velocity threshold for the CRISPS
Hydraulics and Hydrodynamics Periphyton Survey periphyton dataset while Equation C-
11 was used for the analysis of the critical velocity threshold for the CRISPS Study periphyton dataset.

Explicit Posterior Distributions for Primary Producer Biomass Datasets

As noted above, only one dataset quantified primary producer abundance using
biomass estimates rather than cover: periphyton abundance from the Gulf Coast
Springs Survey. We cannot use Equation 2 from the main text to model this dataset
because biomass estimates do not inherently have an upper limit, as is the case with
cover estimates. Instead we use the following model,

\[
P \sim \begin{cases} 
\log N[\mu_1, \sigma_1^2], & v < v_c \\
\log N[\mu_2, \sigma_2^2], & v > v_c 
\end{cases}
\]

where \( P \) is the periphyton biomass, \( \log N[\mu_1, \sigma_1^2] \) is a lognormal distribution with mean
\( \mu_1 \) and variance \( \sigma_1^2 \) for flow velocities, \( v \), below the critical threshold velocity, \( v_c \).
Similarly, $\log N[\mu_2, \sigma_2^2]$ is a lognormal distribution with mean $\mu_2$ and variance $\sigma_2^2$ for $v$ above $v_c$. We use the lognormal distribution for $P$ since it has semi-infinite support between 0 and $\infty$, which corresponds to the possible values of $P$ could take. Using the Heaviside step function, $\Phi(\cdot)$, we can rewrite Equation C-12 as a single distribution with its parameters $\mu(v)$ and $\sigma^2(v)$ as functions of $v$,

$$P(v) \sim \log N[\mu(v), \sigma^2(v)] = \frac{1}{P\lambda \sqrt{2\pi}} e^{-\frac{(\ln P - \eta)^2}{2\lambda^2}}$$

$$\eta = \ln \left( \frac{\mu(v)^2}{\sqrt{\sigma^2(v) + \mu(v)^2}} \right)$$

$$\lambda = \sqrt{\ln \left( 1 + \frac{\sigma^2(v)}{\mu(v)^2} \right)}$$

$$\mu(v) = \mu_1 \Phi(v) + (\mu_2 - \mu_1) \Phi(v - v_c)$$

$$\sigma^2(v) = \sigma_1^2 \Phi(v) + (\sigma_2^2 - \sigma_1^2) \Phi(v - v_c)$$

(C-13)

where $\eta$ and $\lambda$ are the standard lognormal distribution parameters that are defined in terms of the parameters, mean, $\mu$, and variance, $\sigma^2$.

To calibrate Equation C-13 to $N$ values of periphyton biomass and flow velocity observations (i.e., $\{P\}, \{v_i\}$), we use Bayes theorem, written as,

$$p(v_c, \mu_1, \sigma_1^2, \mu_2, \sigma_2^2 | \{P_i\}, \{v_i\}) \propto \left( \prod_{i=1}^{N} \log N[P_i | \mu(v_i), \sigma^2(v_i)] \right)$$

$$p(v_c) p(\mu_1) p(\sigma_1^2) p(\mu_2) p(\sigma_2^2)$$

(C-14)

where $\log N[P_i | \mu(v_i), \sigma^2(v_i)]$ is the probability of a single abundance observation, $P_i$, given the corresponding $v_i$ and Equation S2-13; and $p(\cdot)$ are the prior probability distributions for each parameter. To write the explicit form of Equation C-14 we must assign prior distributions for $p(v_c), p(\mu_1)$, etc. Prior distributions were selected to be the least informative given the known constraints for each parameter. A uniform distribution
was selected for \( v_c \), specifically, \( p(v_c) = U[0, v_{\text{max}}] \). Lognormal prior distributions were chosen for the remaining parameters, specifically, \( p(\mu_1) = p(\sigma_1^2) = p(\mu_2) = p(\sigma_2^2) = \text{Log}N[0, 1000] \). We are now able to write the explicit form of the posterior distribution used for the analysis of the critical velocity threshold for the Gulf Coast Springs Survey periphyton biomass dataset,

\[
p(v_c, \mu_1, \sigma_1^2, \mu_2, \sigma_2^2 | \{P_i\}, \{v_i\}) \propto \left( \prod_{i=1}^{N} \text{Log}N[P_i | \mu(v_i), \sigma^2(v_i)] \right)
\]

\[
U[0, v_{\text{max}}] \left( \frac{1}{\mu_1(1000)\sqrt{2\pi}} e^{\frac{-(\ln \mu_1)^2}{2(1000)^2}} \right) \left( \frac{1}{\mu_2(1000)\sqrt{2\pi}} e^{\frac{-(\ln \mu_2)^2}{2(1000)^2}} \right) \left( \frac{1}{\sigma_1^2(1000)\sqrt{2\pi}} e^{\frac{-(\ln \sigma_1^2)^2}{2(1000)^2}} \right) \left( \frac{1}{\sigma_2^2(1000)\sqrt{2\pi}} e^{\frac{-(\ln \sigma_2^2)^2}{2(1000)^2}} \right)
\]

\[\text{(C-15)}\]

**Sampling of Posterior Distributions**

As was stated in Chapter 4, all posterior distributions were sampled using a random walk Metropolis-Hastings Gibbs Sampling algorithm implemented in the software R. 100,000 samples were drawn from each posterior distribution. The first 20,000 samples were discarded as a “burn-in” period to ensure that the algorithm had converged to the posterior distribution.

**Text C-3**

In this section we develop and describe the models used in the analysis of the growth dynamics of periphyton released from hydraulic control and the test for hysteresis.

**Explicit Posterior Distribution for Periphyton Growth Dynamics**

This analysis uses data of the same format (i.e. relative abundance scores) as the CRISPS Hydraulics and Hydrodynamics Periphyton Survey observational
periphyton dataset. Details about the nature of these data and how they are treated are discussed in Text C-2 and Table C-1. Here we give the explicit forms of the model and posterior distribution. First, we write Equation 4-5 from Chapter 4 in explicit form,

\[ A(t) \sim \beta[\mu(t), \sigma^2] = \frac{\Gamma(a + b)A^{a-1}(1 - A)^{b-1}}{\Gamma(a)\Gamma(b)} \]

\[ a = \frac{-\mu(t)[\sigma^2 + \mu(t)^2 - \mu(t)]}{\sigma^2} \]

\[ b = \frac{[1 - \mu(t)][\sigma^2 + \mu(t)^2 - \mu(t)]}{\sigma^2} \]

\[ \mu(t) = \frac{KA_0e^{rt}}{K + A_0(e^{rt} - 1)} \]  

(C-16)

where \( \Gamma(\ ) \) is the Gamma function and \( a \) and \( b \) are the standard beta distribution parameters that are defined in terms of the parameters, mean, \( \mu \), and variance, \( \sigma^2 \). In order to write the explicit form of the posterior distribution (Equation 4-6 from Chapter 4), we must assign explicit forms for the prior distributions, \( p(A_0), p(K), p(r), p(\sigma^2), p(\varphi_1), p(\varphi_2), p(\varphi_3), \) and \( p(\varphi_4) \). As discussed in Text C-2, prior distributions were selected to be the least informative given the known constraints for each parameter. Uniform distributions, \( U[s,f] \) (Text C-2), were selected for \( A_0, K, \varphi_1, \varphi_2, \varphi_3 \), and \( \varphi_4 \) since all of these parameters have a finite range of possible values they can take (i.e. must be between 0 and 1). Specifically, \( p(A_0) = p(K) = U[0,1], p(\varphi_1) = U[0,\varphi_2], p(\varphi_2) = U[\varphi_1,\varphi_3], p(\varphi_3) = U[\varphi_2,\varphi_4], \) and \( p(\varphi_4) = U[\varphi_3,1] \). Lognormal prior distributions were assigned to \( r \) and \( \sigma^2 \). Specifically, \( p(r) = p(\sigma^2) = LogN[0,1000] \) (Text S2). We can now rewrite Equation 4-6 for the main text as,

\[ p(A_0, K, r, \sigma^2, \varphi_1, \varphi_2, \varphi_3, \varphi_4 | N_1, \{t_{1,i}\}, N_2, \{t_{2,j}\}, N_3, \{t_{3,k}\}, N_4, \{t_{4,w}\}, N_5, \{t_{5,q}\}) \propto \]  

(C-17)
\[
\left( \prod_{i=1}^{N_1} I_{\varphi_1} \left[ \mu(t_{1,i}) \right] \right) \left( \prod_{j=1}^{N_2} I_{\varphi_2} \left[ \mu(t_{2,j}) \right] - I_{\varphi_1} \left[ \mu(t_{2,j}) \right] \right)
\]

\[
\left( \prod_{k=1}^{N_3} I_{\varphi_3} \left[ \mu(t_{3,k}) \right] - I_{\varphi_2} \left[ \mu(t_{3,k}) \right] \right)
\]

\[
\left( \prod_{w=1}^{N_4} I_{\varphi_4} \left[ \mu(t_{4,w}) \right] - I_{\varphi_3} \left[ \mu(t_{4,w}) \right] \right)
\]

\[
\left( \prod_{q=1}^{N_5} 1 - I_{\varphi_4} \left[ \mu(t_{5,q}) \right] \right) U[0,1] U[0,1] U[0,\varphi_2] U[\varphi_1, \varphi_3] U[\varphi_2, \varphi_4] U[\varphi_3, 1]
\]

\[
\left( \frac{1}{r(1000)\sqrt{2\pi}} e^{-(ln(r))^2 \frac{2}{1000}} \right) \left( \frac{1}{\sigma^2(1000)\sqrt{2\pi}} e^{-(ln(\sigma^2))^2 \frac{2}{1000}} \right)
\]

where \( I_x[\mu, \sigma^2] \) is the regularized incomplete beta function (Text C-2).

**Explicit Posterior Distribution for Test for Hysteresis**

This analysis also uses data of the same format (i.e. relative abundance scores) as CRISPS Hydraulics and Hydrodynamics Periphyton Survey observational periphyton dataset. Details about the nature of these data and how they are treated are discussed in Text C-2 and Table C-1. Here we list the explicit posterior distribution for the hysteresis test using Equation 4-9 from Chapter 4,

\[
p(\mu_a, \sigma_a^2, \mu_b, \sigma_b^2, \varphi_1, \varphi_2, \varphi_3, \varphi_4 | N_1,a, N_1,b, N_2,a, N_2,b, N_3,a, N_3,b, N_4,a, N_4,b, N_5,a, N_5,b)
\]

\[
\propto
\left( I_{\varphi_1} \left[ \mu_b, \sigma_b^2 \right] \right)^{N_1,b} \left( I_{\varphi_1} \left[ \mu_a, \sigma_a^2 \right] \right)^{N_1,a}
\]

\[
\left( I_{\varphi_2} \left[ \mu_b, \sigma_b^2 \right] - I_{\varphi_1} \left[ \mu_b, \sigma_b^2 \right] \right)^{N_2,b} \left( I_{\varphi_2} \left[ \mu_a, \sigma_a^2 \right] - I_{\varphi_1} \left[ \mu_a, \sigma_a^2 \right] \right)^{N_2,a}
\]

(C-18)
\[ (I_{\varphi_3} [\mu_b, \sigma_b^2] - I_{\varphi_2} [\mu_b, \sigma_b^2])^{N_{3,b}} (I_{\varphi_3} [\mu_a, \sigma_a^2] - I_{\varphi_2} [\mu_a, \sigma_a^2])^{N_{3,a}} \]

\[ (I_{\varphi_4} [\mu_b, \sigma_b^2] - I_{\varphi_3} [\mu_b, \sigma_b^2])^{N_{4,b}} (I_{\varphi_4} [\mu_a, \sigma_a^2] - I_{\varphi_3} [\mu_a, \sigma_a^2])^{N_{4,a}} \]

\[ (1 - I_{\varphi_4} [\mu_b, \sigma_b^2])^{N_{5,b}} (1 - I_{\varphi_4} [\mu_a, \sigma_a^2])^{N_{5,a}} \]

\[
\frac{\alpha_{\frac{1}{\varphi_1}}}{\Gamma(A_{\frac{1}{\alpha_1}})} e^{-\alpha_1 B_{\frac{1}{\alpha_1}}} \left[ \frac{\beta_{\frac{1}{\beta_1}}}{\Gamma(A_{\frac{1}{\beta_1}})} e^{-\beta_1 B_{\frac{1}{\beta_1}}} \right]^{A_{\frac{1}{\alpha_1}} - 1} \frac{\beta_{\frac{1}{\beta_2}}}{\Gamma(A_{\frac{1}{\beta_2}})} e^{-\beta_2 B_{\frac{1}{\beta_2}}} \left[ \frac{\alpha_{\frac{2}{\varphi_2}}}{\Gamma(A_{\frac{2}{\alpha_2}})} e^{-\alpha_2 B_{\frac{2}{\alpha_2}}} \right]^{A_{\frac{2}{\beta_2}} - 1} \]

where \( N_{1,a}, N_{1,b}, N_{2,a}, N_{2,b}, \) etc. are the number of algal abundance observations of “very low” “low”, “medium”, etc. with \( b \) corresponding to before flow modification and \( a \) corresponding to after flow modification. \( \alpha_{\varphi_1}, \beta_{\varphi_1}, \alpha_{\varphi_2}, \beta_{\varphi_2} \), etc. are distributions parameters of the beta distribution priors for \( \varphi_1, \varphi_2, \varphi_3, \) and \( \varphi_4 \), which are informed from the posterior distribution from the corresponding growth dynamic analysis, (i.e. Equation S3-2). \( B_{\frac{1}{\alpha_1}}, A_{\frac{1}{\alpha_1}}, B_{\frac{1}{\beta_1}}, A_{\beta_1}, \) etc. are distribution parameters of the gamma distribution priors for \( \alpha_1, \beta_1, \alpha_2, \) and \( \beta_2 \) which are to \( \mu_a, \sigma_a^2, \mu_b, \) and \( \sigma_b^2 \) through \( \mu = \frac{\alpha}{\alpha + \beta} \) and \( \sigma^2 = \frac{\alpha \beta}{(\alpha + \beta)^2 (\alpha + \beta + 1)} \). The values of \( B_{\frac{1}{\alpha_1}}, A_{\frac{1}{\alpha_1}}, B_{\frac{1}{\beta_1}}, A_{\beta_1}, \) etc. were all set to 0.001, produces a very wide and flat distribution (except very close to zero), reflecting the lack of prior lack of knowledge of the values of \( \mu_a, \sigma_a^2, \mu_b, \) and \( \sigma_b^2 \).

**Text C-4**

In this section we develop an approximation of the minimum average mixing layer velocity required for the generation of monami and sustained canopy motion. The
mixing layer refers to the turbulent region above the VP canopy [Ghisalberti and Nepf, 2002]. Monami generation occurs when the instantaneous drag force exerted by vortices in the mixing layer exceeds the buoyancy and rigidity of the individual blades of the VP [Nepf, 2012a], causing the blades to undergo a large deflection from their upright position (Figure S3). The maximum restoring buoyant force for the simple bending of an VP blade occurs when it has deflected 90° or \(\frac{\pi}{2}\) radians. This provides a physical threshold for the onset of monami and sustained canopy motion. Specifically, when the vortex-induced instantaneous drag force, \(F_D\), becomes larger than the restoring force from VP blade rigidity and buoyancy at a deflection of \(\frac{\pi}{2}\) radians, \(F_S\), i.e.

\[
F_D = F_S
\]  

(C-19)

This approximation gives the magnitude of the forces required to produce a static endpoint (i.e. blade deflection of \(\frac{\pi}{2}\) radians), which is sufficient for identifying the threshold of motion, but would not be valid for a dynamic analysis. Both \(F_D\) and \(F_S\) depend on the individual structure of the VP blades (i.e. via drag, rigidity, and buoyancy), but also are dependent on the structure of the rest of the VP canopy. The structure of the VP canopy controls the formation of mixing layer vortices and the depth with which the vortices can penetrate the canopy, \(\delta_e\), (Figure C-3), which controls the degree of interaction between the vortices and individual blades VP.

**VP Drag Force**

Assuming the dominant hydrodynamic force on the individual VP blades is form drag, we can write,

\[
F_D = \frac{1}{2} \rho_w C_S W \delta_e v_t^2
\]  

(C-20)
where $\rho_w$ is the density of water, $C_s$ is the drag coefficient of an individual VP blade, $W$ is the width of an individual VP blade, and $v_i$ is the maximum instantaneous velocity generated by the traveling vortices. The dominant VP in spring-fed rivers, *Vallisneria americana* and *Sagittaria kurziana*, are long-bladed grasses with simple leaves and relatively uniform cross section along their length. This allows us to approximate the VP geometry as a flat plate of small aspect ratio, which has a drag coefficient formula of [Ortiz et al., 2015],

$$C_s = 1.11 + 0.02 \left( \frac{W}{\delta_e} + \frac{\delta_e}{W} \right)$$

(C-21)

The relationship between $\delta_e$ and overall VP canopy structure has been shown to be [Nepf, 2012a],

$$\delta_e = \frac{0.23\Delta S^2}{C_D W}$$

(C-22)

where $\Delta S$ is the characteristic spacing distance between VP blades and $C_D$ is the bulk drag coefficient of the whole VP canopy, distinct from $C_s$ [Nepf, 1999].

**VP Restoring Force**

To determine $F_S$, we model rooted VP as a cantilever beam undergoing simple elastic bending (Figure C-4). This is a good approximation for *Vallisneria americana* and *Sagittaria kurziana*, given their simple and relatively uniform geometry. We define the coordinate axes with the x-axis starting at the rooted end of the VP blade and increasing in value to towards the top of the VP and the y-axis start at and perpendicular to the VP blade and increasing in the downstream direction (Figure C-4). The curvature, $\kappa$, of a beam is related to the bending moment in the following manner,
\[ \kappa = \frac{M}{EI} = \frac{\frac{d^2y}{dx^2}}{\left[1 + \left(\frac{dy}{dx}\right)^2\right]^{\frac{3}{2}}} \]  

(C-23)

where \( M \) is the bending moment, \( E \) is Young's modulus, and \( I \) is the second moment of area. In Equation S4-5, \( \kappa \) is also expressed in terms of the x-y coordinate system. Additionally, \( \kappa \) can be expressed in terms of the beam's angle of deflection, \( \theta \), by using \( \frac{dy}{dx} = \tan \theta \), resulting in,

\[ \frac{d(\tan \theta)}{[1 + \tan^2 \theta]^\frac{3}{2}} = \frac{\sec^2 \theta \, d\theta}{[\sec^2 \theta]^\frac{3}{2}} = \cos \theta \, d\theta = \frac{M}{EI} \, dx \]  

(C-24)

Integrating Equation C-24 yields,

\[ \sin \theta = \frac{1}{EI} \int M(x) \, dx + C_1 \]  

(C-25)

where \( C_1 \) is a constant of integration. An exact determination of \( F_S \) could be performed using Equation C-25, however, this would require defining \( M(x) \) in terms of all the moment-generating forces simultaneously acting on the VP blade (i.e. drag and buoyancy), which results in an analytically challenging implicit equation. Importantly, solving this implicit equation would result in a static endpoint approximation, but with a substantial amount of additional complexity. Alternatively, we pursue an analytical approximation of \( F_S \). First, we solve Equation C-25 explicitly for \( \theta(x) \) for an VP blade under load from drag alone. This calculation gives an expression for the magnitude of the restoring force due to rigidity, \( F_R \). We then calculate the magnitude of the restoring force due to buoyancy, \( F_B \), for a VP blade following the deflection profile from drag alone (i.e. \( \theta(x) \)). \( F_S \) is approximated as the sum of these two restoring forces,
Figure C-4 illustrates the geometry of the VP blade, which has a total height, $h$. The drag force is modeled as a uniformly distributed load on the VP blade running from $x = 0$ to $x = \delta_e$, as this is the section of the VP blade that interacts with traveling vortices (Figure S3). To simplify calculations, this distributed load was converted into a point load located at $x = \frac{\delta_e}{2}$, we define new variables $z = x - \frac{\delta_e}{2}$ and $\bar{h} = h - \frac{\delta_e}{2}$, and assume that the deflection angle between $x = 0$ and $x = \frac{\delta_e}{2}$ constant. The shear through the beam, $V_R(z)$, caused by the restoring force due to rigidity, $F_R$, is,

$$V_R(z) = -F_R$$

(C-27)

The internal bending moment profile of the VP blade, $M_R(z)$, is the integral of $V_R(z)$. Integrating Equation C-27 and using the boundary condition $M_R(\bar{h}) = 0$, yields,

$$M_R(z) = -F_R z + F_R \bar{h}$$

(C-28)

We now use Equation C-25 to solve for $\theta_R(z)$, with the boundary condition $\theta_R(0) = 0$, yielding,

$$\sin \theta_R(z) = \frac{-F_R z^2}{2EI} + \frac{F_R \bar{h} z}{EI}$$

(C-29)

By letting $\theta_R(\bar{h}) = \frac{\pi}{2}$ (i.e. the threshold condition), Equation C-29 can be solved for $F_R$,

$$F_R = \frac{2EI}{\bar{h}^2}$$

(C-30)

Next, we solve for the shear caused by buoyancy within the VP blade, $V_B(z)$, with the deflection profile $\theta_R(z)$,

$$V_B(z) = -\int_0^z (\rho_w - \rho_s) W \tau g \sin \theta_R(s) \, ds$$

(C-31)
\[-(\rho_w - \rho_s)W\tau g \int_0^z \left( \frac{-F_RS^2}{2EI} + \frac{F_R\tan s}{EI} \right) ds\]

where $\rho_s$ is the density of VP tissue, $\tau$ is the thickness of the VP blade, $g$ is the acceleration due to gravity, and $s$ is a dummy integration variable. Letting $\Delta\rho = (\rho_w - \rho_s)$ and evaluating Equation C-31 gives,

$$V_B(z) = -\Delta\rho W\tau g \left[ \frac{-F_Rz^3}{6EI} + \frac{F_R\tan^2 z}{2EI} \right]$$  \hspace{1cm} (C-32)

To find $V_B(\tan)$, we substitute Equation C-30 into Equation C-32 giving,

$$V_B(\tan) = -\frac{2}{3} \Delta\rho W\tau g \tan$$  \hspace{1cm} (C-33)

$F_B$ is the sum of $|V_B(\tan)|$ and the additional buoyant force due to the top section of the VP where $\theta_R$ was considered constant (i.e. the section between $x = 0$ and $x = \frac{\delta e}{2}$), which yields,

$$F_B = \frac{2}{3} \Delta\rho W\tau g \tan + \frac{1}{2} \Delta\rho W\tau g \delta e$$  \hspace{1cm} (C-34)

Summing $F_R$ and $F_B$ finalizes the analytical approximation of $F_S$,

$$F_S \approx \frac{2EI}{\tan^2} + \frac{2}{3} \Delta\rho W\tau g \tan + \frac{1}{2} \Delta\rho W\tau g \delta e$$  \hspace{1cm} (C-35)

**Minimum Average Mixing Layer Velocity**

We can now can calculate instantaneous flow velocity required to overcome $F_S$.

Substituting Equations C-20 and C-35 into Equation C-19 gives,

$$\frac{1}{2} \rho_w C_S W \delta e v_i^2 = \frac{2EI}{\tan^2} + \frac{2}{3} \Delta\rho W\tau g \tan + \frac{1}{2} \Delta\rho W\tau g \delta e$$  \hspace{1cm} (C-36)

The second moment of area for a rectangular cross section of the VP blade is, $I = \frac{Wr^3}{12}$.

Substituting in the definitions of $I$ and $\tan$ into Equation C-36 and rearranging, yields,
\[ v_i = \sqrt{\frac{E \tau^3}{3 \rho_w C_s \delta_e \left( h - \frac{\delta_e}{2} \right)^2} + \frac{2 \Delta \rho \tau g (\delta_e + 2h)}{3 \rho_w C_s \delta_e}} \]  

Equation C-37 gives the maximum instantaneous velocity generated by the traveling vortices, however we are interested in the average mixing layer velocity that will produce this velocity. Measurements at the top the VP canopy have shown the velocity varying by a factor of three during vortex passage [Ghisalberti and Nepf, 2006]. This allows us to relate \( v_i \) to the average vortex velocity, \( v_a \),

\[ v_a \cong \frac{2}{3} v_i \]  

Vortex translation velocities are typically higher than the average mixing layer velocity, \( v_m \) [Ghisalberti and Nepf, 2002; Nepf, 2012a]. The ratio of \( v_a \) to \( v_m \) varies with depth of submergence of the VP canopy. It has been found that value of the ratio varies between 1, for pure mixing layers or shallowly submerged canopies, and asymptotically approaches 1.8 for unconfined canopies (i.e. deeply submerged) [Nepf, 2012a]. Using the midpoint of this range (1.4), we write an expression for the minimum average mixing layer velocity required for the generation of monami and sustained canopy motion,

\[ v_m \cong \left[ \frac{1}{1.4} \right] \left[ \frac{2}{3} \right] \sqrt{\frac{E \tau^3}{3 \rho_w C_s \delta_e \left( h - \frac{\delta_e}{2} \right)^2} + \frac{2 \Delta \rho \tau g (\delta_e + 2h)}{3 \rho_w C_s \delta_e}} \]  

which is Equation 4-9 in Chapter 4. Figure C-3 illustrates the relationships between \( v_i \), \( v_a \), and \( v_m \).
Parameterization of $v_m$ for Springs

In order to make estimates of $v_m$ for springs, we need to have representative values for the parameters $E$, $\rho_s$, $h$, $\tau$, $W$, $\Delta S$, and $C_D$. Here we develop appropriate values or ranges of values for each parameter. $C_D$ decreases in value with increasing Reynolds number, asymptotically approaching a value of 1 [Tanino and Nepf, 2008]. This allows us to approximate $C_D \approx 1$, as has been deemed reasonable in previous work [Nepf, 2012b]. In lieu of direct measurements of $E$ and $\rho_s$ for Vallisneria americana or Sagittaria kurziana, we estimated these values from literature values from similar rooted VP. We set $E = 0.883$ GPa and $\rho_s = 850$ kg/m$^3$, by averaging reported values from three seagrass species (Thalassi testudinum, Zostera Marina, and Posidonia oceanica) [Lei and Nepf, 2016]. Values for the VP blade morphology parameters, $h$ and $W$ were assigned from data collected in the CRISPS Study, while $\tau$ was calculated from $W$ using the width to thickness ratio $\frac{W}{\tau}$, which was determined from digital images of VP from the CRISPS Hydraulics and Hydrodynamics Periphyton Survey. The values $h = 787$ mm and $W = 12.0$ mm were set by averaging all measurements of VP length and width. These values can be found in Dataset 3. The value $\tau = 0.7$ mm calculated using a width to thickness ratio $\frac{W}{\tau} = 17$. Finally, a range of $\Delta S$ were estimated from VP canopy from [Hauxwell et al., 2007]. Hauxwell et al. [2007] found that Vallisneria americana shoot areal density ranged between 200 to 800 shoots/m$^2$ and that the leaves per shoot on average ranged from 6 to 11. These values allow for the calculation of the leaf areal density, $l_A$, giving a range 1200-8800 leaves/m$^2$ and midpoint of 4250 leaves/m$^2$. $\Delta S$ can be approximated from $l_A$ using,
\[ \Delta S = \sqrt{\frac{1}{l_A}} \]  

Using Equation C-40, we calculated a range of \( 10.7 \leq \Delta S \leq 28.9 \) mm, with the midpoint value \( \Delta S = 15.3 \) mm.

Using the values for \( \rho_s, h, \tau, W, \) and \( C_D \) and the range of values for \( \Delta S \), we combine Equations S4-3 and S4-4 with Equation S4-21 to calculate a range and midpoint value for \( v_m \). The resulting midpoint value is \( v_m = 0.232 \) m/s, with a range for sparse to dense VP canopies of \( 0.125 \leq v_m \leq 0.326 \) m/s.
Table C-1. Summary of the visual classification scales used with the corresponding datasets.

<table>
<thead>
<tr>
<th>Braun-Blanquet</th>
<th>Range of Cover (%)</th>
<th>Relative Abundance 4 Thresholds</th>
<th>Range of Cover (%)</th>
<th>Relative Abundance 3 Thresholds</th>
<th>Range of Cover (%)</th>
</tr>
</thead>
<tbody>
<tr>
<td>5</td>
<td>75-100</td>
<td>very high (5)</td>
<td>𝜑4-100</td>
<td></td>
<td></td>
</tr>
<tr>
<td>4</td>
<td>50-75</td>
<td>high (4)</td>
<td>𝜑3-𝜑4</td>
<td>high (4)</td>
<td>𝜑3-100</td>
</tr>
<tr>
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<td>25-50</td>
<td>medium (3)</td>
<td>𝜑2-𝜑3</td>
<td>medium (3)</td>
<td>𝜑2-𝜑3</td>
</tr>
<tr>
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<td>5-25</td>
<td>low (2)</td>
<td>𝜑1-𝜑2</td>
<td>low (2)</td>
<td>𝜑1-𝜑2</td>
</tr>
<tr>
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<td>0-5</td>
<td>very low (1)</td>
<td>0-𝜑1</td>
<td>very low (1)</td>
<td>0-𝜑1</td>
</tr>
</tbody>
</table>

Datasets

- **Gulf Coast Springs Survey** – VP and macroalgae
- **Gum Slough Filamentous Algae Survey** – macroalgae
- **Synoptic Springs Study** – VP, macroalgae, and periphyton
- **CRISPS Study** - VP
- **CRISPS Hydraulics and Hydrodynamics Periphyton Survey** - periphyton
- **CRISPS Study** - periphyton
Figure C-1. Flow velocity profiles before (blue) and after (red) the deployment of the flow control structure. The central solid lines give the mean velocity, while dotted line intervals get one standard deviation around the mean. The height of the top of the structure is given by the solid black line. Velocity is reduced to near zero levels behind the flow control structure.
Figure C-2. Images of the flow control structures used in the flow suppression prior to deployment in the field. The frame of the structure is made from PVC piping, while the transparent panels are made from acrylic sheeting. Panels are attached to the frame using stainless steel boat hook clips. Photos courtesy of author.
Figure C-3. Illustration of canopy motion due to traveling vortices (i.e., monami). The vortex penetrates the canopy at a depth of $\delta_e$, which is controlled by the overall structure of the VP canopy. This sets the length of the VP blade that can interact with the drag due to the vortex. Also shown are the relationships between the velocities, $v_m$, $v_a$, and $v_i$, referenced in Text S4. The average mixing layer velocity, $v_m$, is slower than the traveling velocity of the vortex, $v_a$. (a) If $v_i$ is not large enough to overcome the VP rigidity and buoyancy, and monami does not occur even though vortices are present. (b) If the drag force exerted due to $v_i$ is large enough to overcome the VP rigidity and buoyancy, the VP blades bend substantially, and a monami is generated.
Figure C-4. A rooted VP blade model as a cantilever beam undergoing simple elastic bending with the coordinate system and geometry of the VP blade referenced in Text S4. (a) The VP blade prior to the application of the drag force. (b) The VP blade during bending, and restoring force due to blade rigidity and buoyancy.

Figure C-5. Corresponding periphyton biomass and cover measurements from the Synoptic Biological Springs Study dataset. The correlation between the two estimates of abundance is weak as evident from the low $R^2$ value.
Figure C-6. Corresponding macroalgae biomass and cover measurements from (a) the Gulf Coast Springs Survey and (b) the Synoptic Biological Springs Study dataset. The correlation between the two estimates of abundance is weak as evident from the low $R^2$ value.

Figure C-7. Corresponding VP biomass and cover measurements from (a) the Gulf Coast Springs Survey and (b) the Synoptic Biological Springs Study dataset. The correlation between the two estimates of abundance is weak as evident from the low $R^2$ value.

Object C-1. Flow control structures deployed in the field. File name “ms01.mp4”. Size: 86.9 MB. Filmed in the Silver River using GoPro Hero 3+ Black Edition and Hero 5 Session cameras (GoPro, Inc., San Mateo, CA, USA). This video shows different perspectives of one of the flow control structures deployed in the field. The transparent surfaces both divert flow upward and allow light to pass through to the VP and periphyton. There is a very apparent difference in the amount of deflection and the motion of the VP behind the flow control structure versus the VP in the rest of the channel. This is due to the substantial velocity reduction behind the structure as quantified in Figure A-1.

Object C-2. Flow restoration process to the treatment sites. File name “ms02.mp4”. Size: 237 MB. Filmed in the Silver River using a GoPro Hero 3+ Black Edition camera (GoPro, Inc., San Mateo, CA, USA). This video shows the flow restoration process to the sites that had undergo flow suppression. The
transparent surfaces are quickly removed allowing the natural velocity profile to be reestablished. Two perspectives are presented in the video. First, a side view of the process is shown, followed by a top down view of the same event. As soon as flow is restored, the majority of the periphyton is quickly exported. Additional periphyton continues to be exported as abrasive VP blade contact mechanically detaches it. This process happens relatively rapidly, stabilizing the periphyton cover after approximately 1 to 2 days.

Object C-3. Illustration of monami behavior in the Silver River. File name “ms03.mp4”. Size: 72.6 MB. Filmed in the Silver River using a GoPro Hero 3+ Black Edition camera (GoPro, Inc., San Mateo, CA, USA). This video pans across a section of the river bottom showing the extent of the VP canopy and its motion. Traveling depressions in the top of the VP canopy can been seen, indicating monami behavior.
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226


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227


BIOGRAPHICAL SKETCH

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