

ABSTRACT

Title of Dissertation: MECHANISMS REGULATING
GREENHOUSE GAS EMISSIONS AND SOIL
CARBON STORAGE IN MID-ATLANTIC
COASTAL PLAIN WETLANDS

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Wetlands are key components of the global carbon (C) cycle, storing significant amounts of C while emitting methane (CH₄), a greenhouse gas. As wetland restoration emerges as a potential climate mitigation strategy, understanding the factors that influence wetland greenhouse gas exchange across land uses is essential for aligning management with ecology and biogeochemistry. This dissertation investigates variability in soil organic carbon (SOC) storage and CH₄ flux in mid-Atlantic Coastal Plain wetlands, focusing on the roles of hydrology, vegetation, and land-use history in shaping underlying ecosystem processes.

In Chapter 1, I surveyed SOC stocks across neighboring least-disturbed wetlands with similar vegetation and hydrogeomorphology and found substantial variation. Hydrologic regimes and relative topography partially explained variability, highlighting the importance of landscape

heterogeneity in determining wetland C storage capacity. In Chapter 2, I measured CH₄ fluxes across five dominant vegetation patch types in a freshwater wetland using a multi-scale approach. I found that vegetation patches had distinct CH₄ signals throughout the growing season, likely driven by differences in the mechanisms that regulate fluxes. The magnitude of the CH₄ source was linked to patch identity, suggesting that CH₄ fluxes were properties of patch types, and that a patch-explicit representation may be needed for modeling and estimating wetland greenhouse gas exchange. In Chapter 3, I explored the temporal dynamics of CH₄ flux across wetlands with different land-use histories, identifying key biophysical drivers at multiple time scales. I found that after two decades, CH₄ dynamics in a restored wetland appeared to have converged with those at a natural wetland and diverged with those at a cultivated former wetland. Together, these findings demonstrate the importance of acknowledging and accounting for the inherent variability and context-specificity in wetland C dynamics and suggest that wetland management and restoration for climate mitigation requires a detailed understanding of wetland ecosystem processes.

MECHANISMS REGULATING GREENHOUSE GAS EMISSIONS AND SOIL
CARBON STORAGE IN MID-ATLANTIC COASTAL PLAIN WETLANDS

by

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Preface

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Dedication

I dedicate this work to my mother, Jane, a dedicated conservationist; my father, Brian, and grandfather, George, both brilliant scientists; and to the memory of my grandmother, Ruth, who was simply extraordinary.

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Introduction

Wetlands have a significant climate footprint that is predominantly determined by the balance between carbon sequestration and greenhouse gas emissions. Wetlands act as carbon (C) sinks, taking up carbon dioxide (CO₂) via primary production and storing it as organic matter. Decomposition is slowed in anaerobic wetland soils, allowing C stocks to persist, but these same conditions also lead to the production of CH₄, a potent greenhouse gas. Thus, wetlands contain 20–30% of the world’s belowground organic C and contribute ~20% of global CH₄ emissions, despite representing only 5% of the total area (Lal, 2008; Saunio et al., 2020).

Left undisturbed, most wetlands have a long-term cooling effect on the climate, but under anthropogenic pressures, that balance is unclear (Petrescu et al., 2015). Land-use change, agriculture, and drainage have resulted in a loss of than half of global wetland area (Davidson, 2014), and in remaining wetlands, disturbance can alter ecosystem processes, resulting in loss or reduction of important ecosystem functions and services (Zedler, 2003). Wetland drainage exposes soils to aerobic conditions, causing rapid oxidation (i.e., respiration) of organic matter and potentially transforming wetlands into C sources (Jones et al., 2024). As the climate warms, wetland CH₄ emissions are projected to grow, suggesting positive feedback (Gedney et al., 2019).

There is potential for wetland restoration increase the earth’s C sink and mitigate anthropogenic climate change (Griscom et al., 2017). Restored wetlands are

designed to recreate the conditions found in natural wetlands, such as hydrologic regimes and hydrophytic plant communities, that enable the provision of ecosystem services like climate regulation (Mitsch & Wilson, 1996). Despite promise, it is unclear whether restored wetlands can achieve the same climate mitigation function as natural wetlands (Schaller et al., 2022). Meta-analyses have shown consistently lower soil organic carbon (SOC) in restored wetlands (Meli et al., 2014; Yu et al., 2017), and recent work has found slower SOC accumulation in restored wetlands (Loder et al., 2023), which may result from a weakened ability to retain C inputs (Keshta et al., 2021).

Meanwhile, the cost of CH₄ fluxes from restored wetlands is uncertain. Fluxes may remain relatively low from restored wetlands, even several years after re-flooding (Urbanová et al., 2013), but it has also been suggested that restoring wetlands represents a “biogeochemical compromise” of beneficial services (e.g., nutrient removal, flood regulation, biodiversity) against CH₄ emissions (Hemes et al., 2018). Since CH₄ fluxes affect the climate on a shorter time scale than CO₂ uptake, accurately assessing restored wetland CH₄ is an immediate priority (Hemes et al., 2018).

Developing management strategies that promote wetland climate mitigation requires understanding the patterns and drivers of spatiotemporal variability in wetland C cycling. Temporal variability in C storage is low due to slow soil processes, but spatial variability can be high within and between wetlands (Pearse et al., 2018). CH₄ flux, on the other hand, has extreme spatial and temporal variability, making it difficult to predict and model accurately, and resulting in global uncertainty

(McNicol et al., 2023; Saunois et al., 2020). It is therefore imperative to investigate wetland C storage and CH₄ flux in the context of both land-use and environmental variability (Petrescu et al., 2015).

In this dissertation, I address uncertainties in wetland C storage and CH₄ flux with studies in mid-Atlantic Coastal Plain wetlands across different land uses. In Chapter 1, I quantify variability in SOC stocks in natural and restored wetlands and examine how hydrology and topography can help explain differences between wetlands. In Chapter 2, I use a multi-scale approach to contrast CH₄ fluxes from distinct vegetation patch types in a spatially heterogeneous restored wetland. In Chapter 3, I describe the nonlinear temporal relationships between CH₄ fluxes and biophysical drivers over four years of continuous data from a natural, restored, and cultivated former wetland.

Chapter 1: Setting a reference for wetland carbon: the importance of accounting for hydrology, topography, and natural variability

Abstract

Wetland soils are a key global sink for organic carbon (C) and a focal point for C management and accounting efforts. The ongoing push for wetland restoration presents an opportunity for climate mitigation, but C storage expectations are poorly defined due to a lack of reference information and an incomplete understanding of what drives natural variability among wetlands. We sought to address these shortcomings by 1) quantifying the range of variability in wetland soil organic C (SOC) stocks on a depressional landscape (Delmarva Peninsula, USA) and 2) investigating the role of hydrology and relative topography in explaining variability among wetlands. We found a high degree of variability within individual wetlands and among wetlands with similar vegetation and hydrogeomorphic characteristics. This suggests that uncertainty should be presented explicitly when inferring ecosystem processes from wetland types or land cover classes. Differences in hydrologic regimes, particularly the rate of water level recession, explained some of the variability among wetlands, but relationships between SOC stocks and some hydrologic metrics were eclipsed by factors associated with separate study sites. Relative topography accounted for a similar portion of SOC stock variability as hydrology, indicating that it could be an effective substitute in large-scale analyses. As wetlands worldwide are restored and focus increases on quantifying C benefits, the importance of appropriately defining and assessing reference systems is

paramount. Our results highlight the current uncertainty in this process, but suggest that incorporating landscape heterogeneity and drivers of natural variability into reference information may improve how wetland restoration is implemented and evaluated.

Introduction

Carbon (C) storage is an important process in wetlands and is cited as a goal for conservation and restoration efforts worldwide (Erwin, 2009; Poulter et al., 2021; Were et al., 2019). Wetlands contain an estimated 20–30% of global soil organic C (SOC) (Lal, 2008), which varies among wetland ecosystems according to factors such as plant communities and soil properties (Carnell et al., 2018; Davila & Bohlen, 2021; Loder & Finkelstein, 2020). Long recognized for its climate cooling effect, the wetland SOC sink has gained recent attention for its potential to mitigate human-induced climate change (Bossio et al., 2020; Griscom et al., 2017). While conserving pristine wetlands is of immediate concern for protecting global SOC stocks (Griscom et al., 2017; Taillardat et al., 2020), much of the existing wetland acreage has been degraded by human activities (Davidson, 2014), and restoration remains integral to climate mitigation strategies (Bossio et al., 2020). Therefore, there is interest in refining expectations of SOC storage capacity in restored wetlands and ensuring that current practices allow targets to be met (Taillardat et al., 2020; Were et al., 2019).

The extent to which degraded wetlands can regain SOC stocks through restoration is unclear. Few restored wetlands approach SOC levels comparable to least-disturbed wetlands (hereafter, “natural” wetlands), even after decades of recovery (Ballantine & Schneider, 2009; Yu et al., 2017). Soil properties inherently

develop slowly, but evidence of plateauing SOC accumulation well below natural levels has raised concern that restored wetlands may not reach these targets (Moreno-Mateos et al., 2012; Zedler & Callaway, 1999). Hence, there is a need to better understand how SOC stocks in restored wetlands vary compared to natural wetlands (Kreyling et al., 2021; Tangen & Bansal, 2020).

In a restoration context, reference wetlands set the foundation for siting, designing, and evaluating projects for their SOC benefits. Since pre-disturbance conditions are rarely documented, information to guide restoration must come from nearby wetlands of the same type that are relatively undisturbed (Moorhead, 2013). If restoration aims to increase SOC storage, then interventions should reflect an ecological understanding of how SOC accumulates and persists in reference wetlands (Palmer et al., 2016). Further, baseline data on SOC in reference wetlands is essential to set realistic targets and perform C accounting (Brinson & Rheinhardt, 1996; Kentula, 2000). This has become urgent given governmental efforts to create standardized natural capital accounting systems, including those for C storage (e.g., most recently for the US; White House Office of Management and Budget, 2022).

Despite the critical role of reference systems, their use in wetland restoration is complicated by natural variability among individual wetlands (Otte et al., 2021). Wetlands that appear similar can vary widely in hydrological, ecological, and biogeochemical attributes (Dvoretz et al., 2013; LaBaugh et al., 1998), which makes it difficult to select references and introduces uncertainty when evaluating restored systems (Morgan & Short, 2002). Classification systems are used to group wetlands, but high variability is routinely observed within classes (Moorhead, 2013; Otte et al.,

2021), meaning these systems alone may be ineffective at describing natural variability (Stander & Ehrenfeld, 2009). Some researchers have thus argued that the reference condition is best represented by a collection of natural systems (Matthews et al., 2009; Vélez-Martín et al., 2018), or as explicitly dependent on environmental drivers (Johnson et al., 2014).

A better understanding of the hydrologic drivers of wetland SOC may help constrain natural variability and provide valuable ecological information for restoration. Hydrology is considered a “master variable” in wetland processes (Brinson, 1993; Tiner, 2017), and can influence SOC through multiple mechanisms. For example, patterns of saturation and inundation control plant abundance, community composition, and primary production (Day & Megonigal, 1993; S. M. Fennessy et al., 1994; Schalles & Shure, 1989). Anoxic conditions during prolonged saturation and inundation suppress microbial enzyme activity and slow decomposition, promoting the accumulation of plant-derived C in wetland soils (Freeman et al., 2001; Mclatchey & Reddy, 1998). In practice, however, the relationship between wetland hydrology and SOC is less clear (Davila & Bohlen, 2021). Hydrologic regime can differ between otherwise similar wetlands (Dvoretz et al., 2013; McLaughlin & Cohen, 2013; Park et al., 2014), but research is inconsistent as to how this corresponds to variability in SOC (see e.g., Davila & Bohlen, 2021; M. S. Fennessy et al., 2018). Since no single parameter can fully describe complex wetland hydrologic regimes, improving restoration requires knowing which measurable aspects (e.g., average water level, inundation duration) are associated with SOC (Galatowitsch & Zedler, 2014; Zedler, 2000).

Characterizing the role of relative topography in wetland hydrology and ecosystem processes is key to increasing the practical benefits of reference information. Relative topography can indirectly control wetland SOC through its effects on surface and groundwater flows, which in turn determine wetland hydrologic regimes (Winter, 1988, 2001). In restoration, this is reflected in interventions (e.g., plugging ditches, re-grading) that shape the physical landscape to achieve reference hydrologic conditions (Jarzensky et al., 2013; USDA-NRCS, 2010). Terrain analysis is increasingly recognized as an essential tool in wetland management due to its scalability and the accessibility of high-resolution elevation data (Cianciolo et al., 2021; Epting et al., 2018; Horvath et al., 2017).

On low-lying landscapes, natural or anthropogenic variation in topographic relief can create hydrologic conditions that support wetlands with extensive herbaceous vegetation. In addition to vegetation cover, these "emergent" wetlands can differ from nearby forested wetlands in basin morphology, hydrology, and likely other factors that may influence SOC (Kirkman et al., 2000; McFarland et al., 2016). Regardless of their historical vegetation type, wetlands are most often restored as emergent systems to promote biodiversity and wildlife habitat (Yepsen et al., 2014). Certainly, quantifying the links between relative topography, hydrology, and SOC storage will help simplify reference wetland selection and inform restoration initiatives (Branton & Robinson, 2020; Euliss et al., 2008; Johnson et al., 2012).

We measured SOC stocks in wetlands on a depressional landscape and assessed whether hydrology and relative topography explained differences among least-disturbed reference wetlands. We first compared SOC variability between

representative natural and restored wetlands. We then quantified SOC stocks in a broader number of natural wetlands to determine the baseline variability on the landscape. Lastly, we tried to explain this baseline variability by examining relationships between natural wetland SOC stocks, hydrologic metrics, and terrain metrics. Our results provide insight into the collection and interpretation of reference information towards improving wetland restoration practices and evaluation.

Methods

Study system

Our study took place on the Delmarva Peninsula (Maryland, USA) within the mid-Atlantic Coastal Plain province (Figure 1.1a). The Peninsula contains thousands of freshwater depressional wetlands (“Delmarva bays”; Fenstermacher et al., 2014), which exist naturally as either forested or emergent (vegetated) systems. Forested bays are small (~ 1 ha) closed-canopy pools with little to no herbaceous vegetation, while emergent wetlands are larger with diverse meadow-like vegetation in distinct zonal communities (McFarland et al., 2016; Tyndall, 2000). Soils come from sandy or silty parent materials and are dominated by mineral components, although organic soils (i.e., histosols) develop in some natural bays (Stolt & Rabenhorst, 1987). Delmarva bays interact with shallow groundwater, and annual hydrologic patterns are characterized by seasonal (winter–spring) flooding followed by evapotranspiration-driven drawdown in the summer and fall (Phillips & Shedlock, 1993). Owing primarily to agriculture, more than two thirds of Delmarva bays have been at least partially destroyed, and those remaining have likely been hydrologically altered

(Fenstermacher et al., 2014). Recently, however, the Peninsula has seen net wetland gain (Stubbs et al., 2020), due in part to large-scale restoration efforts (e.g., the US Department of Agriculture’s Conservation Reserve Program) (Lee et al., 2020). Common techniques used to hydrologically restore Delmarva bays include ditch plugging, soil surface excavation, and installation of water control structures (Lee et al., 2020; USDA-NRCS, 2010).

Wetland SOC stocks

Our study includes data from two sampling sets to capture the range of variability in Delmarva bays. We initially chose three restored and three nearby least-disturbed (“natural”) wetlands to assess spatial variability in SOC. In this set, hereafter called the “emergent wetlands”, we sampled from three vegetation zones: woody, herbaceous, and open water. After finding high variability in natural wetland SOC, we sampled an additional 19 natural wetlands (hereafter “forested wetlands”) at two sites with similar vegetation, edaphic and topographic conditions (“BC” and “JL”; Figure 1.1). Although emergent wetlands result from most wetland restoration/creation projects, forested wetlands are more common in the study region (Hogan et al., 2004; Yepsen et al., 2014) and were our focus for further baseline data.

In forested wetlands, duplicate soil cores (≥ 1 m depth) were taken from the basin center and separated into five depth intervals (0–10, 10–30, 30–50, 50–75, and 75–100 cm) for analysis. To determine SOC, we first measured organic matter content in all samples by mass loss on ignition (LOI) for 16 hours at 400°C (Nelson & Sommers, 1996). We then chose a 90 sample subset spanning the range of LOI

values to measure C content using dry combustion (CHN analyzer, LECO Corp, St. Joseph, MI). We fit a linear regression between LOI and C content in the sample subset and used the fit equation ($R^2 = 0.99$) to estimate C content from LOI in all samples. Bulk density was determined using the core method (Blake & Hartge, 1986), with linear correction for compaction (Walter et al., 2016).

Stocks were calculated by multiplying C content, bulk density, and sample length. For each core, SOC stocks were summed over all depth increments to 1 m, and wetland values were taken as the average of duplicate cores. The mean difference between duplicates was 3.6 kg C m⁻² (11.6% relative difference).

Because our initial objective was to examine soil spatial variability, our sampling approach differed in emergent wetlands. For each wetland and vegetation zone, we selected one random location and took three soil cores spaced 10 m apart (total $n = 9$ cores per wetland). Cores were taken to a minimum depth of 50 cm (mean = 67 cm) and separated by naturally-occurring horizons. Organic matter was determined by LOI, and C content was estimated using the linear regression fit with forested wetland samples. To compare with forested wetlands, we used a data harmonization approach: SOC density was modeled as a function of LOI using forested wetland data (sensu Holmquist et al., 2018; Morris et al., 2016), and 1 m stocks were estimated by integrating depth functions fit with horizon values (Bishop et al., 1999). Details of soil data harmonization are in supplementary methods.

Water level data and hydrologic metrics

Continuous water level data was collected from 2018 to 2019 in a subset of study wetlands. Shallow wells were established in 12 forested wetlands and instrumented with pressure transducers (HOBO water level loggers; Onset Computer Corporation, Bourne, MA). Water levels were aggregated to daily averages for each wetland. Where necessary, data gaps were filled using nearby wells not included in this study.

We chose six metrics to capture different aspects of the hydrologic regime with potential importance in C cycling (Richter et al., 1996). From 2019, which had average rainfall (1114 mm), we calculated: median, maximum, interquartile range, inundation duration (i.e., hydroperiod), and exposure date (i.e., the first day water level dropped below the surface). From 2018, which was wetter than average (1555 mm) but did not require gap filling, we calculated recession rate as the median daily water level decline during the growing season (May–Oct). We included only days when water levels declined in all wetlands and excluded days following rainstorms. A summary of metrics can be found in Table 1.1a.

Geospatial data and terrain metrics

We analyzed wetland relative topography using a 1 m lidar-derived digital elevation model (DEM) of the study area (Lang et al., 2013). Wetland basins were delineated with a Stochastic Depression Analysis tool (Lindsay, 2016), which has been used to map wetlands in the region (Vanderhoof et al., 2017). Using the delineated wetlands and DEM, we calculated six terrain metrics (Table 1.1b)

associated with wetland presence (Winter, 2001). These included standard descriptors (depth, area, and shape index) as well as other metrics that, based on literature reports, may contain unique information about wetland hydrology (relative topographic position, relative catchment area, and basin profile coefficient as indicators of landscape position; potential runoff inputs; wetland bathymetry; Table 1.1b). Due to an extreme value, relative catchment area was transformed by $-1/x$ for analysis. Geospatial data was processed and analyzed in QGIS (QGIS Development Team, 2022) using tools from Whitebox (Lindsay, 2016) and SAGA (Conrad et al., 2015), and in R (v4.2.0; R Core Team, 2022) using the *sf* (Pebesma, 2018) and *terra* (Hijmans et al., 2022) packages. An extended description of geocomputation is in supplementary methods.

Statistical analysis

Relationships between forested wetland SOC stocks and hydrologic/terrain metrics were quantified using multiple linear regression. Our analysis focused on two models: one with hydrologic metrics (“hydrology model”; $n = 12$ wetlands) and one with terrain metrics (“terrain model”; $n = 19$ wetlands). We included a *site* term in each model to account for unknown differences between our sampling sites. All statistical analysis was done in R using the *car* (Fox & Weisberg, 2018) and *rdacca.hp* (Lai et al., 2022) packages.

We expected multicollinearity, so we examined pairwise correlations and variance inflation factors (VIFs) to select minimum subsets of hydrologic/terrain metrics that characterized differences among wetlands (Zuur et al., 2007). Since our

analysis was exploratory, we did not do further variable selection (Lai et al., 2022; Mac Nally, 2000), and we present regression coefficients descriptively while recognizing their uncertainty due to small sample sizes (Forstmeier & Schielzeth, 2011; Gregorich et al., 2021). Fitted models were validated by visually inspecting residuals (Figures S1.1-1.2).

The relative importance of metrics in regression models was evaluated using variance partitioning methods (Kraha et al., 2012). Specifically, we determined the average contribution of each metric to the total variance explained in the model over all subsets of explanatory variables (i.e., hierarchical partitioning (Murray & Conner, 2009)). Results are expressed as partial R^2 values for each metric, which sum to the multiple R^2 of the model, and as % R^2 , which is the partial R^2 divided by the multiple R^2 .

Commonality analysis was used to compare the variability in SOC stocks explained by hydrologic metrics, terrain metrics, and site differences (Ray-Mukherjee et al., 2014). First, we re-fit both models without *site* and chose the three metrics with the highest partial R^2 in each. We then fit a third model including the selected groups of hydrologic and terrain metrics, and *site* ($n = 12$ wetlands), and partitioned variance using commonality analysis. This technique quantified each group's unique contribution to the model as well as the contributions shared among groups (Ray-Mukherjee et al., 2014). As in hierarchical partitioning, contributions are expressed as proportions of the model's R^2 . Pairwise relationships among all metrics were assessed with Pearson correlation coefficients.

Results

Natural variability in wetland SOC stocks

In forested wetlands, SOC stocks ranged from 19.7 to 51.0 kg m⁻² (mean = 32.2 kg m⁻² SD = 8.40, CV = 26.1%; Figure 1.3). Natural emergent wetland estimates spanned a similar range (14.0–49.4 kg m⁻²), and two of the three wetlands contained soils dominated by organic materials. Restored emergent wetlands had a narrower range of estimated SOC stocks (10.9–28.1 kg m⁻²), although several point estimates fell within the ranges of both types of natural wetlands (Figure 1.3).

There was high spatial variability in emergent wetland SOC. Mean estimated stocks were highest in open water (36.7 kg m⁻²) for natural wetlands and in herbaceous vegetation (24.1 kg m⁻²) for restored wetlands (Figure 1.3). Natural wetlands had higher among-zone variability (i.e., mean of CVs for each wetland; 36.3%) and among-wetland variability (i.e., mean of CVs for each zone; 40.5%) compared to restored wetlands (among-zone CV = 18.9%, among-wetland CV = 27.3%). Variability among natural wetlands was driven more by open water (CV = 46.7%) and herbaceous (CV = 64.4%) than by woody vegetation (CV = 10.6%; Figure 1.3). For the herbaceous zone, all restored SOC stock estimates fell within the natural range.

Wetland SOC stocks as a function of hydrologic metrics

As expected, there was multicollinearity and strong correlations among hydrologic metrics (Figure 1.4). Since water levels in all wetlands followed a similar seasonal pattern (Figure 1.2b), we assumed correlated metrics reflected the same

hydrologic dynamics, and proceeded with a subset containing *duration*, *max*, and *recession*. The strongest correlation in this subset was between *duration* and *max* ($r = 0.44$).

The hydrology model explained variability in SOC stocks ($R^2 = 0.75$, $R^2_{adj.} = 0.61$), but individual metrics differed in their contributions (Table 1.2). *Recession* was the most important, with a higher contribution (37.7%) than the other two combined (20.8%), while *duration* was relatively unimportant. Both *recession* and *max* were positively associated with SOC stocks ($\beta = 0.52 \pm 0.24$ and 0.53 ± 0.23 , respectively); in other words, wetlands with deeper water and slower drying rates tended to have higher SOC stocks. The negligible r^2 value of *max*, however, shows its contribution to the model (% $R^2 = 13.4$) was likely due to suppression of residuals rather than by direct association with SOC stocks. *Recession* was the only metric that explained variability in SOC stocks individually ($r^2 = 0.34$).

Site was an important component in the hydrology model (% $R^2 = 41.6$). SOC stocks were lower in JL than in BC ($\beta = -1.62 \pm 0.62$), and this difference was not explained by hydrologic metrics. Although we did not include interaction terms in the model, pairwise relationships between hydrologic metrics and SOC stocks appeared to depend on *site* (Figure 1.5a-c). Within BC, all three metrics had higher slopes and explained more variability (mean $r^2 = 0.69$) than within JL (mean $r^2 = 0.14$).

Relationships between wetland relative topography, hydrology, and SOC stocks

There were strong correlations between terrain metrics and hydrologic metrics (Figures 1.4 and S1.3). The strongest correlation was between *depth* and *max* ($r =$

0.87), which was expected given that *depth* is effectively an estimate of *max* based on relative topography. *Duration* and *recession* were most strongly correlated with *RTP* and *profile*, respectively ($r = -0.70$ and 0.66). Among terrain metrics, *catchment* and *depth* were correlated ($r = -0.79$) so we excluded the former from further analysis.

As with hydrology, individual metrics contributed unevenly to the terrain model (Table 1.3). *Profile* was the most important ($\% R^2 = 58.0$) and was positively associated with SOC stocks ($\beta = 0.74 \pm 0.34$); that is, wetlands that were more cylindrical (i.e., had flatter bottoms) tended to have higher SOC stocks (Figure 1.5d). Despite correlating with hydrologic metrics, *depth* and *RTP* had minor contributions to the terrain model ($\% R^2 = 12.5$ and 9.5). *Site* was a minor component ($\% R^2 = 7.6$) and relationships between terrain metrics and SOC stocks did not appear to consistently differ between sites (Figures 1.5d-f and S1.4).

Commonality analysis revealed that hydrologic and terrain metrics both explained a common portion of variability in wetland SOC stocks (Figure 1.6). Hydrologic metrics were represented by *duration*, *max*, and *recession*, and terrain metrics by *depth*, *profile*, and *shape*. The largest component was that shared by the hydrologic and terrain groups, which contributed 42.9% of the model's R^2 value. Both groups had similar unique components (hydrologic = 12.8%, terrain = 12.0%). The unique component of *site* was approximately zero (0.2%); nearly all its contribution was shared by terrain or (to a lesser extent) hydrologic metrics. Variability shared among all groups was a small negative value (-5.4%), which was likely due to sampling error and can be considered zero (Reichwein Zientek & Thompson, 2006).

Discussion

Focusing on one of the most common types of wetlands worldwide—seasonal depressional wetlands—we show extensive variability in SOC storage. This was evident in both natural and restored wetlands, and to such an extent that it was difficult to distinguish wetland types based on their SOC content. This finding raises two pertinent questions: how much do SOC stocks vary among wetlands on any landscape? And can we explain SOC variability by quantifying wetland-scale differences in hydrology and relative topography? In the following, we address these questions and discuss the implications of our study for how reference conditions are determined in wetland restoration.

High natural variability in wetland SOC stocks

We measured a wide range of SOC stocks among wetlands that would be considered replicates for most purposes. Wetlands are often classified based on vegetation and hydrogeomorphology, and wetland types are widely used to approximate functions in lieu of empirical data (Sieben et al., 2018). However, despite their shared vegetation type and hydrogeomorphic class (depressional), as well as their proximity to one another, the 19 forested wetlands we sampled had SOC stocks spanning values characteristic of mineral wetlands ($\sim 20 \text{ kg C m}^{-2}$) to those of organic wetlands ($> 50 \text{ kg C m}^{-2}$; Table 1.4). Mean stocks in our forested wetlands were $32.2 \pm 8.4 \text{ kg C m}^{-2}$; in comparison, a recent analysis of 529 inland wetlands, which spanned vegetation types and ecoregions throughout the conterminous US,

estimated mean SOC stocks at $19.7 \pm 10.6 \text{ kg m}^{-2}$ (Uhran et al., 2021). We compiled a list of relevant studies encompassing a range of wetland types and found that high within-type variability is common (Table 1.4). This suggests that caution should be broadly applied when assuming that wetland types, as defined by existing classification systems, reflect variability in ecosystem processes (Bullock & Acreman, 2003; Hruby, 2001; Lisenby et al., 2019; Stander & Ehrenfeld, 2009).

We also found that SOC varied within spatially heterogeneous wetlands. Accounting for spatial variability is essential for accurately assessing wetland functions and can help to identify drivers of function in reference systems (Larkin et al., 2016; Stolt et al., 2001). In our natural emergent wetlands, estimated SOC stocks varied among vegetation zones, but in an inconsistent pattern among wetlands. Spatial variability was lower in restored emergent wetlands, which aligns with studies indicating that soil properties are more spatially homogeneous in restored wetlands (R. P. Brooks et al., 2005; Bruland et al., 2006). While vegetation communities are thought to influence wetland SOC storage (Bernal & Mitsch, 2012; Davila & Bohlen, 2021; Marín-Muñiz et al., 2014), our results suggest that vegetation type may not be a reliable indicator of within-wetland SOC variability. We did not directly measure productivity, but we expect its variability to be dominated by vegetation type, as reported elsewhere (e.g., Osland et al., 2018). Instead, other factors (e.g., flooding patterns and soil properties that affect oxygen availability and decomposition; Owers et al., 2020) likely contribute to spatial variability within these wetlands.

Our observations of high natural variability support a revised strategy for defining reference conditions (e.g., Shackelford et al., 2021). In small datasets like

ours, high variability limits the ability to evaluate restored wetlands relative to references. Incorporating attributes like hydrology can help interpret reference information (as we address in the following section), but significantly increasing precision in reference conditions requires extensive data and a thorough understanding of landscape variability (White & Walker, 1997). Constraints on time and funding often put these conditions out of reach for practitioners. With outcomes unpredictable, restoration assessment would benefit from a more rigorous treatment of uncertainty and a greater focus on the natural range of variability (Brudvig & Catano, 2021; Oliver et al., 2023). For example, strategies like setting targets for groups of wetlands (rather than for individual wetlands) and reducing the precision of targets acknowledge ecosystem dynamism and promote heterogeneity (Hiers et al., 2012, 2016). Importantly, our results also suggest that estimates of restored wetland “C storage potential” should be accompanied by uncertainty analysis based on landscape-scale variability.

Complex role of hydrology in explaining SOC stock variability among wetlands

Water level recession rate had the strongest relationship with SOC stocks, while standard hydrologic descriptors, notably inundation duration (i.e., hydroperiod), explained relatively little variability among wetlands. Measures of duration and average water level are commonly used in wetland restoration to set performance standards and evaluate success (Schlatter et al., 2016; U.S. Army Corps of Engineers, 2005). Although these metrics have been linked to wetland processes (Barksdale et al., 2014; Lewis & Feit, 2015), our results indicate that the most relevant aspects of

the hydrologic regime may depend on the system and process of interest (Johnson et al., 2012).

The importance of recession rate suggests a key role of drying processes in wetland SOC storage. Recession rate represents wetland response to negative water fluxes, mainly evapotranspiration and groundwater outflow (Park et al., 2014).

Human management at the catchment scale has been shown to affect wetland recession rates by altering upland forest evapotranspiration (Golladay et al., 2021).

Wetlands that dry faster may have soils with increased oxygen diffusion, increased temperature sensitivity of respiration, and more frequent wet–dry cycles; all of which can promote C loss through mineralization (Capps et al., 2014; Chapman et al., 2019; Chen et al., 2018). Recent reports have linked recession rates to other ecological and biogeochemical variables (Beaulieu et al., 2018; Botson et al., 2016; Yuan et al., 2017), which implies a broader importance in wetland function that should be examined in future studies.

Interestingly, site-scale differences appeared to modulate hydrology–SOC relationships. Such differences could include, for example, proximity to drainage ditches, absolute elevation, forest age, and adjacent land use (Golladay et al., 2021; Jones et al., 2018; Rains et al., 2016). While studies have established that large-scale factors like climate and geological setting can be important controls of SOC (e.g., Ferreira et al., 2022), these did not vary within our study area. Furthermore, since our forested wetlands lacked emergent vegetation and most had the same soil type (i.e., map unit; Table S1.2), we assumed *in situ* production and soil properties were relatively uniform, but fine-scale spatial variability in these factors could affect SOC

storage (Barksdale et al., 2014; Bruland & Richardson, 2005; M. S. Fennessy et al., 2018; Maynard et al., 2014). For example, soil texture can vary among neighboring wetlands (O'Driscoll & Parizek, 2008; Stolt et al., 2000), including those within the same soil map unit (Lin et al., 2005), and we did note that deeper layers at BC had finer textures than at JL (data not shown). Studies have shown that soil physical properties may interact with water level to influence wetland C processes (Daugherty et al., 2019; Volik et al., 2020), so it is plausible that soil texture contributed to the site differences we observed. Similarly, though *in situ* production was likely a minor source of variability, terrestrial inputs are also important sources of C, and may have interactive effects with hydrology on wetland C budgets (Rubbo et al., 2006; Stoler & Relyea, 2020; Wardinski et al., 2022). Regardless of its cause, spatial variability in wetland hydrology–SOC relationships may occur within limited areas and should be considered when setting expectations for restored wetlands.

Our study joins a growing list that have found complex or unclear relationships between wetland hydrology and SOC (e.g., Carnell et al., 2018; Chanlabut et al., 2020; Davila & Bohlen, 2021; Pearse et al., 2018). In addition to other sources of variability, these results suggest that hydrology is a multifaceted and indirect driver of wetland SOC (Mueller et al., 2016; Straková et al., 2012). Hydrology influences wetland C processes through numerous mechanisms such as dissolved organic matter flows, temperature, and, predominantly, soil oxygen diffusion (Kayranli et al., 2010; Straková et al., 2012; Wardinski et al., 2022). Despite the negative effect of water level on oxygen content (and thus decomposition (Kayranli et al., 2010)), persistent water saturation can maintain anoxia long after

inundation recedes (Megonigal et al., 1993). Further, inundation does not always slow decomposition (Mueller et al., 2016). Decomposition rates also depend on factors such as organic matter chemistry, physicochemical stabilization, microbial communities, and the availability of alternative electron acceptors (Kirwan et al., 2013; Kottkamp et al., 2022; Yarwood, 2018). Overall, though hydrology is a “master variable” in wetland function, its breadth of biogeochemical influence makes it difficult to quantify its role in specific processes.

Relative topography and hydrology provide similar information about wetland SOC stocks

We found that hydrology and relative topography explained much of the same variability in wetland SOC stocks. Relative topography provides the physical basis for wetland hydrology (Jackson et al., 2014; Winter, 1988), and therefore may help characterize wetland ecosystem processes that respond to the hydrologic regime (Richardson et al., 2010). Accordingly, our results support evidence that cylindrical (i.e., flat-bottomed) wetlands have slower recession rates (R. T. Brooks & Hayashi, 2002; Chandler et al., 2017; Hill & Durchholz, 2015) and indicate that these wetlands may also have higher SOC stocks. Relative topography can also reflect other forms of landscape-scale variability (Park et al., 2014; Webster et al., 2011); for example, the basin-forming processes that determine wetland bathymetry may also affect sedimentation and soil texture (Hayashi & van der Kamp, 2000; Lane & D’Amico, 2010). Developing a mechanistic understanding of the relationships between relative

topography, hydrology, and wetland processes is imperative to inform how restoration interventions can support functions like SOC storage.

Hydrology did not offer a clear advantage over relative topography in explaining SOC stock variability among our wetlands. This finding is significant in that relative topography is a far more practical tool for large-scale analyses. Terrain metrics can be rapidly computed over large areas with publicly-available remote sensing data, in contrast to water level data, which is more expensive and time-consuming to obtain (Cianciolo et al., 2021). It should be noted that human-made structures (e.g., ditches, tile drainage) that modify wetland hydrology may not be detected by remotely-sensed terrain metrics (Jones et al., 2018); thus, care should be taken when scaling to broader areas.

Relative topography may even be a preferable indicator when only short-term hydrologic data is available. Although 2019 represented average water conditions, wetland hydrologic tendencies can shift over time with changes in catchment land cover, regional water withdrawals, and climate-driven precipitation patterns (Fay et al., 2016; Lewis & Feit, 2015; McCauley et al., 2015). Hydrologic non-stationarity is especially likely in heavily altered areas, where contemporary conditions may uncouple from “slow” variables like SOC that develop over decades to centuries (Hossler & Bouchard, 2010; Schulte et al., 2019). Relative topography is less responsive to nonlocal disturbance and could therefore more robustly represent reference wetland conditions at these time scales.

Conclusion

Understanding natural variability in ecosystem processes is critical for successful restoration. In wetlands, variability in C cycling is widely recognized, but attention has mainly centered on C fluxes (Kolka et al., 2018). We found that SOC stocks varied substantially among neighboring least-disturbed wetlands with similar vegetation and hydrogeomorphology. In a restoration context, this implies that reference conditions have inherent uncertainty, and that success should be evaluated against the range of natural variability (Oliver et al., 2023). Although hydrologic metrics explained some variability in SOC stocks, our results highlight the complex and context-dependent relationships between wetland hydrology and ecosystem processes. We therefore caution that a reliance on hydrology as the primary predictor of wetland processes risks undervaluing the role of other potential drivers. Lastly, wetland terrain metrics were correlated with hydrologic metrics and explained similar variability in SOC stocks. This result is promising given that the physical landscape can be analyzed at large scales and offers an interface for management to affect wetland processes (Euliss et al., 2008). As focus grows on quantifying C benefits in restoration, the importance of appropriately defining reference conditions is paramount. In the foreseeable future, determining how much SOC a wetland “should have” is likely to remain unfeasible, but C accounting practices can still have robust ecological foundations by integrating natural variability and its drivers into reference frameworks.

Tables

Table 1.1. Metrics assessed as explanatory variables of forested wetland SOC stocks. Hydrologic metrics (a) were selected to represent distinct and fundamental aspects of wetland hydrologic regimes. Terrain metrics (b) were selected based on hypothesized or empirical relationships with hydrologic regimes as reported in literature.

Metric	Definition/description	Mean value (min, max)
a) Hydrologic (n = 12 wetlands)		
<i>duration</i>	Total number of days inundated (i.e., water level > 0)	263 (228, 293)
<i>exposure</i>	Earliest day of year exposed (i.e., water level < 0)	222 (184, 257)
<i>IQR</i>	Interquartile range; robust index of daily water level variability (m)	0.77 (0.49, 1.16)
<i>max</i>	Maximum daily water level (m)	0.76 (0.50, 1.11)
<i>median</i>	Median daily water level (m)	0.43 (0.18, 0.66)
<i>recession</i>	Median daily water level decline during rain-free periods in May–Oct (cm day ⁻¹)	-1.42 (-1.85, -0.86)
b) Terrain (n = 19 wetlands)		
<i>area</i>	Total area of wetland basin (m ²)	930 (144, 2240)
<i>catchment</i>	Total area (wetland + upland) draining internally to wetland basin, given as relative to wetland area	7.78 (2.93, 29.8)
<i>depth</i>	Maximum depth of wetland basin (m)	0.60 (0.21, 1.10)
<i>profile</i>	Index of wetland 3D shape from conical (low) to cylindrical (high) (Hayashi & van der Kamp, 2000)	1.98 (0.80, 3.95)
<i>RTP</i>	Relative topographic position; mean value of deviation from mean elevation within a 500 x 500 m window	-0.87 (-1.46, -0.48)
<i>shape</i>	Size-invariant area-to-perimeter ratio; represents complexity of 2D shape, where 1 is a perfect circle	1.11 (1.02, 1.27)

Table 1.2. Results of multiple linear regression of SOC stocks as a function of hydrologic metrics in natural forested wetlands (n = 12).

Metric	r^2	VIF	β	P	Partial R^2	% R^2
<i>site (JL)</i>	0.28	2.9	-1.62 ± 0.62	0.04	0.31	41.6
<i>recession</i>	0.34	1.6	0.52 ± 0.24	0.07	0.28	37.7
<i>max</i>	<0.01	1.6	0.53 ± 0.23	0.06	0.10	13.4
<i>duration</i>	<0.01	3.1	0.20 ± 0.33	0.57	0.06	7.4
Hydrology model: $R^2 = 0.75$; $R^2_{adj.} = 0.61$; $P = 0.03$						

Model statistics: marginal R^2 , adjusted R^2 ($R^2_{adj.}$), P value (P)

Statistics for each term: squared bivariate correlation with SOC stocks (r^2), variance inflation factor (VIF), beta coefficient ($\beta \pm \text{std. err.}$), P value (P), partial contribution to multiple R^2 , and percent contribution to multiple R^2

Table 1.3. Results of multiple linear regression of SOC stocks as a function of terrain metrics in natural forested wetlands (n = 19).

Metric	r^2	VIF	β	P	Partial R^2	% R^2
<i>profile</i>	0.41	3.0	0.74 ± 0.34	0.05	0.31	58.0
<i>depth</i>	0.07	2.7	-0.30 ± 0.32	0.38	0.07	12.5
<i>RTP</i>	0.10	1.7	-0.02 ± 0.26	0.94	0.05	9.5
<i>shape</i>	0.06	2.3	0.06 ± 0.30	0.85	0.05	8.5
<i>site (JL)</i>	0.07	2.4	-0.03 ± 0.59	0.96	0.04	7.6
<i>area</i>	0.02	1.9	-0.08 ± 0.27	0.77	0.02	3.9
Terrain model: $R^2 = 0.54$; $R^2_{adj.} = 0.30$; $P = 0.10$						

Model statistics: multiple R^2 , adjusted R^2 ($R^2_{adj.}$), P value (P)

Statistics for each term: squared bivariate correlation with SOC stocks (r^2), variance inflation factor (VIF), beta coefficient ($\beta \pm \text{std. err.}$), P value (P), partial contribution to multiple R^2 , and percent contribution to multiple R^2

Table 1.4. Variability in wetland SOC stocks from this study and literature reports. Data are field-measured from natural (least-disturbed) non-tidal freshwater wetlands in temperate climates. Wetland types are as described in the studies, and soil type (O = organic, M = mineral), if indicated, is self-defined by the publication. Only studies reporting 1 m stocks are included. Ranges of values are shown if given. *N* = number of wetlands.

Wetland type	<i>N</i>	1 m SOC stock (kg C m ⁻²)		Reference
		Mean ± std. dev.	Range	
Coastal Plain depressional (O)	3	73.3 ± 47.4	22.1–115.7	Fenstermacher et al., 2016
Seasonally inundated (O)	6	68.3 ± 44.1		Pearse et al., 2018
Fen	6	64.5 ± 8.6		Zhang et al., 2008
Floodplain forest (O)	15	53.3 ± 9.7	38.0–68.7	Ricker & Lockaby, 2015
Forested depressional	19	32.2 ± 8.4	19.7–51.0	<i>This study</i>
Marsh	5	25.2 ± 9.3		Zhang et al., 2008
Forested riparian	29	24.6 ± 9.6	11.7–49.5	Ricker et al., 2013
Coastal swamp oak forest	6	24.1 ± 13.6	13.8–43.3	Kelleway et al., 2021
Coastal Plain depressional (M)	11	21.5 ± 17.2		Fenstermacher et al., 2016
Floodplain forest (M)	15	19.3 ± 10.5		Ricker & Lockaby, 2015
Marshy meadow	5	16.0 ± 2.3		Zhang et al., 2008
Floodplain forest (M)	10	14.9 ± 3.3	9.5–19.2	Heger et al., 2021
Floodplain grassland (M)	5	14.4 ± 3.6	11.2–18.3	Heger et al., 2021
Grassland playa	17	10.6 ± 4.1		O’Connell et al., 2016

Figures

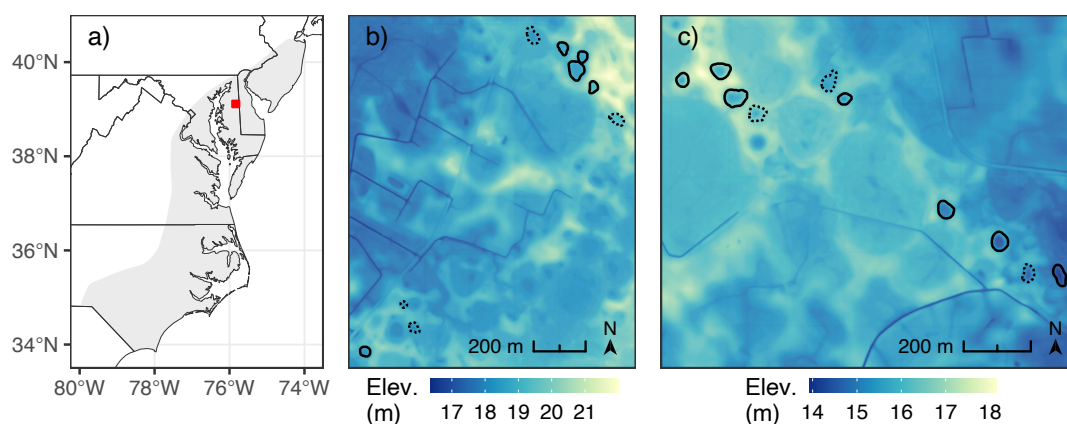


Figure 1.1. Location of study area (red marker) within the mid-Atlantic Coastal Plain of Maryland, USA (a). Terrain maps of the two forested wetland study sites, “BC” (b; 39.06°N, 75.83°W) and “JL” (c; 39.06°N, 75.75°W), which are ~ 7 km apart. Elevation in (b-c) is from a digital elevation model and shown as m above sea level. Natural forested wetlands sampled for SOC stocks ($n = 19$) are outlined, with solid outlines indicating the 12 wetlands in which water level was monitored (emergent wetlands not shown).

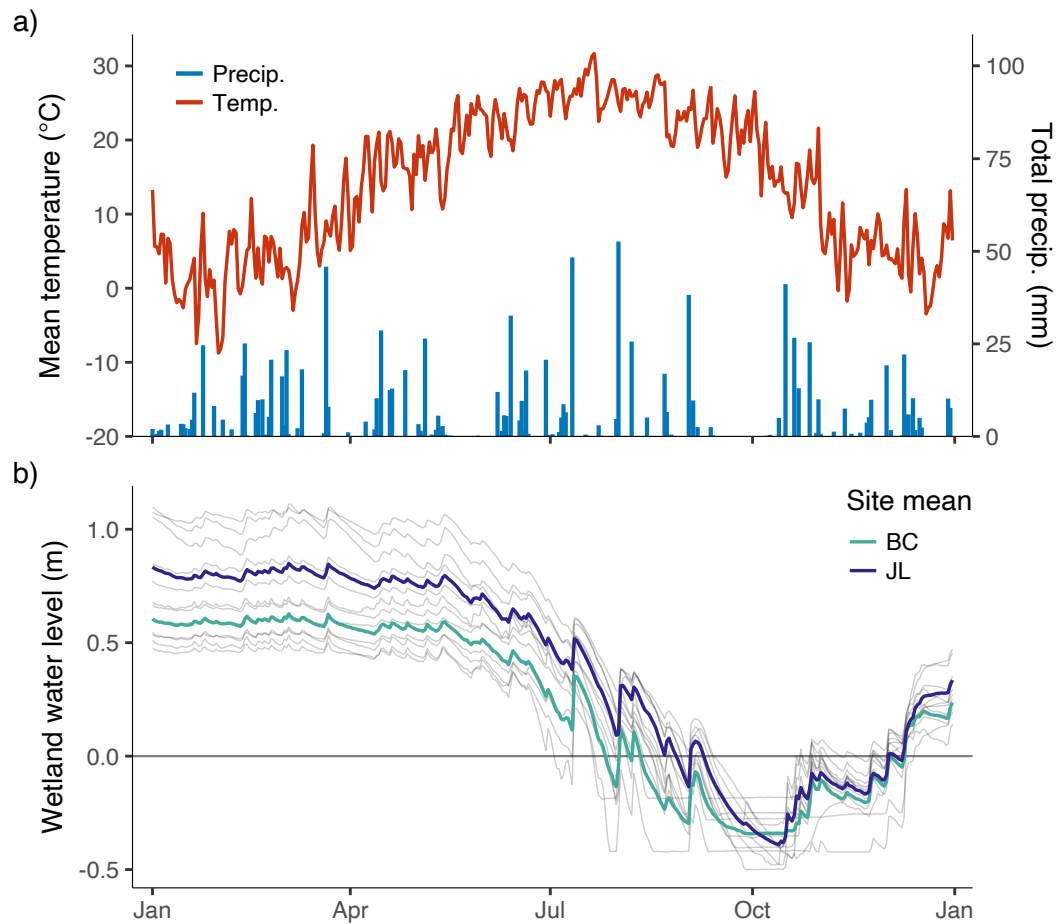


Figure 1.2. Daily 2019 (a) mean temperature and total precipitation, and (b) water level in a subset of forested wetlands. Water levels shown as daily means of wetlands at study sites “JL” and “BC” ($n = 7$ and 5) and for each wetland separately (grey lines). Some wetland water levels appear to flatten as wells dried and transducers read constant values. Climate data was collected at JL weather station.

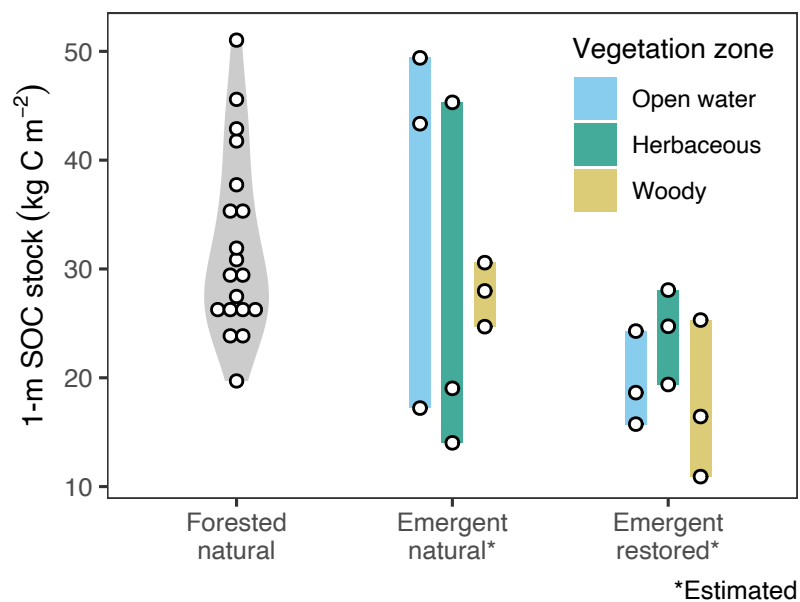


Figure 1.3. Variability in SOC stocks among forested natural wetlands, alongside point estimates from vegetation zones in natural and restored emergent wetlands. Shaded areas show range of values.

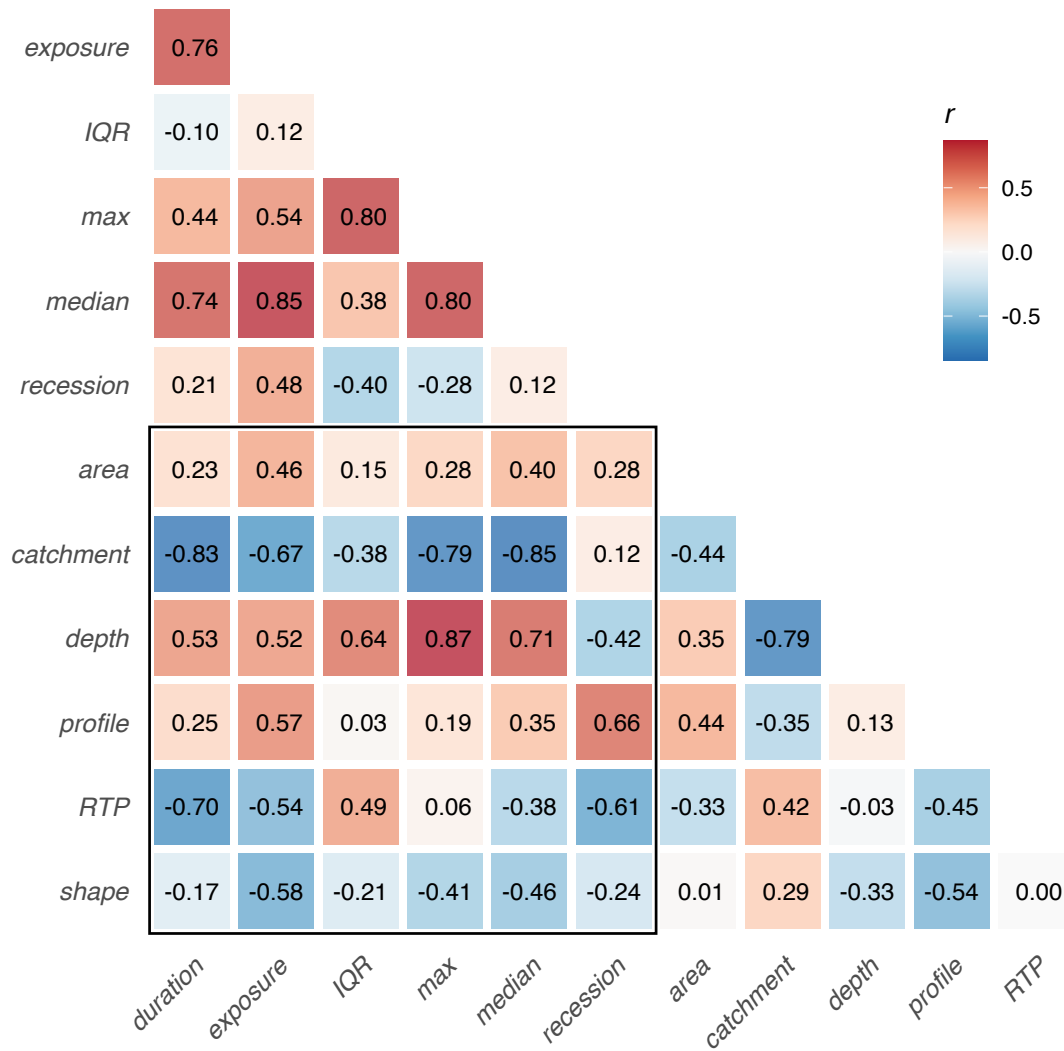


Figure 1.4. Pearson correlation matrix of hydrologic metrics (*duration*, *exposure*, *IQR*, *max*, *median*, *recession*) and terrain metrics (*area*, *catchment*, *depth*, *profile*, *RTP*, *shape*) in natural forested wetlands. Outlined box contains correlations between a hydrologic and a terrain metric. Correlations between two terrain metrics represent data from 19 wetlands; all other correlations represent a 12 wetland subset for which hydrologic data was available. Note that *catchment* was transformed by $-1/x$.

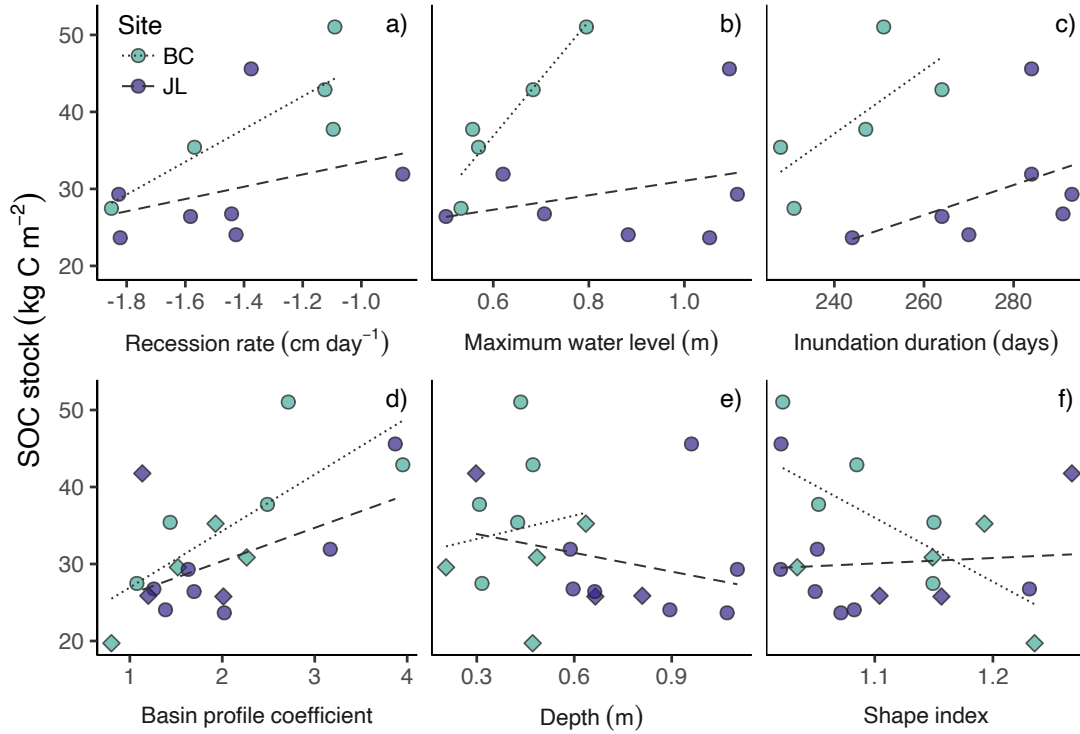


Figure 1.5. Relationships between upper 1 m SOC stocks and hydrologic/terrain metrics in natural forested wetlands ($n = 19$). The three hydrologic (a-c) and three terrain (d-f) metrics that contributed the most to their respective model are shown; diamond-shaped markers are wetlands without water level data (i.e., only included in terrain analysis; $n = 7$). Linear best-fit lines are shown separately for each study site (“BC”, “JL”).

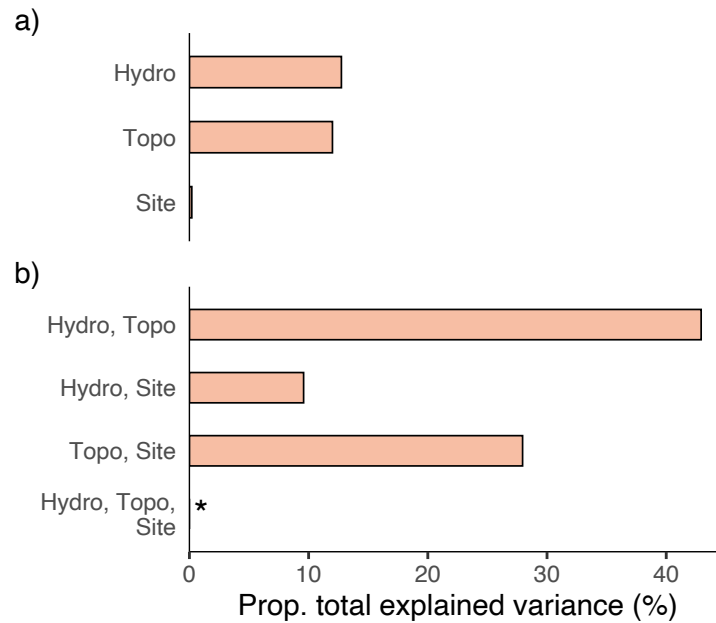


Figure 1.6. Variance partitioning of wetland SOC stocks. Colored bars are proportions of explained variance (a) attributed uniquely to hydrologic metrics ("Hydro"), terrain metrics ("Topo"), and unknown sampling site differences, and (b) shared among those groups. Hydrologic metrics included recession rate, maximum water level, and inundation duration; terrain metrics included basin profile coefficient, depth, and shape index. The asterisk in (b) denotes a component with a negative contribution (-5.4%) shown as zero. The total variability explained by the model (i.e., multiple R^2) was 0.85 ($R^2_{adj.} = 0.60$).

Supplementary materials

Estimating SOC stocks in emergent wetlands

We used a soil data harmonization approach to estimate SOC stocks in emergent wetlands and compare them directly to forested wetlands (Uhran et al., 2021). This was necessary because our sampling approaches were different; specifically, in forested but not emergent wetlands we 1) measured bulk density and 2) split cores into fixed-depth intervals up to 1 m.

To address missing bulk density values, we used forested wetland data to model bulk density as a function of organic matter content and applied the fit to emergent wetland samples. We used a nonlinear “ideal mixing model” (Holmquist et al., 2018; Morris et al., 2016)

$$BD = \frac{1}{\frac{OM}{k1} + \frac{(1 - OM)}{k2}} , \quad (1.1)$$

where BD is bulk density (g cm^{-3}), OM is organic matter content (g g^{-1}), and $k1$ and $k2$ are parameters representing the density of organic and mineral soil components respectively. We recognize that emergent wetlands may have different BD–OM relationships, and restored wetlands in general have higher BD than natural wetlands (Yu et al., 2017), so some predictions may be biased. We estimated parameters using nonlinear least squares; the best fit model had a root mean squared error (RMSE) of 0.12 g cm^{-3} and the $k1$ and $k2$ parameters $\pm$ std. error were 0.096 ± 0.005 and $2.36 \pm 0.13 \text{ g cm}^{-3}$, respectively.

To address the mismatch in depth intervals, we estimated emergent wetland C density at the fixed-depth intervals used for forested wetland samples (i.e., 0–10, 10–

30, 30–50, 50–75 and, 75–100 cm). We fit mass-preserving splines, which is a standard method for harmonizing data from soil cores that were split by horizon in the field (Bishop et al., 1999), to C density profile data in each emergent soil core. Spline fits and fixed-depth interval C density estimates were determined using the R package *mpspline2* (O’Brien, 2022). To calculate 1 m C stocks, we multiplied C density by interval length and took the sum over each core. Final C stock estimates for each wetland/zone were averages of three replicate cores. We treat these values as estimates due to the high uncertainty and potential for bias in the harmonization process.

Geocomputation for terrain metrics

Note: for any computation that used a specific software tool, that tool is referenced as (“Tool”; Developer).

Prior to analysis, the lidar-derived digital elevation model (DEM) was filtered to reduce the effects of systematic and random errors. Lidar cannot penetrate some landscape features (e.g., buildings, dense ground vegetation), resulting in DEM errors that can be problematic in low-gradient landscapes (Hutchinson & Gallant, 2000). We considered these systematic errors because they are always higher than the ground elevation, and we removed them using a specialized filter (“Remove Off Terrain Objects”; Whitebox). The DEM was then filtered to smooth random errors and abrupt changes in slope (“Multi Direction Lee Filter”; SAGA).

Wetland areas were delineated using a probabilistic approach (“Stochastic Depression Analysis”; Whitebox). This method accounts for the vertical accuracy of

the DEM (RMSE = 0.15 m in our case) by generating a distribution of errors, adding a random sample to each cell, then identifying depression cells (Lindsay & Creed, 2006). We ran 500 iterations of this process to estimate the probability of each cell belonging to a depression. In the resulting grid, we masked areas higher than a standard depression probability threshold of 80% (Vanderhoof et al., 2017; Wu et al., 2014), which corresponded with field surveys of maximum inundated extent for most of our wetlands. Depression areas were converted to polygons for further analysis.

Nested depressions (i.e., depressions within depressions) were delineated with a level-set method (Wu et al., 2019). Briefly, this algorithm finds the elevation in a depression at which surface water would form multiple disconnected areas. We considered areas greater than 50 m² as separate wetlands that merge at high water levels, which resulted in four nested wetlands (all located in site BC) among our study set. Note that the interpretation of some terrain metrics may vary between nested and non-nested wetlands. For example, depth and area (calculated as described below) of nested wetlands are likely to be lower than the maximum water level and inundated extent. However, we concluded that for these wetlands, the nested delineation more accurately represented the wetland than the unnested delineation, which in one case was more than 2000% larger in area and contained multiple other wetlands. We did not find any patterns in the residuals of our statistical models that suggested nested and non-nested wetlands should be distinguished during analysis.

We calculated area, depth, and shape index (“*shape*”) as basic morphometric indices for delineated wetlands. Area was the two-dimensional area, and depth was

the difference between the maximum and minimum elevation within each wetland.

Shape index, which is a size-invariant perimeter-to-area ratio, was calculated as

$$Shape\ index = \frac{P}{2\sqrt{\pi \cdot A}} , \quad (1.2)$$

where P is perimeter (m) and A is area (m²).

Wetland catchments were delineated to calculate relative catchment area (“*catchment*”). The filtered DEM was further conditioned by filling depressions (“Fill Depressions”; Whitebox) shallower than 10 cm. Flow was routed using the Deterministic 8 method (“D8 Pointer”; Whitebox), and catchments were delineated as the area draining to the deepest point inside wetland depressions (“Watershed”; Whitebox). Catchment areas were divided by the corresponding wetland areas to better represent the potential influence of catchment size on wetland water balance (Hayashi et al., 2016).

We selected the deviation from mean elevation (“Deviation from Mean Elevation”; Whitebox) as an indicator of wetland relative topographic position (“*RTP*”). This metric was calculated as

$$RTP = \frac{(z_0 - \mu)}{\sigma} , \quad (1.3)$$

where z_0 is the DEM elevation of a cell and mean (μ) and standard deviation (σ) were calculated within a 500 x 500 m window (Newman et al., 2018). The window size was about twice the diameter of the largest depressions identified in stochastic depression analysis. To obtain a single value for each wetland, we took the mean of all values inside the wetland area.

The basin profile coefficient (“*profile*”), which quantifies the curvature of wetland slopes, was estimated using a simple power equation (Hayashi & van der Kamp, 2000)

$$A = s \cdot \left(\frac{h}{h_0} \right)^{\frac{2}{p}}, \quad (1.4)$$

where A is inundated area (m^2); h is water level (m); h_0 is a reference water level, which we took as the maximum depth; s is a scaling constant that equals inundated area at h_0 ; and p is the dimensionless basin profile coefficient. Using the DEM, we simulated “filling up” each wetland basin to its maximum depth and counted the number of inundated grid cells at 5 cm depth increments. This gave us semi-empirical depth-area curves, to which we fit Equation 1.4 with nonlinear least squares to estimate p . The mean RMSE of all nonlinear fits was 23.1 m^2 or 2.5% of wetland total areas.

Table S1.1. Description of emergent wetlands included in analysis of SOC spatial variability. Woody vegetation at all wetlands was a mix of trees and shrubs. Soil map units are those reported in the USDA-NRCS Web Soil Survey (Soil Survey Staff, 2022).

Wetland	Approx. area (ha)	USDA soil map unit	Dominant herbaceous vegetation	Year restored	Restoration methods
Rest. 1	4.3	Lenni loam	Grasses, sedges	2003	Ditch plugging, tree removal
Rest. 2	1.3	Hammonton- Fallsington- Corsica complex	Rushes, sedges	2003	Ditch plugging, microtopography construction, organic matter addition, tree planting
Rest. 3	0.4	Whitemarsh silt loam	<i>Phragmites</i> , <i>Typha</i>	2004	Scraping, tree planting
Natu. 1	1.0	Hammonton- Fallsington- Corsica complex	Grasses, sedges	-	-
Natu. 2	2.5	Corsica mucky loam	Sedges	-	-
Natu. 3	0.4	Hammonton- Fallsington- Corsica complex	Sedges	-	-

Table S1.2. Description of natural forested wetlands included in analysis of SOC stock variability. Soil map units are those reported in the USDA-NRCS Web Soil Survey (Soil Survey Staff, 2022). Note: for wetlands mapped as Hammonton-Fallsington-Corsica complex, soil series is likely Corsica due to landscape position at the bottom of depressions (Goldman et al., 2020).

Site-wetland	Well	Min elev. (m.a.s.l.)	USDA soil map unit
BC-1		17.91	Hammonton-Fallsington-Corsica complex
BC-2		18.01	Hammonton-Fallsington-Corsica complex
BC-3		18.04	Hammonton-Fallsington-Corsica complex
BC-4	X	18.50	Hammonton-Fallsington-Corsica complex
BC-5	X	18.37	Hammonton-Fallsington-Corsica complex
BC-6	X	18.54	Hammonton-Fallsington-Corsica complex
BC-7		18.88	Hammonton-Fallsington-Corsica complex
BC-8	X	19.00	Hammonton-Fallsington-Corsica complex
BC-9	X	18.10	Hammonton-Fallsington-Corsica complex
JL-1		14.50	Lenni loam
JL-2		15.55	Hammonton-Fallsington-Corsica complex
JL-3	X	15.27	Hammonton-Fallsington-Corsica complex
JL-4	X	15.35	Hammonton-Fallsington-Corsica complex
JL-5	X	13.84	Lenni loam
JL-6	X	14.86	Hammonton-Fallsington-Corsica complex
JL-7	X	14.40	Hammonton-Fallsington-Corsica complex
JL-8	X	15.63	Corsica mucky loam, Carolina Bay
JL-9	X	15.48	Corsica mucky loam, Carolina Bay
JL-10		15.61	Corsica mucky loam, Carolina Bay

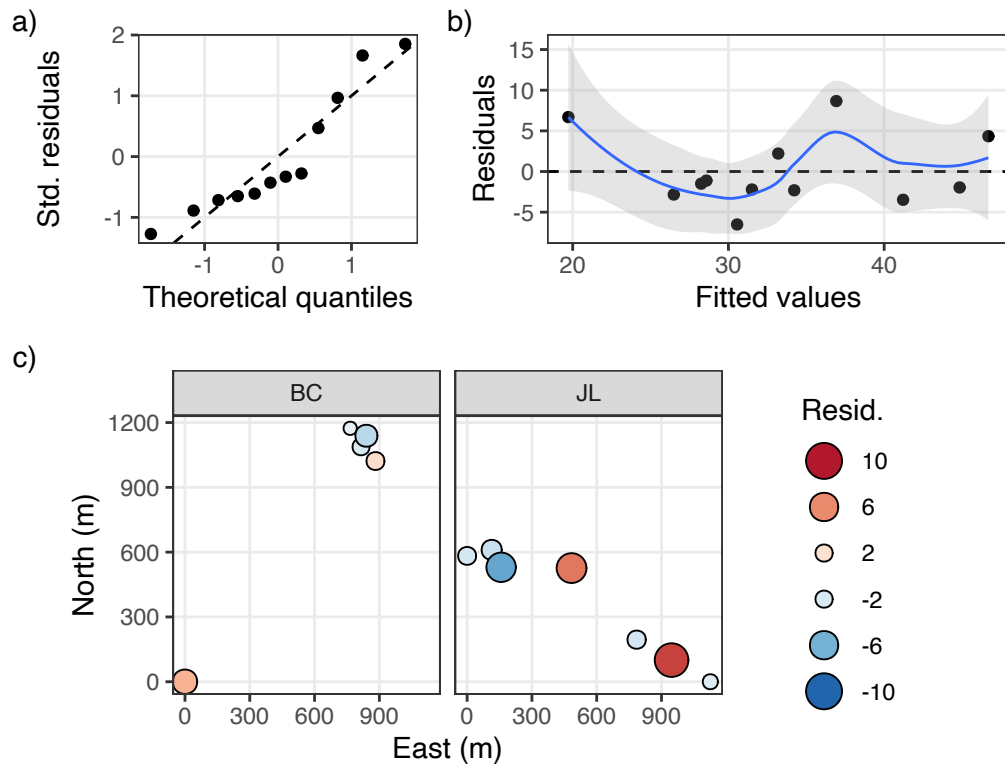


Figure S1.1. Hydrology model residual diagnostics. (a) Normal Q-Q plot. (b) Residuals vs. fitted values with a LOESS smoother and 95% confidence band. (c) Residuals by location at study sites BC and JL showing no spatial dependence; coordinates relative within each site area.

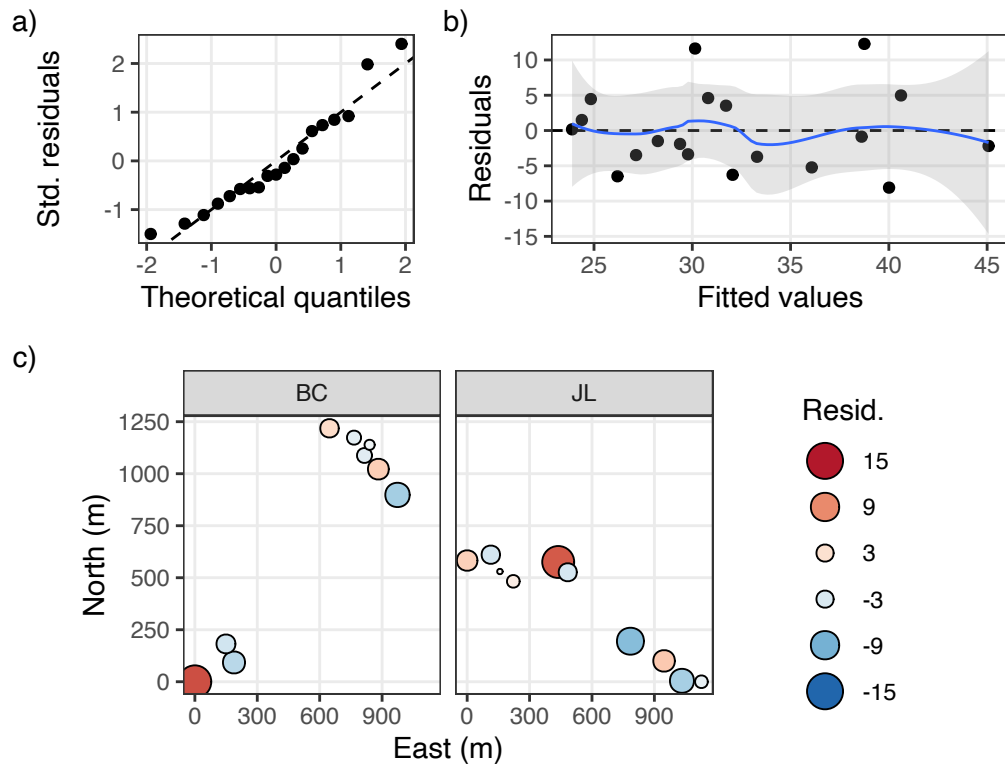


Figure S1.2. Terrain model residual diagnostics. (a-c) As in Figure S1.1.

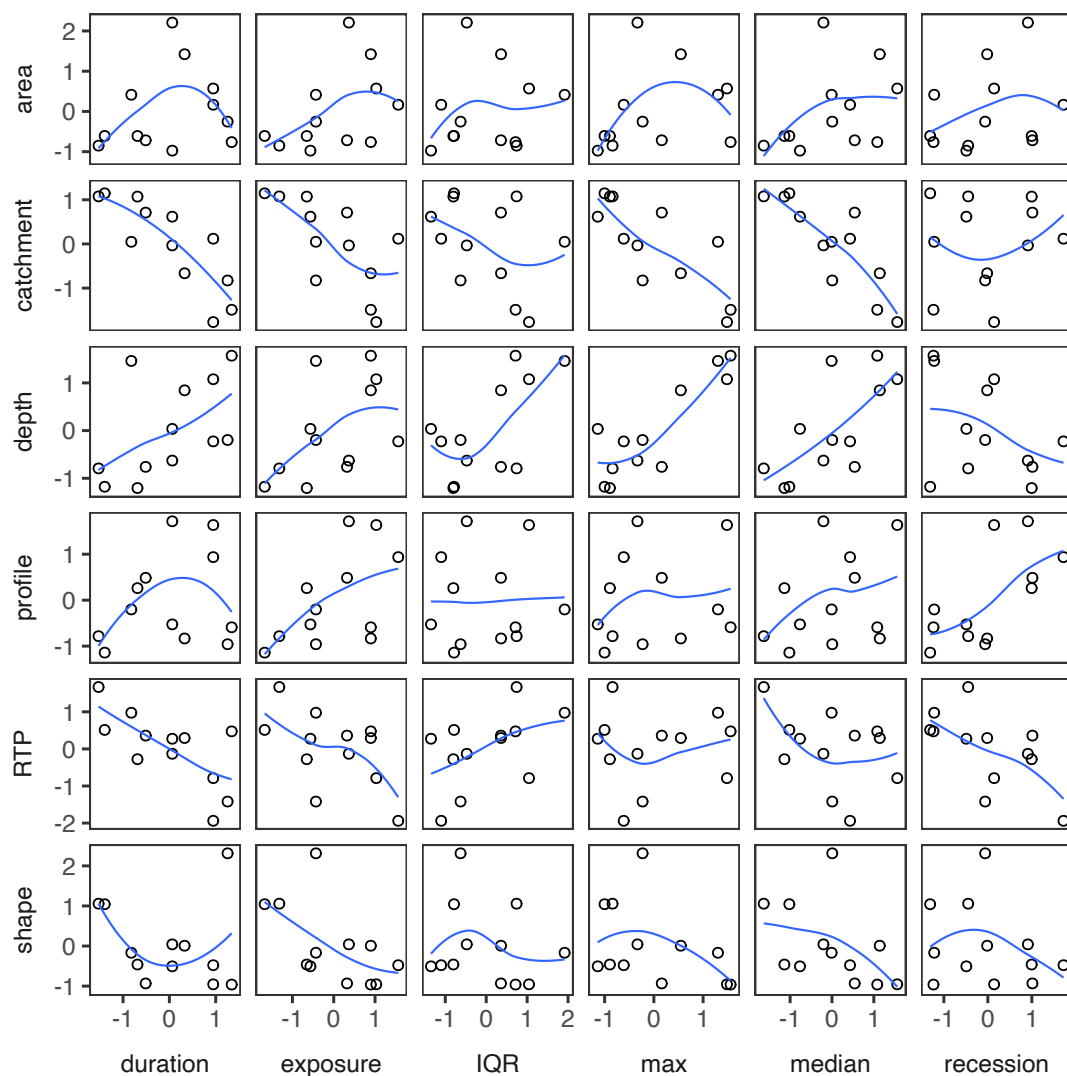


Figure S1.3. Scatterplot matrix of hydrologic (x-axes) and terrain (y-axes) metrics. Metrics were scaled and centered to simplify visualization and local polynomial regression lines are shown to approximate shapes of relationships.

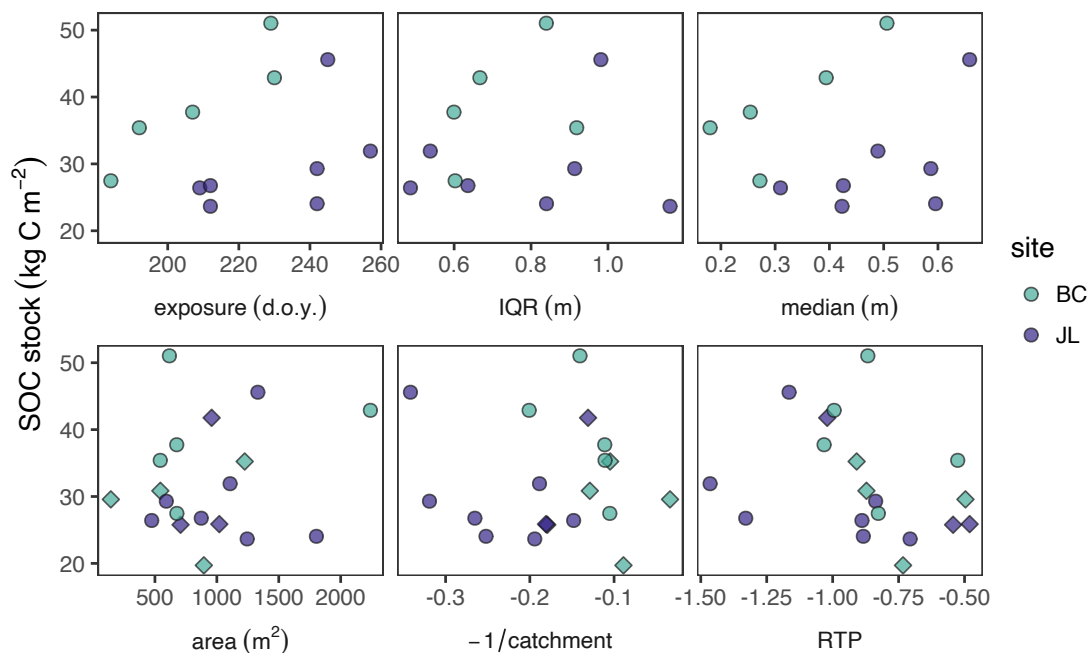


Figure S1.4. Scatterplots of SOC stocks and the hydrologic (top row) and terrain (bottom row) metrics not included in commonality analysis. IQR is the water level interquartile range; RTP is the relative topographic position. Diamond-shaped markers are wetlands without water level data (i.e., were only included in terrain analysis; $n = 7$) and colors indicate separate study sites (“BC”, “JL”).

Chapter 2: High spatial variability in wetland methane fluxes is tied to vegetation patch types

Abstract

Wetlands are the largest natural source of methane (CH_4), but spatial variability in fluxes complicates prediction, budgeting, and mitigation efforts. Despite the many environmental factors identified as CH_4 drivers, the overall influence of wetland spatial heterogeneity on CH_4 fluxes remains unclear. We identified five dominant patch types—submersed aquatic vegetation (SAV), emergent forbs, sedges/rushes, grasses, and open water—within a freshwater wetland in Maryland, USA, and measured CH_4 fluxes using a combined chamber and eddy covariance approach from June to September 2021. Because patch types integrate co-occurring environmental factors, we hypothesized that CH_4 flux is best characterized at the patch scale. Chamber measurements from representative patches showed distinct CH_4 signals; fluxes from grasses and sedges/rushes were highest, while fluxes from SAV and forbs were lower but skewed, suggesting episodic emission pulses. Open water had the lowest fluxes. Differences between patches were consistent over time, and spatial variability was greater between patches than within them, highlighting patches as key drivers of flux variability. By combining chamber fluxes with eddy covariance data in a Bayesian framework, we provide evidence that patch-type fluxes scale over space and time. Understanding spatial heterogeneity is essential for quantifying wetland contributions to global biogeochemical cycles and predicting the impacts of environmental change on wetland ecosystem processes. Our study demonstrates the

importance of vegetation patch types in structuring spatial variability and supports a patch-explicit representation to reduce uncertainty in wetland CH₄ fluxes.

Introduction

Wetlands are hotspots of biogeochemical activity and are characterized by spatially variable processes (Capps et al., 2014; Marton et al., 2015; McClain et al., 2003). Methane (CH₄) flux, in particular, is highly scrutinized in wetlands because of its potency as a greenhouse gas (Whiting & Chanton, 2001). Most wetlands contain sufficient organic carbon (C) substrate, reducing conditions, and methanogenic archaea to produce CH₄ (Bridgham et al., 2013), but fluxes within wetlands can exhibit extreme spatial variability (Yavitt et al., 2018). As a result, scaling up flux measurements is an acute challenge (McNicol et al., 2023), and wetlands are a major source of uncertainty in the global CH₄ budget (Bousquet et al., 2006). Alongside efforts to identify spatial drivers of variability (e.g., Girkin et al., 2019; Praetzel et al., 2021), a comprehensive framework is required to understand the relationship between environmental heterogeneity and CH₄ flux.

In many wetlands, spatial heterogeneity is organized into discrete patch types (Marani et al., 2006). Wetlands are often described as patterned mosaics (e.g., Matthes et al., 2014; Morin et al., 2017), with patches distinguished by physical features like microtopography and plant community (Keshta et al., 2023; Lampela et al., 2016). The mechanisms of patch formation vary but are thought to involve self-reinforcing feedback among plants, soil, and hydrological regimes. Through this

process, local conditions that initially favor a particular plant assemblage can become increasingly distinct as the plants modify their environment, leading to persistent patches (Marani et al., 2006). In addition to their ecological importance, patches are an accessible means of describing spatial heterogeneity because they can be detected visually and with remote sensing (Dronova et al., 2011).

Wetland vegetation patches integrate co-occurring drivers of spatial variability in CH₄ flux (Davidson et al., 2016). Spatial heterogeneity in abiotic factors, such as flooding regime and soil nutrients, regulates the distribution of wetland vegetation (Day et al., 1988); thus, patch types represent the physicochemical conditions that favor their dominant plants (Couwenberg et al., 2011). Over time, positive feedbacks may further differentiate patches. Plant inputs modify soil chemistry (Palozzi & Lindo, 2017), and some wetland plants engineer their physical environment to favor their own dominance (Caraco et al., 2006), resulting in stronger aboveground-belowground linkages and additional spatial variation (Jones et al., 1994). Altogether, the interactions between plants and the abiotic environment shape microbial communities (Berg & Smalla, 2009), providing the basis for CH₄ variability among patch types (Sharp et al., 2024).

Plants directly influence patch CH₄ fluxes through physiological mechanisms. The release of oxygen and root exudates into the rhizosphere affects rates of CH₄ production and oxidation, and in emergent plants with porous aerenchyma tissue, vascular gas transport can be an efficient pathway for CH₄ emission (Laanbroek, 2010; Vroom et al., 2022). These processes are mediated by species-specific traits, such as internal conductance and the chemical composition of root exudates (Girkin

et al., 2018; Villa et al., 2020). Plants may also regulate CH₄ fluxes through microbial community composition, for example, by favoring certain groups of soil methanogens (Sharp et al., 2024; Waldo et al., 2022) or supporting epiphytic methanotrophs (Yoshida et al., 2014). A plant's net effect on flux is thus determined by its impact on multiple interacting—and often competing—processes (Bastviken et al., 2023; Noyce & Megonigal, 2021). Plant functional groups and traits can partially explain interspecific variability (Kao-Kniffin et al., 2010; Sutton-Grier & Megonigal, 2011), but accuracy depends on how groups are classified and which traits are measured (Gray et al., 2013; Laine et al., 2022).

Variation in CH₄ drivers may lead to different temporal flux dynamics between vegetation patches. Patch structure may determine the dominant emission pathway; for example, in one study plant-mediated transport accounted for the most flux in emergent vegetation, whereas ebullition (i.e., bubbling) was more important in deep water with floating vegetation (Desrosiers et al., 2022). Patch types may also respond differently to environmental fluctuations or long-term changes, modulating patch effects on fluxes (Noyce & Megonigal, 2021; Whitaker et al., 2021). In vegetated patches, recent studies have suggested that plant phenology is a strong driver of seasonal flux patterns (Ge et al., 2023; Helfter et al., 2022).

Here, we investigated the link between vegetation patches and CH₄ flux in a spatially heterogeneous wetland. Vegetation patches, as “environmental integrators” of CH₄ drivers, may be most effective at explaining spatial patterns in CH₄ fluxes (Davidson et al., 2016). Further understanding how vegetation patches influence spatially variable processes is essential for estimating the contributions of wetlands to

global biogeochemical cycles amid widespread environmental change in these systems. Specifically, we asked: 1) How do fluxes vary among different vegetation patches? 2) How does variability among patches compare with other sources of spatial and temporal variability? and 3) Can patch-type fluxes be estimated at the wetland scale?

Methods

Site description and patch types

We conducted our study in a wetland within the Choptank River watershed on the Mid-Atlantic Delmarva Peninsula (Caroline County, MD, USA). The climate is humid subtropical, with an annual mean temperature of 13.3°C and precipitation of 1210 mm distributed evenly across months (30-year normal, 1991–2020; PRISM climate mapping system). Non-tidal wetlands in this region are freshwater mineral-soil depressions, with seasonal hydrology characterized by inundation for most of the year with a period of evapotranspiration-driven water table drawdown from late summer to autumn (Phillips & Shedlock, 1993). The study wetland (2.08 ha) was briefly drained and used as a pasture in the 1980s, and was ecologically restored in 2003 by plugging drainage ditches, felling encroaching woody vegetation, and removing nonnative plants (Spadafora et al., 2016).

Patch types were selected based on their prevalence in the study wetland, importance in wetlands throughout the region, and representation of plant growth forms (Schultz & Pett, 2018; Table 1). Unvegetated open water appeared only in the

deepest central part of the wetland. Submersed aquatic vegetation (SAV), such as rooted *Juncus repens* or *Proserpinaca palustris*, formed dense mats in deep areas surrounding open water. Emergent forbs, mainly *Persicaria hydropiperoides*, occupied interstitial spaces between graminoid patches or shallow water near the forested margin of the wetland. We divided graminoid vegetation into two types: grass patches dominated by *Panicum hemitomon* and sedge/rush patches with multiple dominant species (e.g., *Carex striata*), which often grow together. Grasses formed dense monospecific stands underlain by mats of semi-decomposed litter, while sedges/rushes (henceforth “sedges”) clustered in tussocks and occupied shallower areas toward the wetland margin. These distinctions are commonly used in wetland studies to represent plant morphological differences (e.g., De Steven et al., 2006; Johns et al., 2015), and may be associated with functional differences (Pan et al., 2020; Williams et al., 2020).

Patch vegetation parameters

Aboveground plant biomass and leaf area index were measured to quantify physical differences in patch vegetation. We chose these parameters because they are easily measured, detectable with remote sensing, and linked to spatial variability in plant productivity and CH₄ flux (Goud et al., 2017, 2022; Villa et al., 2020). In late September, during the late growing season, we sampled vegetation from 0.25 m² quadrats in emergent patch types (forbs, sedges, and grasses; n = 3 each). Quadrats were positioned away from chamber collars to prevent disturbance in research plots. Plant stems were cut above the soil surface, standing litter was separated, and samples

were dried and weighed to determine aboveground biomass (g m^{-2}). To estimate leaf area, we selected ten stems from each quadrat. Leaves were digitally scanned, and area was measured using ImageJ (Schneider et al., 2012) then scaled to the full quadrat by species. Leaf area index ($\text{m}^2 \text{m}^{-2}$) was calculated as the total one-sided leaf area in a quadrat, normalized by quadrat area.

To assess the potential role of plant phenology in patch fluxes, we monitored seasonal greenness patterns of the dominant graminoid species. Using a fixed digital camera (StarDot NetCam), we captured a time series of images and defined homogeneous regions of interest (ROIs) for each species. The camera's field of view did not cover emergent forbs and SAV, so our analysis focused on dominant graminoids (Table 2.1). Following PhenoCam network protocols (Richardson et al., 2018), greenness was calculated for each ROI as the mean pixel green chromatic coordinate (G_{CC}) value, and time series for 2021 were constructed using the 90% cumulative G_{CC} over 3-day windows. Plant active phase was defined as the period when G_{CC} exceeded 10% of its seasonal amplitude (Richardson et al., 2018). This analysis was conducted in R using the *phenopix* and *phenocamr* packages (Filippa et al., 2016; Hufkens et al., 2018).

Flux measurement

We adopted a combined static chamber and eddy covariance (EC) approach to quantify patch-type CH_4 fluxes. The two methods are considered complementary; chambers directly measure fluxes at discrete points, providing high precision but low spatiotemporal coverage, whereas EC offers continuous ecosystem-scale

measurements (Morin et al., 2017). Our primary aim was therefore to synthesize rather than contrast their information. Here, we used a Bayesian approach, which allowed us to draw from both chamber and tower data and obtain robust estimates of patch-type fluxes across space and time.

Patch flux point measurements were collected using chamber incubations. We established research plots in one representative of each patch type; plots had three chamber locations approximately 2 m apart (total $n = 15$ chambers) and were accessed by raised boardwalks to minimize disturbance. We sampled from two types of chambers. In the grasses and sedges, we used static chambers ($0.5 \times 0.5 \times 0.7$ m) consisting of aluminum frames covered by clear polycarbonate sheeting, with aluminum lids, to accommodate tall (> 0.5 m) vegetation. In the forbs, SAV, and open water plots we used floating chambers ($0.4 \times 0.4 \times 0.35$ m) made from clear acrylic aquaria to avoid inducing mixing in deeper (> 0.3 m) water. Battery-powered fans were placed in the larger static chambers to ensure a well-mixed headspace. For both chamber types, sampling ports were located on top.

Chambers were sampled over a series of three campaigns in the summer of 2021. Campaigns were held in June, July, and September to target the early, peak, and late phases of the growing season, respectively. During each weeklong campaign, we selected three sampling days with similar weather forecasts (see Supplementary Table S2.1 for more information on sampling conditions). All chambers were sampled each day in full sunlight between 08:00 h and 18:00 h and in random order by patch. We conducted an additional sampling day in November but did not include it in the main analysis (data shown in Supplementary Figure S2.1). Water depth was

monitored continuously with pressure transducers (Onset Computer Corporation, Bourne, MA, USA) in shallow wells at our research plots in each patch type (Supplementary Figure S2.2).

Chamber fluxes were measured with 30-min incubations. Gas samples were taken at 10-min intervals ($n = 4$ per incubation) and stored in 12 mL evacuated vials (Labco, UK). Methane concentrations were determined using gas chromatography (SRI Instruments, Torrance, CA, USA) and corrected with in-chamber temperature measurements. The average temperature change over the course of incubations was 2°C in static chambers and 3°C in floating chambers. Fluxes were calculated as the linear rate of change in concentration, accounting for chamber volume and surface area (Holland et al., 1999). Quality control was performed by visual inspection, with the goal of ensuring linearity while retaining as many fluxes as possible. We removed points suspected to be affected by vial leakage, chamber headspace saturation, or excessive disturbance as indicated by deviation from linear trends (7.5% of total points). Flux curves were retained if at least three points had an $R^2 > 0.9$ (Nahlik & Mitsch, 2011) or if the rate was near zero ($\pm 1 \text{ mg CH}_4\text{-C m}^{-2} \text{ h}^{-1}$). We retained near-zero fluxes (including negative fluxes) to avoid biasing our results toward higher fluxes (Repo et al., 2007). Because we took care to minimize effects of disturbance, fluxes with large concentration jumps, presumably due to ebullition, were retained unless they failed our statistical criteria. Out of 150 measured fluxes, 102 were calculated using all four points, 45 had three points, and three were discarded.

Continuous wetland-scale CH_4 fluxes were measured using EC (Baldocchi et al., 2001). A 2.9 m tall flux tower located in the open-canopy area of the wetland was

equipped with an open-path CH₄ analyzer (LI-7700; LI-COR, Lincoln, NE, USA) and a sonic anemometer (WindMaster Pro; Gill Instruments, UK) to measure turbulent fluctuations. Raw 10 Hz data was processed at 30-min intervals in EddyPro 7.0.9 (LI-COR) using standard methods for sonic anemometer tilt correction, time series detrending, time lag compensation, and statistical screening (Moncrieff et al., 2004; Vickers & Mahrt, 1997; Wilczak et al., 2001). Fluxes were corrected for frequency response (Moncrieff et al., 1997, 2004) and air density fluctuations (Webb et al., 1980).

As with chamber measurements, we restricted our analysis to the summer (June–September), which accounted for about 70% of 2021 CH₄ emissions at our site (Supplementary Figure S2.3). Fluxes were quality checked using standard tests for stationarity and sufficient turbulence (Foken et al., 2012). We further removed periods during which a plausible time lag was not identified (Eugster et al., 2011), the CH₄ mixing ratio varied excessively (Erkkilä et al., 2018), or the friction velocity was $< 0.1 \text{ m s}^{-1}$ (Kljun et al., 2015). No gap filling was attempted.

Source areas of 30-min tower fluxes were estimated using a two-dimensional analytical footprint model (Kljun et al., 2015). Given the micrometeorological conditions during each flux averaging period, the model applied a source weighting function to assign relative flux contributions to a 1-m grid around the tower (Schmid, 1997). All input variables were derived from tower data, except for atmospheric boundary layer height, which was acquired from ERA5 climate reanalysis data (Hersbach et al., 2020). A description of the model including its definition and parameterization can be found in Kljun et al. (2015).

Although explicitly valid for homogeneous land cover, analytical footprint models are commonly used in heterogeneous environments to attribute EC fluxes to spatial features (Neftel et al., 2008). Studies examining flux uncertainty from footprint calculations in such environments have found it to be relatively low (Morin et al., 2017; Stoy et al., 2021); however, we acknowledge that flow inhomogeneities across patch types can introduce error into our footprint estimates (Finnigan, 2004). We took several steps to mitigate this bias. Aerodynamic roughness parameters were determined empirically for each flux averaging period to account for the dependence of flow conditions on wind direction (Neftel et al., 2008). Footprints were rejected if excessive roughness concentrated the source area at the tower (peak crosswind-integrated distance < 1 m). We also removed periods with negatively skewed absolute humidity, indicating a potential low-frequency influence on fluxes from outside the footprint area (Esters et al., 2021). Our final dataset included 2605 half-hourly CH₄ fluxes and footprints (2219 day; 386 night).

Flux footprints were superimposed on a patch cover map to determine the relative influence of each patch type on tower flux measurements (Figure 2.1). Patch cover was mapped by hand using GPS-referenced field surveys and aerial imagery (0.6 m resolution, color near-infrared; National Agriculture Imagery Program 2021). For each 30-min period, footprint weights were summed by patch type within the tower's source area (Forbrich et al., 2011). Because the footprint model does not define a 100% source area limit, we constrained our analysis to an 80% cumulative footprint and rescaled weights to sum to unity (Chu et al., 2021).

To estimate patch-type fluxes at a broader scale, tower flux data was modeled as a simple weighted average:

$$F_t = \sum_{i=1}^n \bar{f}_i \phi_{it} \quad (2.1)$$

where F_t is the observed tower flux at time t which integrates a source area composed of n ($= 5$) patch types, ϕ_{it} is the source area fraction of patch type i at time t (i.e., a patch type's weighted contribution to the tower flux, determined with footprint analysis as detailed above), and $\bar{f}_i$ is the mean flux from patch type i . We excluded an intercept because we assumed that the observed fluxes were influenced only by the defined patch types (J. Kim et al., 2018). This model is widely used to “disaggregate” fluxes in landscape-scale analyses (e.g., from airborne eddy covariance systems; Hutjes et al., 2010) but less commonly within a single ecosystem. Equation 2.1 can be made temporally explicit by including environmental response functions in a hierarchical structure (e.g., with soil temperature; Levy et al., 2020); however, because our focus was on estimates of $\bar{f}_i$ (rather than predictions of F_t), we did not add parameters that could complicate the interpretation of $\bar{f}_i$. As such, $\bar{f}_i$ should be considered an estimate of the average flux from a patch type over the study period.

The model was parameterized using Bayesian linear regression. Bayesian methods provide a robust representation of uncertainty and, importantly, allowed us to incorporate prior knowledge on parameter distributions (Ellison, 2004). We set normal priors on $\bar{f}_i$:

$$\bar{f}_i \sim \mathcal{N}(\mu_i, \sigma_i) \quad (2.2)$$

where μ_i and σ_i are the median and median absolute deviation of chamber-measured fluxes from patch type i , respectively. Posterior distributions of $\bar{f}_i$ were estimated iteratively using Markov chain Monte Carlo (MCMC) sampling with tower data. To examine model sensitivity to the chamber prior, we ran a second version using weakly informative priors (i.e., normal distributions with a large spread centered at zero). We also ran the model separately for daytime and nighttime data (Supplementary Figure S2.4). Models were evaluated by comparing the observed data distribution with simulated datasets from the posterior predictive distribution (Conn et al., 2018; Supplementary Figure S2.5). Models were fit in R using the *rstanarm* package (Goodrich et al., 2020), based on the Stan probabilistic programming language (Carpenter et al., 2017).

A potential concern with the model was multicollinearity among source area fractions, hindering the independent identification of parameters. At our site, source area fractions were correlated because patch types were unevenly distributed around the flux tower (Figure 2.1). Although informative priors can mitigate multicollinearity issues in Bayesian analyses (Pesaran & Smith, 2019), parameters in our model without the chamber prior likely had some degree of dependence. Parameter identifiability was assessed by examining pairwise correlations between MCMC samples (Ogle & Barber, 2020; Supplementary Figures S2.6-2.7).

Statistical analysis

Variance in chamber flux data was partitioned into components using a linear random effects model (Harrison et al., 2018). The model included terms for patch

type, chamber (nested within patch type), and sampling campaign. We also evaluated the patch type $\times$ campaign interaction. Days were considered replicates because we intentionally selected sampling days with similar weather conditions. The model was fitted with restricted maximum likelihood using the R package *lme4* (Bates et al., 2015). Fluxes were power transformed (Yeo-Johnson) to stabilize variance.

Results

Patch vegetation

Graminoid patch types (sedges and grasses) were most productive according to both aboveground biomass and leaf area index (Table 2.2). Emergent forbs and SAV had greater leaf area relative to biomass than did graminoids, indicating more allocation of resources to leaf tissue, but aboveground biomass was lower overall in these patches. Sedges had the highest aboveground biomass and leaf area index (361 g m⁻² and 3.20 m² m⁻², respectively) and were further characterized by a long growing season (Table 2.2). Compared with the dominant grass, the dominant sedge in our research plots (*Carex striata*) began green-up earlier, peaked earlier, senesced later, and had a longer active phase (Figure 2.2). Phenology also differed between *C. striata* and other dominant sedges/rushes, with all three species exhibiting unique greenness patterns (Figure 2.2).

Empirical distributions of patch-type fluxes

Chamber flux distributions had distinct shapes among patches (Figure 2.3). Most open water fluxes were low (median flux = $0.591 \text{ mg CH}_4\text{-C m}^{-2} \text{ h}^{-1}$); some negative fluxes were observed but were likely below the detection limit. Graminoid patches (grasses and sedges) had the highest median fluxes ($16.1, 16.3 \text{ mg CH}_4\text{-C m}^{-2} \text{ h}^{-1}$, respectively) and were positively skewed. Fluxes from SAV and forbs (median = $6.50, 7.09 \text{ mg CH}_4\text{-C m}^{-2} \text{ h}^{-1}$, respectively) were centered between open water and graminoids, spanned almost the full range of fluxes, and had a strong positive skew. The maximum flux was between 32 and $46 \text{ mg CH}_4\text{-C m}^{-2} \text{ h}^{-1}$ for all vegetated patches.

Temporal variability in fluxes within patches

Relative differences between patch fluxes were generally consistent over time (Figure 2.4). Graminoid (sedge and grass) fluxes were always highest and never fell below $5 \text{ mg CH}_4\text{-C m}^{-2} \text{ h}^{-1}$. Forbs and SAV were most variable among campaigns, but their median fluxes never exceeded those of graminoids. All patch fluxes peaked in July, except for grasses, which decreased with time. Fluxes from forbs and SAV were positively skewed for all campaigns, i.e., these patches had occasional elevated fluxes throughout the summer. Open water fluxes never exceeded $2.2 \text{ mg CH}_4\text{-C m}^{-2} \text{ h}^{-1}$ and were always lowest.

Variability among patches was the largest source of chamber flux variability in our study design (Supplementary Table S2.2). According to our variance component model, *patch* accounted for 65.4% of the variance in power-transformed

flux, followed by *chamber* (4.1%) and *campaign* (2.2%). The *patch* $\times$ *campaign* interaction had a negligible effect on the model fit and was removed from the analysis. We suspected that low open water fluxes were partially responsible for the large *patch* contribution, so we repeated the analysis with vegetated patches only (Supplementary Table S2.2). This reduced the *patch* component, but *patch* (19.8%) remained larger than *chamber* (10.8%) and *campaign* (7.0%). In other words, patch variability was greater than temporal variability (among campaigns) and spatial variability within patches. Excluding open water increased the residual unaccounted variance (including among sampling days within *campaign*) from 28.3% to 62.4%.

Summer patch-type fluxes

Over an expanded spatial and temporal inference space, flux tower data supported the patch variability identified with static chambers (Figure 2.5). Tower estimates had a similar pattern to chamber data, with highest fluxes from graminoid patches, lowest from open water, and both SAV and emergent forbs falling somewhere in between. Incorporating tower data reduced the uncertainty around mean patch type fluxes, as we expected given the amount of flux tower data relative to chamber measurements. Sedge uncertainty remained relatively high, likely because sedge patches were concentrated furthest from the tower and thus had a small contribution to the flux footprint (Figure 2.1; mean source area fraction = 0.6%). Prior distributions specified using chamber data had little effect on patch-type flux estimates; that is, our model produced similar results regardless of whether prior information on patch fluxes was provided. The most notable departure from chamber

data was the lower model estimate for grasses. Our model also indicated a small but nonnegligible source of CH₄ from open water, greater than what we measured with floating chambers.

Discussion

Patches have distinct CH₄ flux distributions

Chamber sampling in our wetland revealed that the distribution of CH₄ fluxes had distinct shapes among patch types. This suggests strong spatial variability in the processes driving CH₄ fluxes and supports a patch-specific framework for wetland ecosystem flux. Below, we describe the observed flux distributions and mechanisms that may differentiate them.

Fluxes from sedge and grass (graminoid) patches were consistently highest and had few extremes. Studies across ecoregions and wetland types have shown that graminoid vegetation is a strong source of CH₄ (Akhtar et al., 2020; Bao et al., 2021; e.g., Turetsky et al., 2014). This is partly because dominant graminoids are generally productive, which is considered a driver of wetland CH₄ fluxes (Whiting & Chanton, 1993). In our wetland, graminoid productivity was indicated by greater aboveground biomass and leaf area index (Table 2.2). These traits have been linked to, for example, inputs of litter and root exudates (Goud et al., 2017; Sutton-Grier & Megonigal, 2011), which can fuel methanogenesis directly as substrate and indirectly by priming the decomposition of complex soil organic matter into compounds more readily accessible to methanogens (Waldo et al., 2019). We did not measure

belowground biomass, which interacts more directly with CH₄-cycling microbes and does not always correlate with aboveground vegetation parameters (Määttä & Malhotra, 2024). However, the relationship between biomass and CH₄ fluxes depends on species and abiotic factors (Bhullar, Iravani, et al., 2013; Kao-Kniffin et al., 2010), indicating that productivity alone is insufficient for explaining plant influences on fluxes.

Plant-mediated transport may also be a factor in high graminoid fluxes. Although all the dominant plants in our wetland develop aerenchyma, graminoid species have highly conductive vascular tissue and extensive root systems, making them effective conduits for CH₄ to the atmosphere (Bhullar, Edwards, et al., 2013; Ge et al., 2023). The same traits can also increase radial oxygen loss and stimulate CH₄ oxidation (Kao-Kniffin et al., 2010; Sutton-Grier & Megonigal, 2011); however, given the high fluxes in graminoid patches, the net effect of these patches on fluxes was evidently positive (McEwing et al., 2015). Along a porewater depth gradient in our study wetland, CH₄ concentrations were reduced in graminoid rooting zones (Sharp et al., 2024), which is characteristic of plant-driven CH₄ transport and rhizosphere oxygenation (van den Berg et al., 2020).

The efficiency of plant-mediated transport can suppress other flux pathways (e.g., ebullition; van den Berg et al., 2020), resulting in a CH₄ signal dominated by plant ventilation. The graminoids in our wetland exchange gases passively, so their influence on CH₄ is likely to be steady rather than, for example, driven by intermittent plant processes (Vroom et al., 2022). Standing litter was abundant in graminoid patches (e.g., 115 g m⁻² on average in *Carex striata* quadrats; data not shown) and

can be an additional passive conduit for CH₄ (Carmichael et al., 2014). Thus, plant-mediated transport may explain the relative consistency (i.e., few outliers) in our graminoid flux measurements.

Fluxes from emergent forbs and SAV were strongly skewed, indicating that episodic emissions may account for a large proportion of fluxes from these patches. Compared with graminoids, leaf area index of emergent forbs and SAV was lower (Table 2.2), possibly reflecting less potential surface area for gas exchange and reduced plant-mediated flux (Villa et al., 2020). Root traits such as shallow depth, low surface area, and higher tissue density may also limit vascular gas transport in both emergent forbs and SAV (Andrews et al., 2013; Bhullar, Edwards, et al., 2013). Nevertheless, C inputs in these patches could support high CH₄ production (Theus et al., 2023), and without an efficient plant conduit, CH₄ can quickly accumulate in the sediment. These conditions promote CH₄ oversaturation and ebullition (Grasset et al., 2019), which could account for episodic fluxes. Others have noted the importance of ebullition in SAV patches (Barbosa et al., 2021; e.g., Jeffrey et al., 2019; but see Villa et al., 2021), and our results highlight that the primary flux pathway may differ between patch types.

Despite being flooded for the length of the study, open water (no vegetation) fluxes remained close to zero. Although we cannot rule out unmeasured pulses, concurrent work in our study wetland revealed high soil porewater CH₄ concentrations beneath open water (Sharp et al., 2024), which could suggest an increased residence time of CH₄ produced in the soil. Open water was found in the deepest areas of our wetland (Table 2.1), and, without ebullition and plant conduits as

efficient transport pathways, most flux likely occurred via slow diffusion. These factors increase the opportunity for CH₄ oxidation by methanotrophs (Rey-Sanchez et al., 2018), and may have moderated open water fluxes in our system.

Patches are an important source of variability in CH₄ flux

Fluxes varied more between than within patches, suggesting that vegetation patchiness is important in explaining spatial heterogeneity in wetland CH₄ flux. Our chambers were placed approximately 2 m apart within patches, so spatial autocorrelation was likely a factor; however, extreme variability has been observed at even shorter distances (Teh et al., 2011; Yavitt et al., 2018). Within vegetated patches, spatial variability in fluxes may be related to local heterogeneity in soils (Briones et al., 2022) or plant density (Theus et al., 2023). Stem counts varied among chambers within our emergent vegetation patches (e.g., coefficient of variation = 38% for grasses; data not shown), but this was not accompanied by a similar degree of flux variability. Thus, differences between patch types appear to outweigh any effects of within-patch biotic and abiotic heterogeneity on CH₄ fluxes.

Variability among summer sampling campaigns was low. Our results follow Turner et al. (2020) and Korrensalo et al. (2022), who observed low intraseasonal variability in CH₄ fluxes from vegetated patches during the growing season. The relative differences between patches were consistent during the summer and on an additional sampling day in November (Supplementary Figure S2.1), suggesting that patches responded similarly to shifts in seasonal conditions. One exception, however, was a decrease in fluxes from grasses relative to sedges (Figure 2.4), which may be

related to phenological differences. The dominant grass, *Panicum hemitomon*, had a steeper decline in greenness than *Carex striata*, the dominant sedge in our chamber plots (Table 2.2; Figure 2.2). This could result in lower CH₄ fluxes, for example, due to reduced C input to the rhizosphere (Helfter et al., 2022).

Over a full annual cycle, variation in patch plant phenology may be an important determinant of a wetland's annual CH₄ budget. Plant phenology is a functional quality of vegetation patches with respect to CH₄ flux, and temporal dynamics in general should be considered intrinsically linked to spatial heterogeneity in wetlands (Hammond & Kolasa, 2014). In our temperate depressional wetland, active phase (indicated by the temporal pattern in greenness) varied among graminoid species and was 67 days longer for the dominant sedge than for the dominant grass (Table 2.2; Figure 2.2). A longer active phase could imply an extended supply of fresh substrate and a prolonged time when aerenchyma tissue is fully developed and can optimally transport gases (Vázquez-Lule & Vargas, 2021). Based on this difference, we expect sedges to be a greater per-area CH₄ source relative to grasses than our summer measurements would suggest (Figure 2.5).

Patch variability scales over space and time

By incorporating flux tower data, we found that our chamber measurements signified a broader pattern of spatial variability in the study wetland, where CH₄ fluxes varied systematically by patch type. Our results support previous studies suggesting that wetland vegetation patches serve as “environmental integrators”, representing distinct arrays of co-occurring CH₄ drivers (Couwenberg et al., 2011;

Davidson et al., 2016). Thus, it is likely that wetland-scale CH₄ fluxes depend on patch composition, and efforts to model and inventory wetland CH₄ should account for differences among patch types.

The persistence of a patch signal across a wide range of spatial and temporal variability suggests that CH₄ flux is a functional property of vegetation patches. Our flux tower footprint covered an area of heterogeneous patch composition across a hydrologic gradient within the wetland depression (Figure 2.1). Temporally, our data spanned fluctuations in temperature, water level, and other environmental variables within the growing season (Supplementary Figures S2.2-2.3). Diel variability was also captured, although to a limited extent as most nighttime fluxes were removed by quality control measures (as is common in EC; Y. Kim et al., 2020). Therefore, it is likely that the patch variability in our wetland is driven by differences in underlying CH₄ dynamics that influence fluxes irrespective of spatial and temporal context.

Unvegetated open water was a minor source of CH₄ in our study. Our model estimate of open water fluxes was higher than chamber measurements alone (Figure 2.5), suggesting that chamber sampling may have missed a small but nonnegligible CH₄ source from this patch type. This underscores the need for high-frequency measurements to capture “hot moments” in CH₄ fluxes, which can contribute disproportionately to CH₄ budgets (Anthony & Silver, 2021). Nevertheless, open water fluxes were the lowest of the patch types. Flux estimates from our model closely resembled measurements from forested, closed-canopy Delmarva bay wetlands that lacked emergent vegetation (Hondula et al., 2021). This suggests that flux estimates for specific patch types may have broader applicability across

landscapes, although literature on this topic is limited. Some previous studies also reported low open water fluxes (e.g., McNicol et al., 2017; Rey-Sanchez et al., 2018), while others found them to be relatively high (e.g., Villa et al., 2021). Further investigation is warranted to determine the factors driving variability in patch-type fluxes among wetlands, and the extent to which patch influence can be generalized across landscapes.

Although the chamber and tower data were remarkably consistent with respect to patch-type fluxes (Figure 2.5), there were some differences between the two methods. These results highlight the importance of combining, rather than contrasting, measurements at different scales to interpret wetland fluxes (Morin et al., 2017). Bayesian methods provide an intuitive means of incorporating prior information, and we recommend these methods for studies aiming to reconcile flux measurement approaches.

Tower estimates were generally lower than chamber fluxes (Figure 2.5), which is a common finding in studies using both methods (Erkkilä et al., 2018; e.g., Krauss et al., 2016). For emergent forbs, within-type spatial variability may have contributed to this discrepancy. This patch type had multiple dominant species; our forb chambers were placed in a *Persicaria hydropiperoides* patch, but we observed other patches near the flux tower dominated by *Ludwigia sphaerocarpa* and *Proserpinaca* spp. that may have had lower fluxes. Because CH₄ fluxes can vary among species within vegetation types (Ström et al., 2005), we expect within-type variability to increase with the number of dominant species in a wetland. However, mapping wetlands at the species level may be an impractical solution for scaling

fluxes, and may limit the geographic applicability of flux estimates (Gray et al., 2013). Instead, research should focus on identifying plant or environmental attributes that efficiently distinguish patches based on their CH₄ fluxes (Laine et al., 2022).

Grass fluxes estimated by our tower model were considerably lower than our median chamber measurement (Figure 2.5). This difference may reflect unmeasured spatial heterogeneity (e.g., in plant density or soil chemistry), but an alternative explanation is that our intermittent chamber sampling did not adequately capture the temporal dynamics specific to the dominant grass, *Panicum hemitomon*. Between our July and September sampling campaigns, water levels receded below the soil surface in some areas (Supplementary Figure S2.2), which may have disproportionately affected CH₄ fluxes from grass patches. *P. hemitomon* grows optimally under flooded conditions (Holm & Sasser, 2008), and we observed a rapid decline in its greenness concurrent with drying, followed by a recovery upon flooding (midway between Jul '21 and Oct '21 in Figure 2.2). This response was similarly pronounced for only one of the three dominant sedge/rush species and not for the sedge found in our chamber plot (*Carex striata*; Figure 2.2). Hence, grasses may have undergone a disturbance that temporarily reduced their ability to facilitate CH₄ flux and resulted in a lower estimate than our chamber data. This hypothesis could be tested to determine the importance of disturbance events on wetland patch fluxes.

Our study conceptualized a spatially heterogeneous wetland as a mosaic of fixed patch types. Although this framework revealed an important pattern of patch variability, it can be extended in several ways. We suggested that plant phenology may contribute to patch differences, and, in general, overlaying temporal

environmental data (e.g., water level, temperature, nutrients) may be necessary to fully understand how fluxes vary among patches (Levy et al., 2020). The spatial distribution of patches is dynamic, especially when wetlands are newly restored, recovering from disturbance, or influenced by external stressors (Antonijević et al., 2023; McKown et al., 2021; Taddeo & Dronova, 2020). Intra-annual shifts in patch distribution may even occur in some systems (Jeffrey et al., 2019). Patches may interact, meaning that configurational aspects such as patch size, shape, and arrangement can influence processes (M. G. Turner, 2005). This has been largely unexplored in the context of wetland CH₄ fluxes, but Matthes et al. (2014) found that the fractal dimension of vegetated patches explained variability in fluxes beyond patch composition alone. Finally, vegetation patches may not fully capture the spatial variability of CH₄ drivers (Briones et al., 2022), and the best representation of spatial heterogeneity likely involves a combination of discrete and continuous approaches (Gustafson, 1998).

Interdependence of vegetation and environmental influences

We have proposed various biogeochemical mechanisms that may contribute to patch variability in CH₄ fluxes, but we were unable to determine whether vegetation or the environment were the dominant drivers. Distinguishing these sources of variability is an important avenue for future research on, for example, the impacts of non-native plant colonization (Bezabih Beyene et al., 2022) and strategies to minimize CH₄ emissions in restored or created wetlands (Silvey et al., 2019). However, separating vegetation and environmental effects may not always be

feasible. The abiotic environment (e.g., hydrology, soil physicochemical properties) controls plant survival and growth, while plants, in turn, modify the environment through processes like transpiration and root exudation (Moor et al., 2017). Further, many plant functional traits reflect both species identity and environmental context (i.e., “response traits”; Engelhardt, 2006). For example, root aerenchyma development is a species-specific trait that can affect CH₄ cycling, but its expression depends on flooding and oxygen availability during growth (Smirnov & Crawford, 1983). A reductionist approach may therefore overlook the entanglement of vegetation and environmental influences, and a more nuanced understanding of spatial heterogeneity may be gained by exploring how these factors interact to shape ecosystem processes.

Conclusions

We showed that wetland vegetation patches exhibit distinct CH₄ signals throughout the growing season, likely driven by differences in the mechanisms that regulate fluxes. Our results demonstrate that patch types are important for understanding spatial variability in wetland CH₄ fluxes and support the incorporation of a patch-explicit representation to reduce CH₄ uncertainty in process-based models and inventories (Dinsmore et al., 2009). Amidst global change, accounting for patch variability is essential even when ecosystem-scale flux measurements are available as shifts in vegetation cover are expected to affect greenhouse gas exchange, and certain patch types may respond disproportionately to wetland-scale disturbance (Rietl et al., 2017; Urbanová et al., 2012). Attributing patch-specific CH₄ fluxes could also inform

practices to minimize greenhouse gas emissions in managed and restored wetlands (Tak et al., 2023), although these strategies must be balanced with targeted ecosystem services (e.g., nutrient retention; Kasak et al., 2020). In addition to CH₄ flux, other consequential wetland processes may be best represented at the patch scale, and further research should address the extent to which patches drive spatial heterogeneity in wetland ecosystem processing.

Tables

Table 2.1. Description of wetland patch types. Plant species in bold were dominant in our study plots. Open water patches had no visible plants. Note that *P. palustris* has both aerial and aquatic growth forms.

Patch type	Dominant plant species	Avg. water depth (m) ^a	Chamber type	Approx. coverage ^b
Submersed aquatic vegetation (SAV)	<i>Juncus repens</i> , <i>Proserpinaca palustris</i> , <i>Utricularia sp.</i>	0.41	Floating	28%
Emergent forbs	<i>Persicaria hydropiperoides</i> , <i>Proserpinaca spp.</i> , <i>Ludwigia sphaerocarpa</i>	0.32	Floating	17%
Sedges/ rushes	<i>Carex striata</i> , <i>Juncus effusus</i> , <i>Eleocharis quadrangulata</i>	0.18	Static	35%
Grasses	<i>Panicum hemitomon</i>	0.24	Static	10%
Open water	n.a.	0.44	Floating	11%

^aJune–September

^bExcluding forested area around wetland margin

Table 2.2. Plant productivity in vegetated patches. Biomass and leaf area index are means with standard errors in parentheses (n = 3 quadrats) for live material only, sampled on DOY 259. Peak greenness and active phase were determined by analyzing digital repeat photography as described in Section 2.2. n.r. = not recorded.

Patch type	Aboveground biomass, g m ⁻²	Leaf area index, m ² m ⁻²	Peak greenness, DOY	Active phase length, days
Submersed aquatic vegetation ^a	34.9 (6.9)	0.61 (0.10)	n.r.	n.r.
Emergent forbs	83.6 (15.3)	0.93 (0.18)	n.r.	n.r.
Sedges/rushes ^b	361 (30.9)	3.20 (0.27)	181	239
Grasses	255 (15.8)	2.15 (0.14)	195	172

^aBiomass data from Sharp et al. (2024); leaf area estimated using a scaling relationship for *Juncus bulbosus* (morphologically similar to *J. repens*; Jamoneau et al., 2017)

^b*Carex striata*-dominated patches

Figures

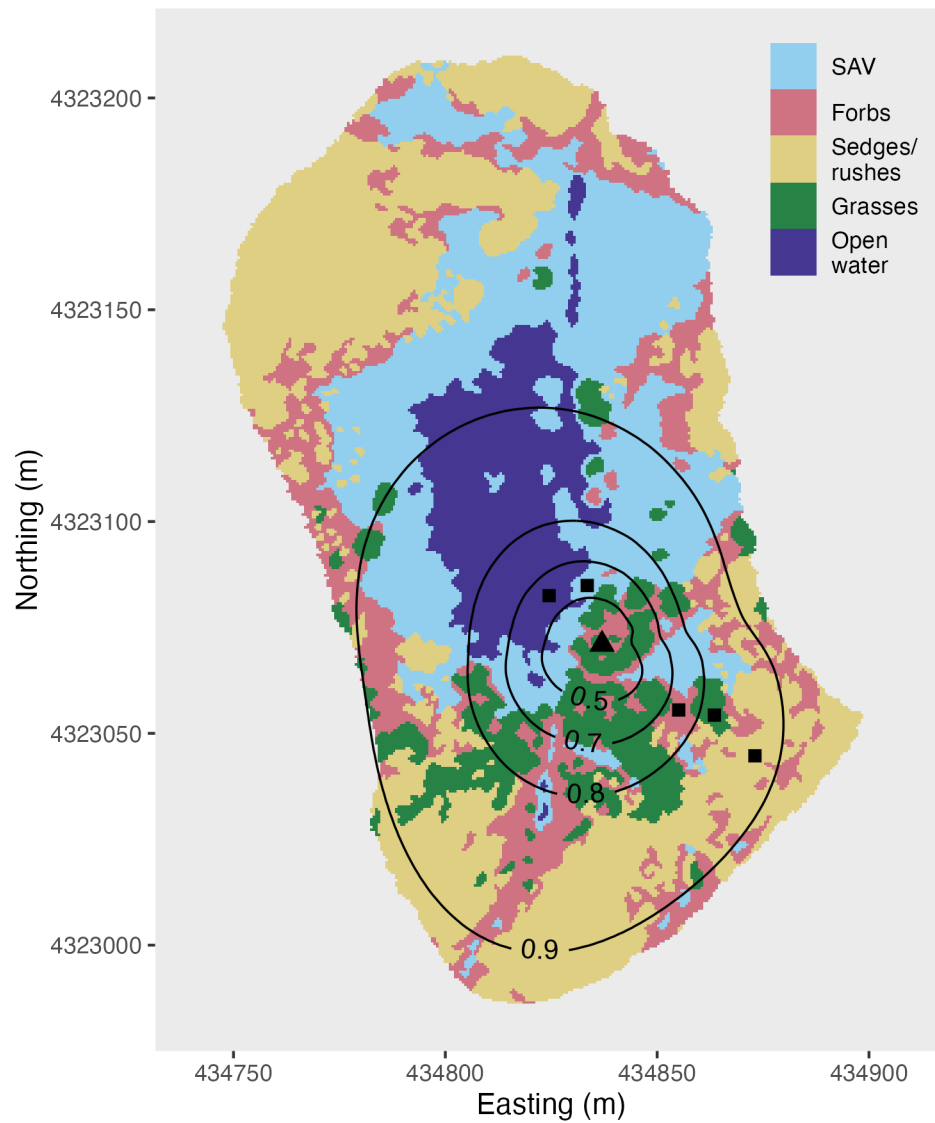


Figure 2.1. Distribution of patch types and flux tower source area in the study wetland. The triangular symbol indicates the location of the flux tower. Contour lines refer to the cumulative flux footprint from all half-hourly measurements ($n = 2605$). All static chambers plots (square symbols) were located within the 90% footprint contour. SAV = submersed aquatic vegetation.

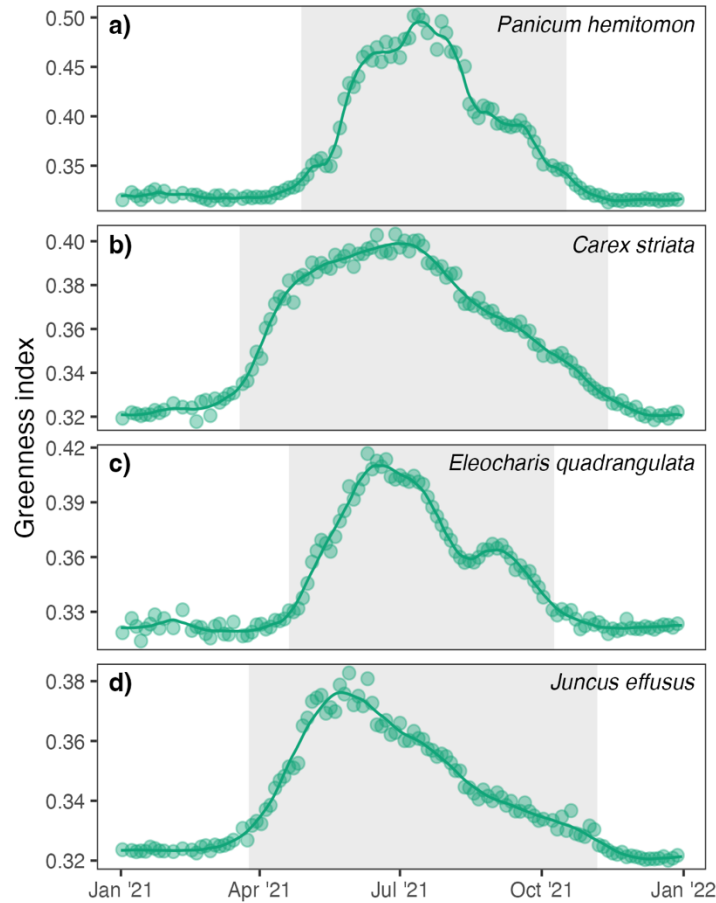


Figure 2.2. Species-specific phenology for dominant grasses (a) and sedges/rushes (b–d) in the study wetland in 2021. Greenness index is the green chromatic coordinate (GCC) derived from digital repeat photography and is shown as smoothed curves on top of 3-day point values. Species are shown on different GCC scales to emphasize individual temporal patterns. Shaded areas denote a plant’s active phase, defined as the period when GCC is greater than 10% of its seasonal amplitude.

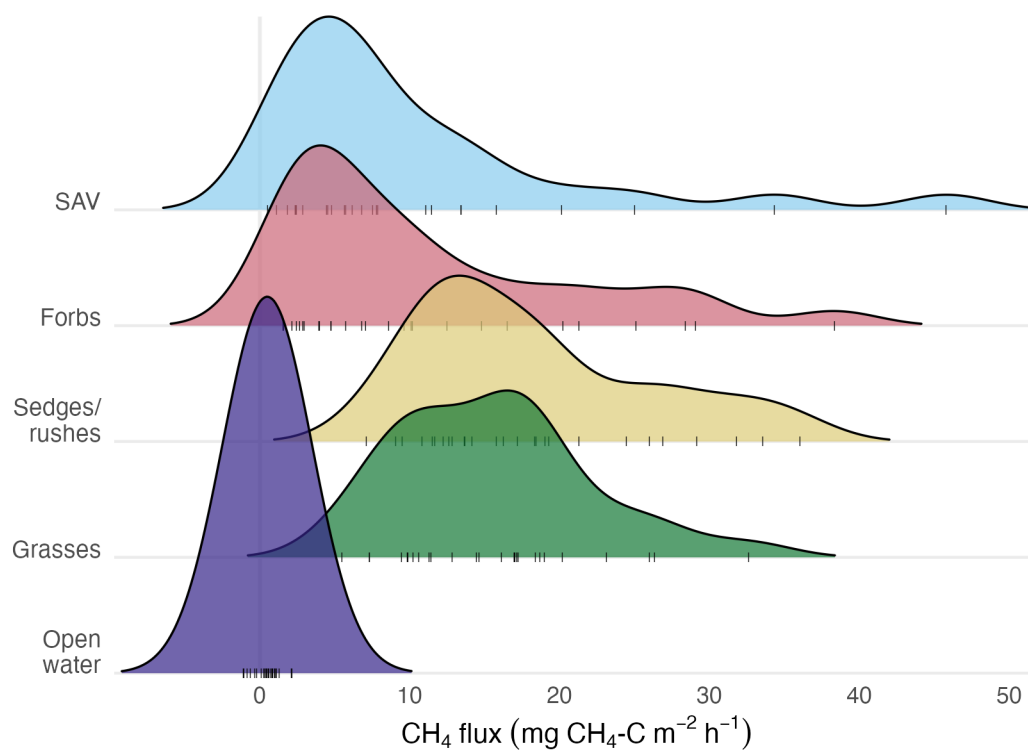


Figure 2.3. Patch chamber flux distributions. Individual measurements ($n = 25\text{--}27$ per patch) are shown as tick marks below smoothed density curves. Density was estimated using a joint bandwidth for all patches. SAV = submersed aquatic vegetation.

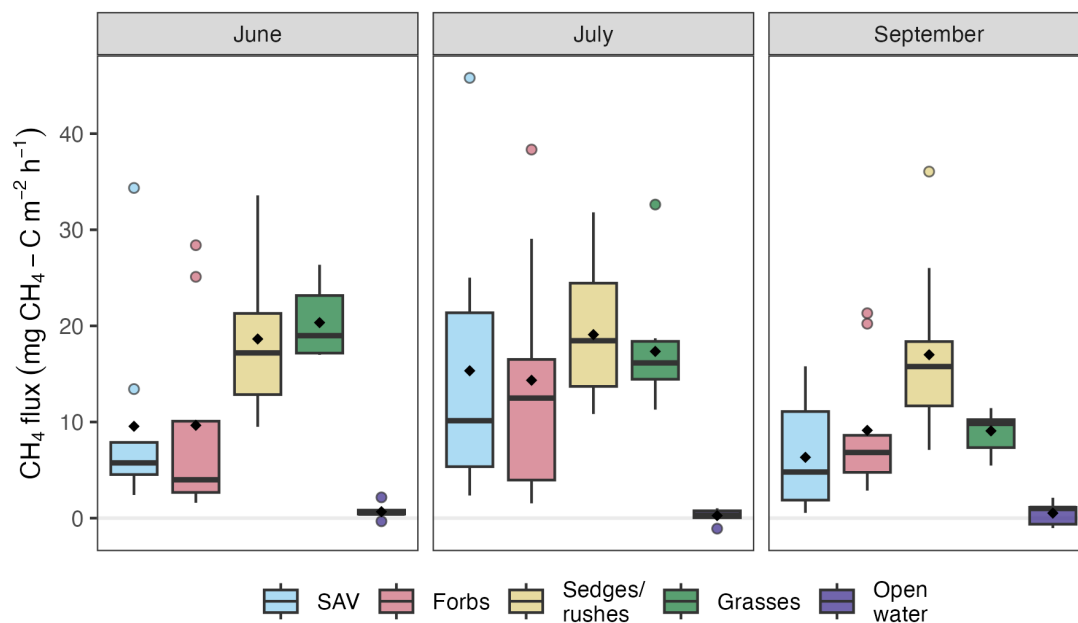


Figure 2.4. Patch flux boxplots for the three sampling campaigns. Fluxes ($n = 8-9$ for each patch per campaign) were measured using chambers in 2021. Campaigns consisted of three sampling days during which three chambers were sampled in each patch. Diamonds are patch-campaign means and colored points lie outside 1.5 times the interquartile range. SAV = submersed aquatic vegetation.

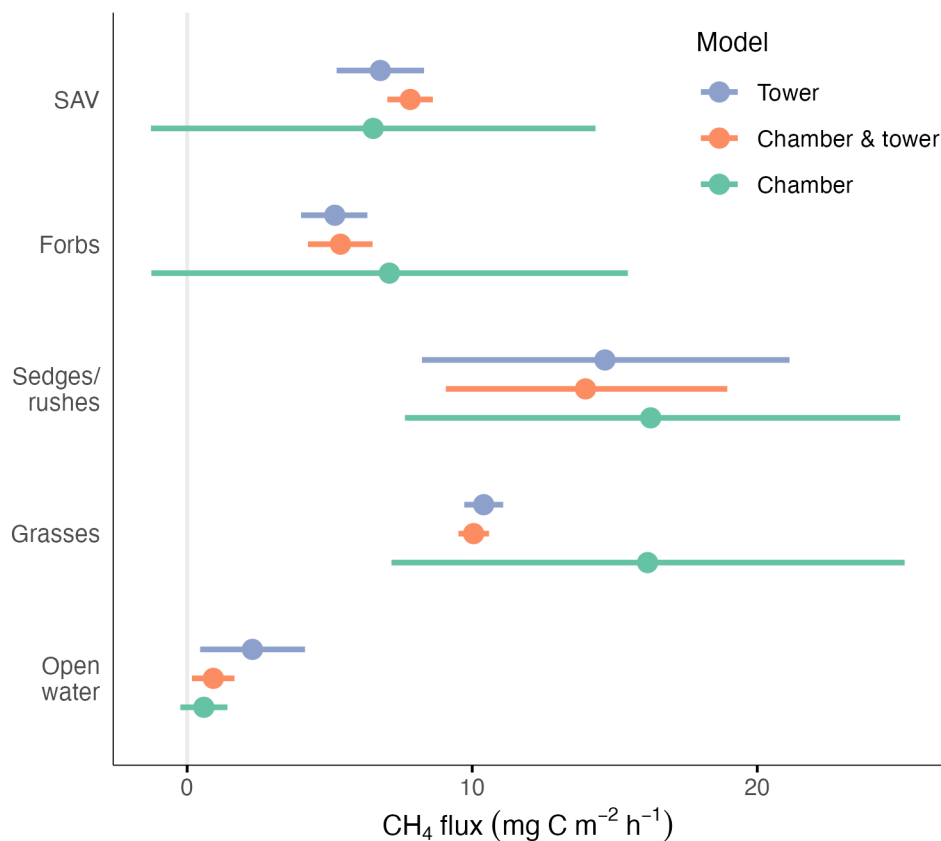


Figure 2.5. Estimates of average growing season CH₄ fluxes for wetland patch types from a model using both chamber and tower data (“Chamber & tower” model). The model was a Bayesian linear regression of tower flux on patch source area fraction data, with chamber data as priors on patch flux parameters. Estimates from a model with weakly informative priors (“Tower” model) and from prior probability distributions (“Chamber” model) are also shown. Points and intervals are medians and 80% uncertainty. SAV = submersed aquatic vegetation.

Supplementary materials

Table S2.1. Wetland conditions during chamber sampling campaigns in 2021. Values are given for each day as means and ranges over the time chambers were sampled. Ranges are omitted for soil temperature and water level as diel variability was low. All variables were measured at the flux tower, located centrally in the wetland. Note that these do not necessarily represent chamber conditions. PPFD = photosynthetic photon flux density, a measure of sunlight intensity.

Campaign-Day	Air temp., °C	Soil temp., °C	Relative humidity, %	PPFD, $\mu\text{mol m}^{-2} \text{s}^{-1}$	Water level, m
June-1	29.2 (26.1–30.9)	23.0	75 (67–87)	1045 (518–1482)	0.27
June-2	21.6 (19.1–23.0)	21.6	44 (40–54)	1548 (1083–1809)	0.28
June-3	23.2 (22.4–23.7)	21.3	48 (46–54)	1553 (1017–1833)	0.27
July-1	29.5 (28.0–31.9)	22.7	70 (52–83)	814 (125–1222)	0.15
July-2	31.7 (30.1–32.9)	22.8	56 (52–66)	1451 (1171–1701)	0.14
July-3	27.7 (25.7–29.7)	22.8	79 (73–86)	978 (825–1138)	0.12
Sept.-1	28.1 (26.4–29.7)	22.2	66 (62–72)	1057 (753–1301)	0.40
Sept.-2	28.9 (26.1–30.6)	23.0	67 (57–82)	1216 (884–1451)	0.39
Sept.-3	25.1 (23.4–26.2)	23.5	85 (82–91)	493 (335–579)	0.39
Nov.-1	15.3 (15.1–15.7)	16.5	46 (37–61)	974 (781–1128)	0.38

Table S2.2. Variance component analysis of power transformed chamber CH₄ flux data. Variance was partitioned between patch types (*patch*), June, July, and September sampling campaigns (*campaign*), and flux chamber nested within patch (*chamber*). Days within campaigns (n = 3 each) were considered replicates in the study design. Analysis was conducted with all patch types and separately with only vegetated patches.

Component	All patches			Vegetated patches		
	N groups	Variance	% of total variance	N groups	Variance	% of total variance
<i>patch</i>	5	2.00	65.4	4	0.290	19.8
<i>chamber</i>	15	0.125	4.09	12	0.159	10.8
<i>campaign</i>	3	0.0666	2.18	3	0.103	7.04
Residual	-	0.866	28.3	-	0.916	62.4

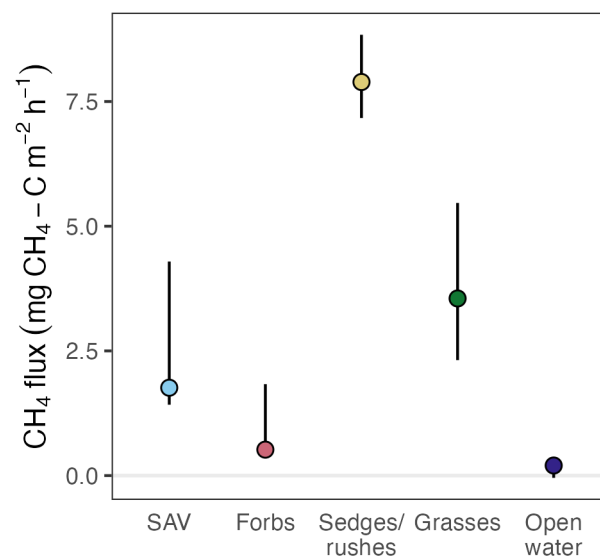


Figure S2.1. Patch CH₄ fluxes sampled with chambers in November 2021 (n = 3 per patch over one day). Points are medians; lines are ranges. Note the different scale from Figure 2.4 in main text. SAV = submersed aquatic vegetation.

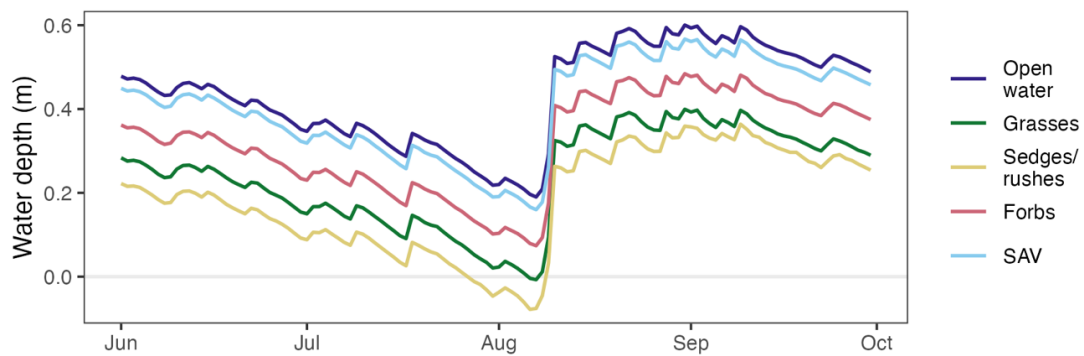


Figure S2.2. Variation in patch water depth during the study period in 2021. Measurements were taken using pressure transducers at research plots and averaged daily. SAV = submersed aquatic vegetation.

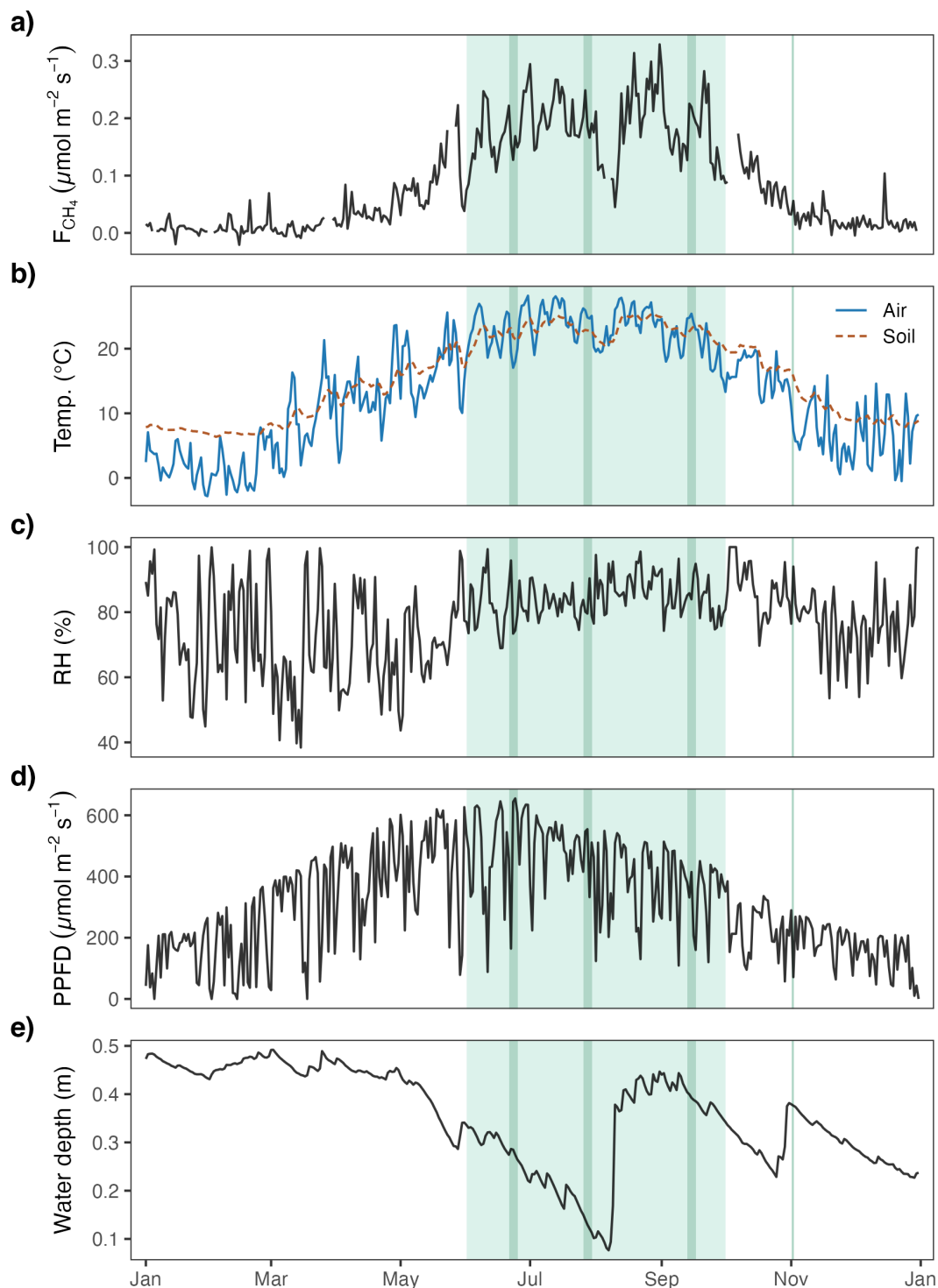


Figure S2.3. Variation in 2021 of wetland a) methane flux, b) air and soil temperatures, c) relative humidity, d) photosynthetic photon flux density, and e) water depth. All variables were measured at the flux tower and averaged daily. The light shaded area is our study period (Jun.–Sep.); dark shaded areas mark sampling campaigns.

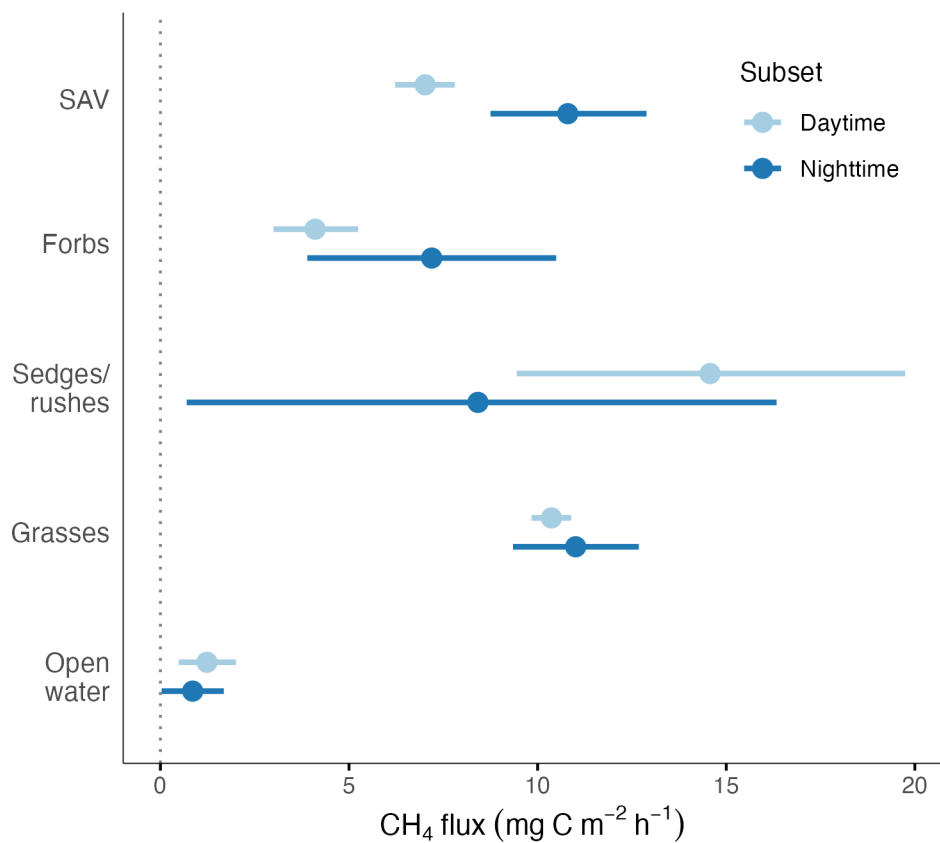


Figure S2.4. Estimates of average summertime CH_4 fluxes for patch types from daytime ($n = 2219$) and nighttime ($n = 386$) subsets. SAV = submersed aquatic vegetation.

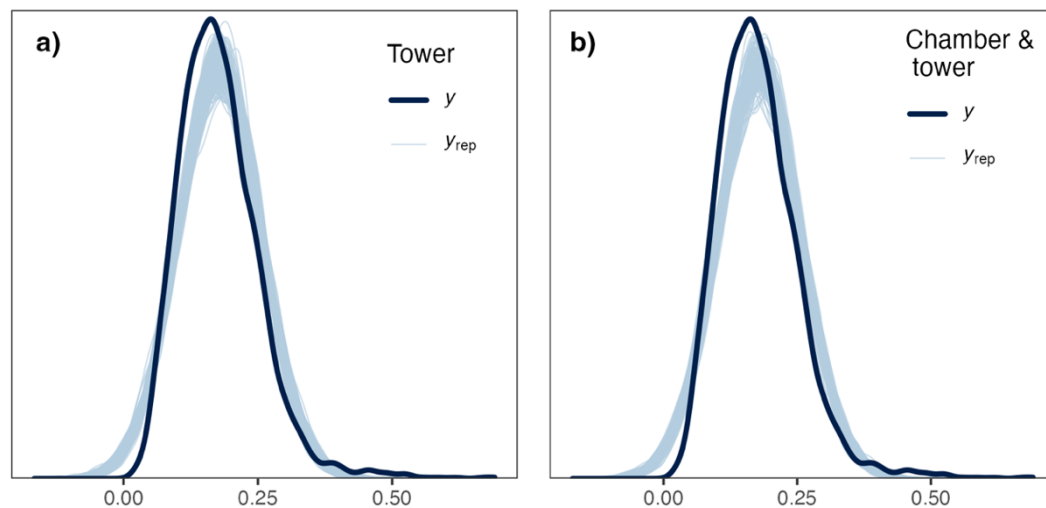


Figure S2.5. Posterior predictive checks for patch flux models without (a) and with (b) chamber priors. Posterior predictive distributions of CH₄ flux (y_{rep} ; $n = 200$) were simulated by drawing from the posterior distributions of patch-type flux parameters.

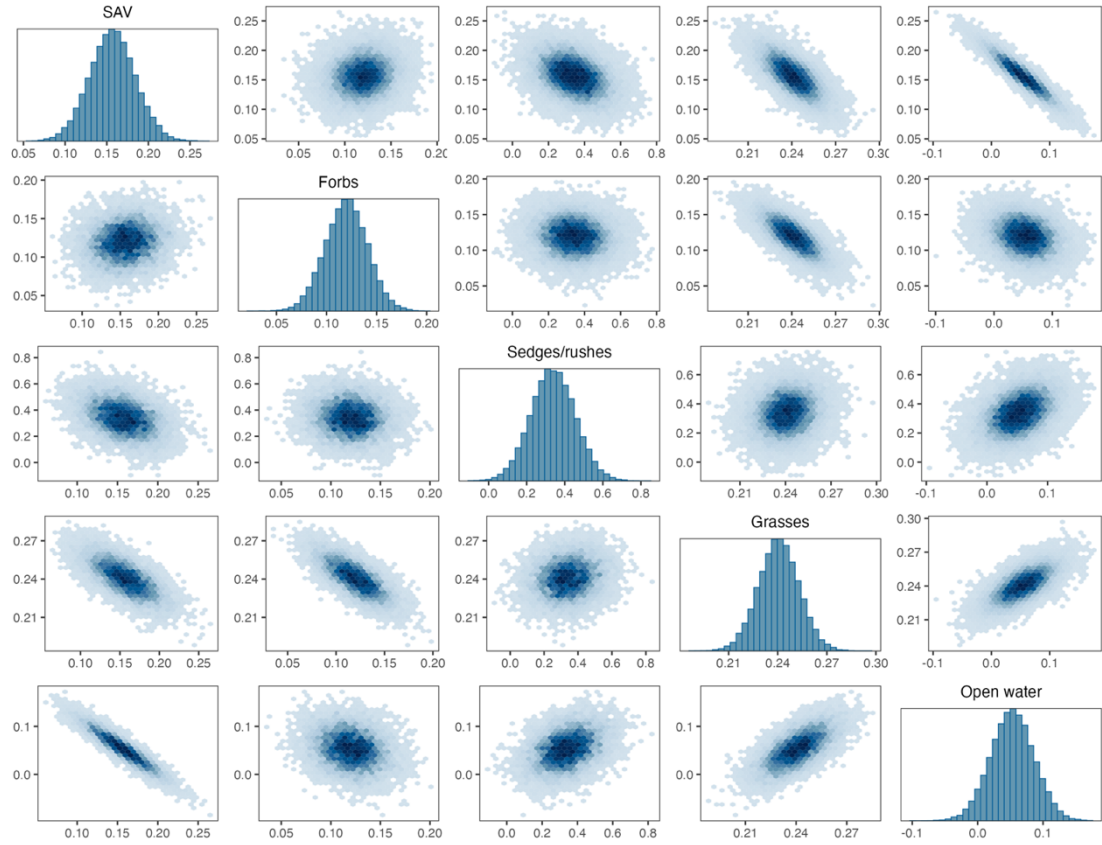


Figure S2.6. Bivariate distributions of Markov Chain Monte Carlo samples of patch flux parameters. SAV = submersed aquatic vegetation.

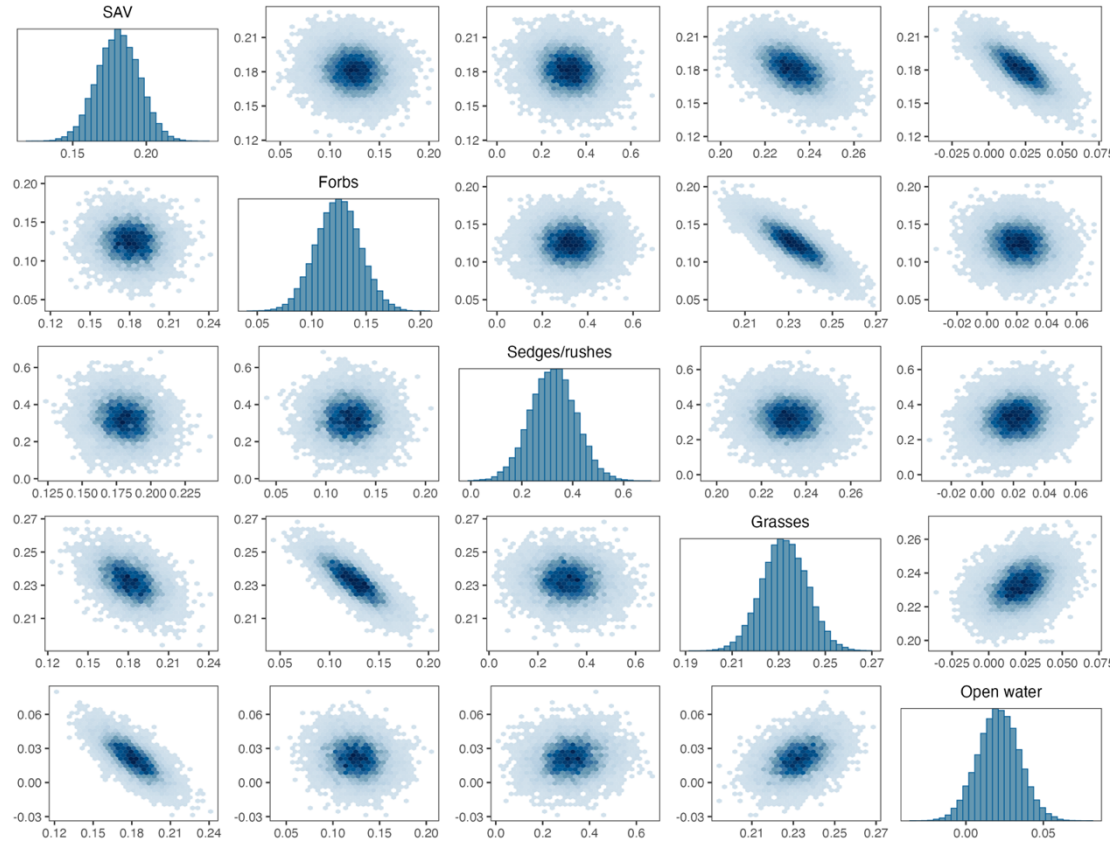


Figure S2.7. Same as previous, but for model with chamber priors. Specifying chamber priors reduced the correlation between some posterior distributions, notably SAV-grasses, SAV-open water, and grasses-open water.

Chapter 3: Contrasting temporal drivers of methane flux across land uses in freshwater wetlands

Abstract

Wetlands are collectively the largest natural source of methane (CH_4), and CH_4 fluxes complicate the climate mitigation potential of wetland restoration. While land-use change has well-documented effects on wetland features such as soils, vegetation, and hydrology, it is unclear how the collective disturbance influences CH_4 fluxes. We investigated temporal dynamics of CH_4 fluxes across three freshwater mineral-soil wetlands with distinct land-use histories: a natural wetland, a restored wetland, and a cultivated former wetland. Using four years of continuous eddy covariance data, we quantified interactions between biophysical drivers, including soil temperature, gross primary productivity (GPP), and hydrologic variables and CH_4 flux at multiple time scales. We found that GPP was the primary driver of diel CH_4 fluxes at the wetlands, but diel CH_4 fluxes were inversely related to GPP, with higher fluxes at night. At the seasonal scale, wetland CH_4 flux was strongly influenced by soil temperature and water level, with state dependency evident in these drivers. Overall, 20 years after restoration, the restored wetland had similar CH_4 dynamics to the natural wetland, indicating convergence in underlying processes. As human activities continue to impact wetlands globally, understanding how wetland processes vary among land uses is imperative for predicting and managing wetland greenhouse gases.

Introduction

Wetland restoration has been cited as a way to enhance the Earth's carbon (C) sink, but methane (CH₄) emissions from restored wetlands complicate the net climate impact of these systems (Hemes et al., 2018). Globally, >50% of all wetland area has been lost, primary by drainage and conversion to agricultural land uses (Davidson, 2014; Zedler & Kercher, 2005). Undisturbed wetlands can be strong C sinks due to high primary productivity and low rates of decomposition in saturated soils (Brinson et al., 1981); thus, wetland restoration may be an effective method for capturing and storing C from the atmosphere (Valach et al., 2021). However, this potential climate benefit comes at the cost of CH₄ emissions. CH₄, a potent greenhouse gas, is produced under reducing conditions found in saturated wetland soils (Bridgham et al., 2013). The radiative forcing of CH₄ acts on a shorter time scale than CO₂, so the climate effects of CH₄ emission are felt more immediately than those of CO₂ uptake (Neubauer, 2014). There is currently no clear consensus on the net impact of wetland restoration on short-term climate mitigation goals (Günther et al., 2020; Hemes et al., 2018; Schuster et al., 2024). Therefore, a better understanding of CH₄ fluxes from restored wetlands is urgently needed to accurately estimate greenhouse gas budgets as well as develop management strategies for restored wetlands to optimize their climate mitigation (Laine et al., 2024).

The role of disturbance legacy in wetland CH₄ fluxes is highly uncertain (Abdalla et al., 2016; Petrescu et al., 2015). Generally, drained wetlands emit less CH₄ than undrained wetlands (Sakabe et al., 2018), and fluxes increase when flooding

and reducing conditions are reestablished (Audet et al., 2013). Studies comparing restored wetland fluxes to those of least-disturbed (hereafter “natural”) wetlands, however, have yielded a wide range of conclusions. For example, differences have been attributed to ecosystem properties, such as C substrate chemistry (Wang et al., 2021), microbial abundance (Juottonen et al., 2012), and flooding duration (Pereyra & Mitsch, 2018). Other studies have found similar fluxes from restored and natural wetlands (Badiou et al., 2011; Morse et al., 2012). Importantly, the development trajectories of restored wetlands are unique and cannot be assumed to progress towards “natural” or historical reference conditions (Kreyling et al., 2021; Matthews, 2015).

Understanding ecosystem processes is central to restoration (Marín-Spiotta & Ostertag, 2016). Wetland processes are altered by disturbance (Moreno-Mateos et al., 2012), and often exhibit nonlinear and lagged responses to restoration (Ballantine & Schneider, 2009; Moreno-Mateos et al., 2015). Ecosystem structure (e.g., geomorphology, plant composition) can recover quickly following wetland restoration; thus, the convergence of ecosystem structure towards reference conditions does not ensure the same for ecosystem processes (Sutton-Grier et al., 2010).

Relationships with temporal drivers may improve our understanding of CH₄ processes in restored wetlands. While static measures such as average fluxes and annual budgets are important for calibrating greenhouse gas inventories, these approaches only capture discrete time periods and may overlook important dynamics of wetland processes (Zedler & Callaway, 1999). Instead, a more complete picture of

restored wetland CH₄ flux may be achieved by investigating how fluxes respond to environmental drivers (Suding et al., 2016). Few studies to date (e.g., Bortolotti et al., 2019) have compared drivers of processes in restored and natural wetlands, and more are needed to assess how processes evolve in actively developing restored wetlands (Kalhori et al., 2024). This approach is especially relevant given that climate change and other anthropogenic pressures will likely shift baseline conditions for key CH₄ flux drivers (Erwin, 2009; Moomaw et al., 2018).

There are numerous drivers of CH₄ flux, but temperature, vegetation, and hydrology represent fundamental constraints on wetland CH₄ dynamics (Delwiche et al., 2021; Turetsky et al., 2014). Temperature limits enzyme activity, which determines the maximum metabolic rates of methane-cycling microbes (Yvon-Durocher et al., 2014). Vegetation, specifically its primary productivity, provides a supply of organic matter that ultimately serves as a substrate for methanogens and fuels CH₄ production (Whiting & Chanton, 1993). Plant productivity is also linked to the flow of gases through plant tissues, which can both suppress fluxes by oxygenating the rhizosphere and enhance fluxes by allowing an efficient route for CH₄ to the atmosphere (Laanbroek, 2010). Finally, the hydrologic regime represents the soil redox state and the presence of anaerobic conditions, which affect the balance between CH₄ production and oxidation (Whalen, 2005).

Despite established mechanisms linking biophysical drivers to CH₄ flux, empirical relationships are complex and difficult to disentangle (Guo et al., 2024). Temporal dynamics in relationships largely arise from nonlinear and synergistic responses to drivers (Runge et al., 2019). For wetland CH₄ flux, temporal dynamics

often appear as lag effects (e.g., Tangen & Bansal, 2019), time scale emergence (e.g., Rinne et al., 2018), and hysteresis (e.g., K.-Y. Chang et al., 2021). Accounting for temporal dynamics is important for identifying relationships, and doing so may reveal additional details about the mechanisms involved in a process (Ryo et al., 2019). For example, lags between changes in water level and CH₄ flux have been linked to alternative electron acceptor availability and methanotroph activity (Tangen & Bansal, 2019). As a result of this complexity, observed relationships between CH₄ flux and biophysical drivers vary among individual wetlands, depend on analysis technique, and are generally poorly constrained (Knox et al., 2021; Murguía-Flores et al., 2023).

In this study, we investigated the temporal dynamics of CH₄ flux in a natural wetland, a restored wetland, and a drained former wetland that is now cultivated. We asked: *how do CH₄ fluxes respond to biophysical drivers in wetlands with varying land use histories?* We examined four years of continuous flux data along with measurements of soil temperature, primary productivity, and hydrologic variables as biophysical drivers. Our results offer insight into the ecosystem processes involved in CH₄ flux and how a legacy of disturbance may influence fluxes from restored wetlands.

Methods

Study sites

This study was performed on the Delmarva Peninsula, within the mid-Atlantic US coastal plain region. The climate is humid subtropical, with a mean annual temperature of 13°C and a mean annual precipitation of 1200 mm (30-year normal, PRISM climate mapping system). The low-gradient landscape contains thousands of freshwater depressional wetlands (i.e., “Delmarva bays”; Fenstermacher et al., 2014). Delmarva bays typically have mineral soils and exhibit seasonal hydrologic patterns that are coupled to the local groundwater table and largely driven by evapotranspiration and precipitation (Phillips & Shedlock, 1993). Heavy agricultural activity in the region has resulted in the conversion of an estimated two-thirds of Delmarva bays to cultivated land uses since colonization (Fenstermacher et al., 2014). Recently, government programs (e.g., USDA Natural Resource Conservation Service’s Wetland Reserve Program and Conservation Reserve Program) have initiated the ecological restoration of some cultivated wetlands (Yepsen et al., 2014).

We collected data from three sites representing distinct land use types. All sites were located within 1.5 km of each other. One is a least-disturbed (hereafter “natural”) wetland. Although this wetland has likely been affected by regional-scale disturbance such as groundwater withdrawal (Lee et al., 2019), according to historical imagery, it has not been directly impacted by agriculture since at least the 1950s and has been used as a reference system in previous studies (e.g., Spadafora et al., 2016). Herbaceous vegetation in the natural wetland is dominated by *Carex striata* and interspersed with woody *Clethra alnifolia* and *Vaccinium corymbosum*, which are

increasingly abundant towards the forested margin. The second site (“restored”) was briefly drained and used as a pasture in the 1980s and was restored in 2003 by plugging drainage ditches, felling encroaching trees, and planting native vegetation (Spadafora et al., 2016). Vegetation in the restored wetland is more heterogeneous, with patches of *C. striata*, *Panicum hemitomon*, and *Persicaria hydropiperoides*, among others, and a large area of submersed vegetation and open water in the center of the depression. The third site (“cultivated”) is ditch-drained and cultivated with a corn/soy rotation. The drainage ditch contains emergent and submerged herbaceous vegetation and has a ~10 m vegetated buffer strip that is mowed every year in the late summer.

Instrumentation and data acquisition

We measured continuous ecosystem-scale fluxes from 2019 to 2022 using the eddy covariance (EC) method. Flux towers were installed in 2018 at each site, positioned centrally, and are approximately 3 m tall. On each tower, turbulent fluctuations were measured using a sonic anemometer (Windmaster Pro; Gill Instruments). CH₄ concentration was measured using an open-path near-infrared gas analyzer (LI-7700; LI-COR, Inc.). CO₂ and H₂O concentrations were measured using an open-path CO₂/H₂O infrared gas analyzer (LI-7500; LI-COR, Inc.). Data was collected at 10 Hz and stored on-site with a data logger system (LI-7550; LI-COR, Inc.).

Biophysical variables were monitored continuously using sensors located on or around the flux towers. Soil temperature was taken as the average measurement of

three replicate probes (Stevens Water Monitoring Systems, Inc.; Portland, OR) at 5 cm depth. The soil probes also measured volumetric soil water content (SWC) which we used to represent hydrologic conditions at the cultivated site. At the wetland sites, we represented hydrology as the depth of water above the soil surface (hereafter “water level”), measured with HOBO pressure transducers (Onset; Bourne, MA). We monitored various other environmental parameters to use as covariates for filling data gaps in CH₄ flux (see Supplementary methods for a list of variables and corresponding sensors).

Data processing

Raw EC data was processed with the EddyPro 7.0.9 software (LI-COR, Inc.). Data processing followed standard methods, including de-spiking (Vickers & Mahrt, 1997), double rotation for sonic anemometer tilt correction (Wilczak et al., 2001), block averaging for detrending, compensation of air density fluctuations (Webb et al., 1980), time lag compensation by covariance maximization, and high- and low-pass spectral corrections (Moncrieff et al., 1997, 2004). Fluxes were storage-corrected based on single-point profile estimation (Hollinger et al., 1994).

Flux quality control followed the same procedure at all sites. Fluxes that failed steady state and integral turbulence characteristics tests were removed (Foken et al., 2004). If were further removed when were removed during periods when a plausible time lag was not detected (Eugster et al., 2011), gas analyzer signal strength was low (<10% for CH₄, <70% for CO₂/H₂O), or any flux dependency (i.e., variable used in flux calculation) fell outside plausible bounds. Low-resolution spikes in non-CH₄

fluxes (CO₂, latent heat, and sensible heat) were removed following Papale et al. (2006) and implemented with the *openeddy* R package v. 0.0.0.9008 (Šigut, 2018/2024). Extreme outliers in CH₄ flux were removed by applying absolute limits at the wetland sites (-0.15, 0.85 $\mu\text{mol m}^{-2} \text{s}^{-1}$) and the cultivated site (-0.15, 0.3 $\mu\text{mol m}^{-2} \text{s}^{-1}$). These thresholds were outside the 0.1% and 99.9% quantiles at the sites. We did not determine an empirical friction velocity threshold but instead applied a nominal threshold (0.05 m s^{-1}), which is appropriate for low tower and canopy heights (Krauss et al., 2016). The amount of original CH₄ fluxes remaining after quality control was 45.7%, 44.7%, and 48.9% at the natural, restored, and cultivated site, respectively. These values are within the typical range for EC data (Irvin et al., 2021).

Gap filling

Data gaps due to instrument malfunction and quality control were filled using statistical techniques. This was necessary as some of our analysis methods required continuous time series. Gaps in CH₄ flux were filled using random forest regression following Irvin et al. (2021). Predictor variables included non-CH₄ fluxes and a suite of environmental covariates (see supplementary methods for full list of predictor variables). Random forests were trained using the H2O machine learning platform through the R package interface (h2o v. 3.44.0.3; Fryda et al., 2024). The mean absolute error in predicted CH₄ flux (average of 20 resampled hold-out sets) was 0.0263, 0.0279, and 0.00912 $\mu\text{mol m}^{-2} \text{s}^{-1}$ for the natural, restored, and cultivated sites, respectively.

Prior to CH₄ flux gap-filling, gaps in non-CH₄ fluxes and other biophysical variables were filled according to FLUXNET methodology (Pastorello et al., 2020). Gaps in non-CH₄ fluxes were filled using the marginal distribution sampling algorithm with air temperature, incoming shortwave radiation, and vapor pressure deficit as covariates (Reichstein et al., 2005). Gap-filled CO₂ flux (i.e., net ecosystem exchange) was partitioned into ecosystem respiration and gross primary productivity (GPP) using the “daytime” method (Lasslop et al., 2010). Marginal distribution sampling and flux partitioning was conducted in R using the *ReddyProc* package v. 1.3.3 (Wutzler et al., 2018). Gap-filling for environmental covariates included linear interpolation, mean diurnal course estimation, substitution from nearby sites, and substitution of downscaled ERA5 climate reanalysis data (Pastorello et al., 2020).

Data analysis

Here, we use a framework (“multiresolution mutual information”) developed for analyzing drivers of EC CH₄ fluxes (Sturtevant et al., 2016), which has since been widely adopted and is notably featured in a recent synthesis of freshwater wetland CH₄ fluxes (Knox et al., 2021). We extend this approach with empirical dynamic modeling (EDM) to account for state-dependency and distinguish between causal relationships and spurious correlation. A summary of our analysis is presented in Figure 3.1.

Multiresolution mutual information

Signals at varying time scales were extracted from 30-min data using maximal-overlap discrete wavelet transform (Percival & Walden, 2000). Wavelet detail was summed into hourly (1–2 h), diel (4 h to 1 d), multi-day (3–21 d), seasonal (43–341 d) time scales (Sturtevant et al., 2016). We did not further analyze the hourly wavelet scale because it can be dominated by noise (Knox et al., 2021). For the diel and multi-day scales, we focused our analysis on the 2021 growing season (d.o.y. 100–300). This year had the greatest amount of original data for all sites, and hydroclimatic conditions did not strongly deviate from those during the other three years of our study (Figure 3.2). Wavelet decomposition was conducted in R with the *wavelets* package v. 0.3-0.2 (Aldrich, 2020).

Interactions were quantified using relative mutual information (MI), which is a measure of (undirected) dependency between paired observations of two variables (Ruddell & Kumar, 2009). Interaction time lag was determined by finding maximum MI across successive shifts in the driver time series. This approach is analogous to maximum cross-correlation. The range of lags considered were up to 6 h at the diel scale, 10 d at the multi-day scale, and 60 d at the seasonal scale. Following Sturtevant et al. (2016), we also examined MI in the case that the putative driver lags behind CH₄ flux (i.e., the driver x is shifted by both negative and positive values of k in $x[t+k]$). We thus denote lags as negative when the driver precedes CH₄ flux, and positive when CH₄ flux precedes the driver. Note that because MI is not causal analysis, the latter case does not mean x is not a true driver of CH₄ flux. MI was calculated using the *entropy* R package v. 1.3.1 (Hausser & Strimmer, 2021).

MI has positive bias that increases with the degree of autocorrelation relative to time series length (Sturtevant et al., 2016). We accounted for this bias by simulating 100 pairs of “surrogate” time series. Surrogates were generated using iterative amplitude adjusted Fourier transform, which preserves spectral characteristics but otherwise randomizes the original series (Schreiber & Schmitz, 1996). We then applied wavelet decomposition and repeated MI analysis on surrogate pairs, creating a null distribution of MI values. We corrected bias in real MI by subtracting the mean surrogate MI (Sturtevant et al., 2016), and calculated p-values using a Monte Carlo approach (North et al., 2002). Specifically, $p = (n + 1)/(k + 1)$, where n is the number of surrogate pairs with MI greater than the real value, and k is the total number of surrogates.

Empirical dynamic modeling

Mutual information quantifies statistical dependency, but it does not distinguish causation from correlation. To assess whether relationships between CH₄ flux and biophysical variables were causal, we used empirical dynamic modeling (EDM), which has recently been applied to EC CH₄ flux data (Hill et al., 2024). We preferred EDM over other causal methods (e.g., transfer entropy) because EDM retains system dynamics and therefore can be used to identify nonlinear (i.e., state-dependent) interactions that vary under different environmental or temporal conditions (Runge et al., 2023). **EDM relies on Taken’s theorem** Much literature has been devoted to describing the theoretical basis for EDM and its computation algorithms (e.g., C.-W. Chang et al., 2017; Munch et al., 2023). In this section, we

outline our implementation and briefly summarize relevant background information. EDM was conducted in R using the *rEDM* package v. 1.15.4 (Park et al., 2024).

Wavelet detail reconstructions were highly autocorrelated at the original 30-min resolution (especially at the seasonal scale), which can mask nonlinear dynamics in time series (Hsieh et al., 2005). To minimize redundant information and reduce computation time, we downsampled wavelet detail to once hourly for diel, once every six hours for multi-day, and once daily for seasonal scales. We applied first-differencing to the seasonal scale to further reduce autocorrelation, ensure stationarity, and amplify nonlinear dynamics (C.-W. Chang et al., 2017). Strictly, this means that we investigated causes of *changes* in seasonal CH₄ flux; however, change in a variable naturally affects the variable itself. The length of analysis series was 4824 points, 804 points, and 1460 points for diel, multi-day, and seasonal scales, respectively. We did not re-introduce gaps because continuous time series were necessary for state space reconstruction.

State space reconstruction in EDM is achieved using time delay embedding and requires the selection of two parameters. Time delay τ determines the length of lags and embedding dimension E determines the number of lags. To capture respective time scales in delay embedding, we set τ to 1 h for diel, 1 d for multi-day, and 15 d for seasonal scales. Following standard EDM, we then selected E using simplex projection (Sugihara & May, 1990). Simplex projection is a forecasting technique that predicts future values in an embedded time series by examining the behavior of nearest neighbors in the state space, and E is tuned to optimize prediction accuracy. We evaluated the presence of nonlinear dynamics (as opposed to, e.g.,

purely high-dimensional stochasticity) in CH₄ flux using S-map forecasting (Sugihara, 1994). This method tunes a local weighting parameter, θ , to determine whether predictions improve if nearby points in the state space are given more influence in forecasts. If prediction skill is higher for nonlinear ($\theta > 0$) than linear ($\theta = 0$) solutions, there is evidence of state dependency (C.-W. Chang et al., 2017).

A key premise of EDM is that an adequate approximation of the system state (i.e., delay embedding) implicitly accounts for the influence of other observed or latent variables, allowing causation to be distinguished from mutual dependency (Runge et al., 2023). In the EDM framework, causal interactions are identified using convergent cross mapping (CCM; Sugihara et al., 2012). CCM employs the simplex projection algorithm to assess whether states of the response variable can estimate states of the driver, assuming that a true driver leaves an indelible “imprint” of its dynamics on the response (Sugihara et al., 2012).

Causal interaction strength is expressed as cross-map skill (ρ), which measures the accuracy of CCM predictions. We accounted for potential lag effects by varying the prediction time in CCM (Ye et al., 2015) and report the maximum ρ across a range of lags (same as with MI; see Multiresolution Mutual Information). The E for CCM was determined by optimal prediction of cross-mapping (C.-W. Chang et al., 2017). We set a maximum E of 20 to allow state vectors to span up to most of a day for diel interactions (20 h at $\tau = 1$ h) and most of a year for seasonal interactions (300 d at $\tau = 15$ d). To assess the degree of state dependency in interactions, we compared ρ to the maximum linear cross-correlation over the same

range of lags (Newcomb & Godsey, 2023). Cross-correlation provides a benchmark to quantify the extent that CCM improves prediction over a purely linear approach.

We evaluated cross-mappings against surrogate data and calculated p-values as with MI. For diel and seasonal scales, we generated surrogates by preserving the periodic signal of the time series and shuffling the residuals. This type of surrogate is designed to distinguish forcing from coincidental periodicity (Deyle et al., 2016). For the multi-day scale, we generated surrogates using a phase randomization technique, which preserves statistical time series properties (namely autocorrelation) but is otherwise random (Ebisuzaki, 1997). These surrogate tests are essential for inferring causation from CCM because they ensure that the observed interactions are inherent to the system dynamics rather than artifacts of coincidental trends or autocorrelation. We determined that a relationship was causal if 1) $p < 0.05$ and 2) ρ did not peak in the positive time domain (i.e., changes in CH₄ flux did not precede changes in the putative driver; Díaz et al., 2022).

Results

Temporal variability in CH₄ flux and biophysical drivers

Across four years of continuous measurement (2019–2022), all sites were net CH₄ sources. Fluxes were highly variable but similar in magnitude at the restored and natural wetland, with distinct seasonal patterns (Figure 3.2a). The natural wetland was a greater CH₄ source by an estimated average of 3.9 g CH₄-C m⁻² per year (Table S3.1). Fluxes were lower at the cultivated site with a seasonal amplitude well below

that of the wetlands. Mean daily fluxes ($\pm$ std. dev.) during the 2021 growing season were 168 ± 65 mg CH₄-C m⁻² d⁻¹ at the natural wetland, 161 ± 74 mg CH₄-C m⁻² d⁻¹ at the restored wetland, and 17 ± 13 mg CH₄-C m⁻² d⁻¹ at the cultivated site.

As expected, T_{soil} and GPP followed clear seasonal cycles, with increase beginning in spring, peak in late summer, and low in mid-winter (Figure 3.2b-c). GPP was more variable than T_{soil} within the seasonal course, although both variables responded to perturbations (i.e., weather) throughout the year. Annual GPP was greater at the natural wetland than the restored wetland, and greater still at the cultivated site. Hydrologic variables were less adherent to seasonal cycles (Figure 3.2d). There were large water level drawdowns in 2019 and 2022, which corresponded to periods in the late summer and early autumn with little or no precipitation. The other two years were relatively wet (Table S3.1), and wetlands remained flooded throughout.

During the 2021 growing season, CH₄ flux in the restored and natural wetland had similar diel patterns (reconstructed from wavelet detail; Figure 3.3). Fluxes were highest at night, with peaks in both the early morning and early evening. Fluxes dropped rapidly during the morning and rose rapidly in the late afternoon. At the cultivated site, CH₄ fluxes were also highest at night, but rose steadily throughout the day from a minimum in mid-morning to a maximum before midnight. Of the biophysical variables, diel cycling was by far the most pronounced in GPP. Diel variation in T_{soil} and hydrologic variables was negligible.

Total variation in wetland CH₄ flux was dominated by seasonal-scale fluctuations (Table S3.2). The seasonal scale accounted for 81% and 75% of wavelet

variance in the natural and restored wetlands, respectively. At the cultivated site, seasonal variance accounted for 26%; CH₄ flux varied more at the hourly (36%) and diel (31%) scales. Multi-day variation was the smallest component at all sites (<8%), regardless of whether all data or a growing season subset was considered.

Interactions between CH₄ flux and biophysical drivers

Interactions between CH₄ flux and biophysical drivers varied by site and time scale (Figure 3.4; $p = 0.01$ unless otherwise noted). During the 2021 growing season, GPP had the strongest diel interactions with CH₄ flux at all sites. MI was highest at the restored and cultivated sites (both 0.049), with the natural wetland somewhat lower (MI = 0.036); maximum MI occurred without lag at all sites (Table S3.3). The natural wetland generally had the weakest diel interactions, but all were still highly probable. Diel T_{soil} was particularly weak at the natural wetland (MI = 0.008) compared to the restored and cultivated sites (MI = 0.029 and 0.040, respectively).

At the multi-day scale, T_{soil} dominated interactions with wetland CH₄ flux (Figure 3.4). MI values for T_{soil} (0.16 and 0.17 at the natural and restored wetland, respectively) were several times higher than other drivers. At the cultivated site, T_{soil} also had the strongest multi-day interaction (MI = 0.055), but by a much smaller margin. Multi-day GPP and hydrology interactions were weaker but highly probable ($p \leq 0.02$) at all sites. The strength of these interactions did not differ greatly by site or from each other. CH₄ flux had a greater lag time with multi-day hydrology at the wetlands (-6 to -6.5 d), while maximum MI occurred without lag at the cultivated site. Multi-day CH₄ flux lagged GPP by -1 to -2.5 d and led T_{soil} by +12 h to +1 d. In

general, lagged multi-day interactions with hydrology and GPP were stronger and more probable than contemporaneous ones (Table S3.3).

T_{soil} also had strong seasonal interactions with CH_4 flux (Figure 3.4). At the wetland sites, this was the strongest interaction, while GPP dominated at the cultivated site ($\text{MI} = 0.24$). CH_4 flux lagged GPP by -16 d at the cultivated site compared to a small lag (-1 d) at the natural wetland and a small lead (+4 d) at the restored wetland (Table S3.3). Seasonal MI with GPP at the natural (0.14) and restored (0.16; $p = 0.06$) wetland were similar to seasonal MI with T_{soil} at the cultivated site (0.16; $p = 0.02$). MI with hydrologic variables was low and potentially spurious at all sites ($p = 0.33, 0.43$, and 0.13 at the natural, restored, and cultivated sites, respectively).

CH_4 flux displayed state dependency at all sites and time scales (Table S3.4). The strongest state dependency was found at the diel scale for all sites, followed by the seasonal scale for the restored and cultivated sites and the multi-day scale for the natural wetland. Seasonal and multi-day state dependency were both strongest at the natural wetland; at the multi-day scale, restored and cultivated site fluxes had relatively weak state dependency. Further, relationships between CH_4 flux and biophysical drivers were state dependent. This was particularly evident at the seasonal scale, where relationships showed hysteresis (Figure 3.5), and all cross-mappings had higher predictive skill than the equivalent linear cross-correlation (Table 3.1).

Accounting for state dependency, convergent cross mapping identified interactions that were likely causal (Table 3.1). Cross-mapping was significant for diel-scale GPP and CH_4 flux at all sites, and marginally stronger at the wetlands (*rho*

= 0.50, 0.59 for natural and restored; both $p = 0.01$) than the cultivated site ($\rho = 0.47$, $p = 0.02$). Maximum cross-mapping with GPP occurred at -12 h for the natural wetland and at -2 h for the restored and cultivated sites, although lagged ρ was only marginally greater than ρ without lag (Table S3.5). At the cultivated site, T_{soil} was the dominant driver of diel CH_4 flux ($\rho = 0.58$, $p = 0.01$). T_{soil} also had a relative strong causal interaction at the restored wetland ($\rho = 0.40$, $p = 0.01$). At the natural wetland, diel T_{soil} was significant, but causation was weak ($\rho = 0.15$) and lower than the maximum cross-correlation (0.17), indicating a lack of nonlinear dynamics. Diel causal interactions with hydrology were all significant but relatively weak.

Most causal relationships at the multi-day scale should be interpreted with caution since ρ was lower than the maximum cross-correlation (Table 3.1). This suggests that, although cross-mapping was significant, nonlinear methods may not be appropriate for analyzing these interactions. The exceptions were multi-day T_{soil} at the natural and cultivated sites; in these cases, ρ was marginally greater than cross-correlation. Regardless, multi-day CCM results largely followed the same patterns found in MI. T_{soil} dominated wetland causal interactions with CH_4 flux at this scale, while causal strength more even among drivers at the cultivated site. Causal interactions at the restored wetland with GPP ($\rho = 0.52$) and hydrology ($\rho = 0.32$) were stronger than those at the natural wetland ($\rho = 0.17$ and $\rho = 0.19$, respectively; all $p = 0.01$). At both wetlands, maximum cross-mapping with hydrology occurred at greater lag times (-5.5 to -7.5 d) than at the cultivated site (-12 h).

T_{soil} dominated causal interactions with wetland CH_4 flux at the seasonal scale (Table 3.1). There was a similar degree of causation at the wetlands (both $\rho = 0.87$, $p = 0.01$); however, this interaction could not be distinguished from coincidental seasonality at the cultivated site ($\rho = 0.73$, $p = 1.00$). Cross-map lag with T_{soil} was greater at the restored wetland (-39 d) than the natural wetland (-9 d). Without time lag, ρ was only marginally smaller at both sites, but this cross-mapping was not statistically significant at the restored wetland ($p = 0.67$; Table S3.5); thus, a time lag was necessary to identify a causal interaction with T_{soil} at the restored wetland. Despite sharing little information with CH_4 flux, seasonal water level had a significant nonlinear causal interaction at both wetlands. This interaction was stronger at the restored wetland ($\rho = 0.44$ compared to $\rho = 0.38$ at the natural wetland; both $p = 0.01$) and acted with a shorter lag time (-5 d compared to -11 d at the natural wetland; Table 3.1). Surrogate testing indicated that strong links between CH_4 flux and GPP at the seasonal scale were caused by mutual dependency and not a causal link. No significant seasonal causal interactions were identified at the cultivated site.

Discussion

This study aimed to evaluate CH_4 fluxes at three sites with contrasting land-use histories through the lens of biophysical drivers and temporal dynamics. Over four years, CH_4 fluxes at the natural and restored wetland were consistently higher and dominated by variability at larger time scales than at the cultivated site. At all sites, GPP drove diel-scale CH_4 fluxes, while T_{soil} dominated at multi-day and seasonal scales, especially in wetlands. Hydrology was a relatively weak, but

significant, driver of seasonal CH₄ fluxes in the wetlands. Convergent cross mapping indicated likely causal links from biophysical drivers to fluxes.

Since interactions were state-dependent, we cannot strictly attribute directions to driver effects on CH₄ flux. In other words, depending on the system state, the effects of a driver on CH₄ flux may have been either positive or negative. In the following, we hypothesize mechanisms contributing to the relationships we found and encourage the reader to bear in mind that our analysis of causality, while robust, was based on observation data. We focus most of our discussion on diel and seasonal interactions, as these were the most important scales for CH₄ variability included in our analysis (Table S3.2). We conclude by revisiting the question: what can relationships with biophysical drivers tell us about wetland CH₄ flux across land uses?

Diel CH₄ flux variation driven by GPP

GPP was the primary driver of diel CH₄ fluxes at the wetlands. However, the diel cycle of CH₄ flux in both wetlands was inverse that of GPP, with higher fluxes at night (Figure 3.3). This pattern has been previously reported (Dooling et al., 2018; Goodrich et al., 2011; Lhosmot et al., 2023), but is contrary to expectation for herbaceous wetlands, where vascular plants are generally thought to have a positive effect on CH₄ fluxes, and fluxes tend to peak during the day when GPP is highest (e.g., Hatala et al., 2012). While GPP was a significant diel driver, T_{soil} was the dominant diel driver at the cultivated site.

Our findings are consistent with a twofold control of GPP on diel CH₄ fluxes, where plant photosynthesis 1) reduces daytime fluxes by oxygenating the rhizosphere and 2) increases nighttime fluxes by releasing root exudates (Lhosmot et al., 2023). During the day while plants are actively photosynthesizing, oxygen can escape from roots into the rhizosphere (i.e., radial oxygen loss), leading to diel redox fluctuations (Nikolausz et al., 2008). Light intensity and plant CO₂ uptake rates are positively correlated with radial oxygen loss (Nikolausz et al., 2008), and inhibition of photosynthesis can increase CH₄ emissions from vegetated areas (Ding et al., 2004b), suggesting that this is an active process that can dominate the overall plant effect on CH₄ flux (Noyce et al., 2023). Radial oxygen loss may stimulate aerobic methanotrophy (Ding et al., 2004a), resulting in oxidation of, in some cases, >90% of total CH₄ production (Ström et al., 2005). Rhizosphere oxygenation can also regenerate alternative terminal electron acceptors (e.g., Fe³⁺, SO₄²⁻), which may enable microbes with more thermodynamically favorable metabolic pathways to outcompete methanogens, effectively suppressing CH₄ production (Sutton-Grier & Megonigal, 2011). Rhizosphere oxygen concentrations have been shown to peak ~2 hours after light intensity (Dong et al., 2011), and a subsequent decrease in CH₄ concentration may occur less than an hour after oxygen addition (Ndanga et al., 2016), suggesting that this process likely suppresses fluxes during the day, while plants are photosynthesizing.

Plant photosynthesis also leads to exudation of bioavailable organic compounds into the rhizosphere. Root exudates are a preferred substrate for methanogens and can fuel a large proportion of CH₄ fluxes from wetlands (King &

Reeburgh, 2002). Recent studies suggest that root exudation may additionally increase fluxes by priming the microbial decomposition of soil organic matter into components more readily assimilated by methanogens (Waldo et al., 2019), and by promoting competition among microbes that effectively outcompete methanotrophs and reduce CH₄ oxidation (Turner et al., 2020). Importantly, any effects of root exudation on CH₄ fluxes involve multi-step processes; thus, there is likely to be a delay between CO₂ uptake and CH₄ emission (Dooling et al., 2018). Isotopic labelling studies have found that peak ¹⁴CH₄ emissions occur several days after plant assimilation of ¹⁴CO₂ (King & Reeburgh, 2002), but can begin in <12 h (Megonigal et al., 1999), and as soon as 4 h after substrate is introduced to the soil (Ström et al., 2003). The range of reported lag times are therefore consistent with the possibility that plant photosynthesis during the day can enhance CH₄ fluxes at night (Dooling et al., 2018; Lhosmot et al., 2023).

CH₄ fluxes can also be enhanced by plant-mediated gas transport. Diel patterns in CH₄ flux have been linked to plant stomatal aperture and conductance (Morrissey et al., 1993), and plants with pressurized ventilation systems can trigger CH₄ spikes around sunrise (Chanton et al., 1993). In plants that exchange gases passively, like the *Carex* species that dominates our natural wetland, plant-mediated transport is not regulated by GPP at the diel scale (Vroom et al., 2022). This means that we cannot infer the role of plant-mediated transport in diel CH₄ flux; however, it is possible that it is an important CH₄ emission pathway at our sites, though fluctuations are unlikely to be visible at the diel scale.

State-dependent control of seasonal CH₄ flux

At the wetlands, seasonal CH₄ flux was driven by soil temperature (T_{soil}) and water level. T_{soil} was the dominant seasonal (and multi-day) driver at both wetlands, with similar causal strength. This finding is unsurprising, as the temperature dependence of CH₄ flux is well documented (Knox et al., 2021; Yvon-Durocher et al., 2014). Water level had a secondary, but significant effect on seasonal wetland CH₄ flux, and did not follow a consistent seasonal cycle like that in T_{soil} and GPP. These results support a relatively simple model of state-dependent seasonal CH₄ dynamics in the wetlands, where fluxes largely followed T_{soil} , but were modulated by water level under certain conditions. The effects of water level were evident during large evapotranspiration-driven drawdown events, which occurred some years during the late summer through fall (e.g., Figure 3.5a). Conversely, in relatively wet years without water level drawdown, there was less hysteresis in the T_{soil} relationship (e.g., Figure 3.5b). Our results support previous studies suggesting that the temperature sensitivity of CH₄ flux depends on water level (Chen et al., 2021), and that hysteresis in temperature sensitivity is explained by seasonal water level variation (Feng et al., 2020; Holl et al., 2020).

Wetland CH₄ fluxes exhibited a lagged response to water level. At the seasonal scale, fluxes at the natural wetland were more lagged than at the restored wetland (-11 d compared to -7 d), although CCM without lag was significant at both wetlands. However, at the multi-day scale, interactions were stronger and more probable when time lags were applied. This was the case for both wetlands, and for both MI and CCM. Further, the lag at which the strongest interaction occurred was

consistent across sites and methods, between -5.5 d and -7.5 d. These lags are within the range of previously-reported lags in wetlands, which are generally between -3 and -10 d (Chamberlain et al., 2016; Goodrich et al., 2015; Olefeldt et al., 2017). The multi-day effect of hydrology on CH₄ flux appeared to have little or no time lag at the cultivated site, although we cannot exactly compare this interaction to the wetlands since hydrology was represented by soil water content.

Time lag in the effect of water level on CH₄ flux reflects the indirectness of this interaction. For example, for water level to affect CH₄ flux via soil redox state, changes in water level must be followed by changes in soil oxygenation, redox conditions, and activity of methanogens and/or methanotrophs (Whalen, 2005). The time necessary for an effect to appear in CH₄ flux may be extended further by other factors. For example, periods of low water level may increase the availability of alternative electron acceptors in the soil (e.g., ferric iron, nitrate). Following an increase in water level and return of reducing conditions, methanogens may be at a competitive disadvantage until pools of alternative electron acceptors are depleted, resulting in a delayed return of CH₄ emissions (Tangen & Bansal, 2019).

A threshold effect of water level may contribute to state dependency in seasonal relationships. Previous work has identified a critical water level below which CH₄ fluxes decrease rapidly (Calabrese et al., 2021), and suggested that water level control on CH₄ flux may be better represented as a binary effect (i.e., an “on-off switch”; Christensen et al., 2003) rather than a continuous relationship (Hassett et al., 2024). This is further supported by studies that have failed to identify interactions between water level and CH₄ flux at any scale in perpetually flooded wetlands (e.g.,

Rinne et al., 2007; Sturtevant et al., 2016). The threshold or binary effect may relate directly to soil reducing conditions, or it may act on the sensitivity of fluxes to other biophysical drivers such as temperature (Brown et al., 2014; Goodrich et al., 2015) and atmospheric pressure (Whalen, 2005). In wetlands with elevation gradients, like our depressional wetlands, variation in water level can be accompanied by variation in the flooded area, and ecosystem-level CH₄ fluxes may reflect the size of the CH₄ source area (Hondula et al., 2021).

We did not identify a significant interaction between seasonal water level and CH₄ flux using MI. Following the existing multiresolution mutual information framework, we did not apply differencing to time series prior to MI analysis. This means that we cannot separate the effects of differencing and state dependency in comparing MI with CCM; however, given the complexity of water level as a driver of CH₄ flux (Brown et al., 2014; Olefeldt et al., 2017), we encourage researchers to consider how temporal dynamics may influence this relationship in future analyses.

Despite strong seasonal interactions between GPP and CH₄ flux, we did not find evidence of causality in this relationship using CCM. This result is contrary to recent studies finding that GPP, rather than temperature, was the dominant control on wetland seasonal CH₄ flux (Mitra et al., 2020), and that seasonal hysteresis in the temperature sensitivity of CH₄ flux was explained by substrate availability (K.-Y. Chang et al., 2020). Seasonal fluctuations in GPP primarily represent plant phenological cycles, which control rates of root exudation, litterfall, and plant-mediated gas transport (Ge et al., 2023; Helfter et al., 2022). Our results suggest that any effect of substrate limitation likely occurs at shorter time scales; GPP was a

significant diel and multi-day driver at all sites. Further, the dominant plants in our wetlands left standing litter, which can be a conduit for CH₄ (Kim et al., 1999). The lack of a seasonal effect of GPP could suggest that plant-mediated transport at our wetlands, if it is an important emission pathway, occurs in both live and dead tissue.

We did not identify any causal seasonal relationships with CH₄ flux at the cultivated site. However, this site had strong seasonal interactions with T_{soil} and GPP, suggesting that seasonality was present, but driven by one or more unmeasured variables (i.e., external forcing). It is possible that there was a mismatch between our measurements of biophysical drivers and the source of CH₄ in this system. The cultivated site flux tower was located next to an agricultural drainage ditch that likely contributed a large proportion, if not all, of the CH₄ measured at the tower (Köhn et al., 2021). While agricultural fields can be modest CH₄ sources (Chu et al., 2014), ditches are considered CH₄ hotspots because they collect sediment, organic matter, and nutrients from runoff, and low flow rates allow anoxic conditions to develop (Peacock et al., 2021). Our T_{soil} and soil water content sensors, however, were positioned directly below the flux tower outside the ditch. Although our measurements likely covaried with conditions inside the ditch, EDM is sensitive to nonlinear dynamics which may not have been represented at the seasonal scale from outside the ditch.

CH₄ dynamics in natural vs. restored wetland

Our study suggests that 20 years after restoration, processes governing CH₄ flux in a restored wetland resemble those in a natural wetland. Fluxes at the restored

wetland were of similar magnitude, followed similar temporal patterns, and responded similarly to scale-dependent biophysical drivers compared to the natural wetland. Overall, we found little evidence that CH₄ dynamics differed strongly between the natural and restored wetland; differences between the wetlands and cultivated site were far more apparent. This result is in line with a study showing a shift in the factors driving variation in CH₄ flux after restoration by raising the water table (Luan et al., 2018), and reflects alteration in underlying ecosystem processes due to disturbance. Another study found that restored wetlands were more sensitive to external forcing than natural wetlands (Wilson et al., 2016). Although CH₄ flux and biophysical drivers shared more information at our restored wetland, suggesting stronger interactions, we found that key interactions had similar causal strengths to the natural wetland. Rather than stronger external forcing, this suggests that unmeasured drivers may have a larger role at the restored wetland. These could involve diel scale mechanisms such as turbulent and convective mixing of the water column (Godwin et al., 2013; Poindexter & Variano, 2013), and multi-day to seasonal drivers such as the availability of secondary fermentation products (K.-Y. Chang et al., 2020; Wilmoth et al., 2021).

Tables

Table 3.1. Results of convergent cross mapping for biophysical drivers and CH₄ flux. Cross-map skill (*rho*) is the strength of causation; evidence of causation (+) or no evidence of causation (–) was evaluated with the criteria outlined in methods. Lag is negative if cross-map skill peaked when the driver preceded CH₄ flux. x-corr is the magnitude of the maximum lagged linear cross-correlation. Seasonal interactions were evaluated over first-differenced data from 2019 to 2022; diel and multi-day interactions are from the 2021 growing season (DOY 100–300). T_{soil} = soil temperature; GPP = gross primary productivity; WL = water level; SWC = soil water content.

Scale	Site	Driver	x-corr	<i>rho</i>	p-value	Lag	Causation
Diel	Natural	T _{soil}	0.165	0.145	0.01	-2 h	+
		GPP	0.383	0.500	0.01	-12 h	+
		WL	0.090	0.115	0.01	-2 h	+
	Restored	T _{soil}	0.308	0.397	0.01	-4 h	+
		GPP	0.434	0.589	0.01	-2 h	+
		WL	0.169	0.226	0.01	-12 h	+
	Cultivated	T _{soil}	0.332	0.575	0.01	-11 h	+
		GPP	0.337	0.465	0.02	-2 h	+
		SWC	0.189	0.192	0.01	-12 h	+
Multi-day	Natural	T _{soil}	0.725	0.760	0.01	-0.5 d	+
		GPP	0.331	0.165	0.01	-2.5 d	+
		WL	0.225	0.191	0.02	-5.5 d	+
	Restored	T _{soil}	0.765	0.690	0.01	-0.5 d	+
		GPP	0.596	0.517	0.01	-1.0 d	+
		WL	0.379	0.319	0.01	-7.5 d	+
	Cultivated	T _{soil}	0.390	0.409	0.01	-1.5 d	+
		GPP	0.393	0.270	0.01	-1.0 d	+
		SWC	0.376	0.305	0.02	-0.5 d	+
Seasonal	Natural	T _{soil}	0.615	0.874	0.01	-7 d	+
		GPP	0.608	0.709	1.00	+60 d	–
		WL	0.271	0.381	0.01	-11 d	+
	Restored	T _{soil}	0.738	0.869	0.01	-38 d	+
		GPP	0.671	0.787	0.28	-1 d	–
		WL	0.266	0.441	0.01	-5 d	+
	Cultivated	T _{soil}	0.464	0.730	1.00	+30 d	–
		GPP	0.643	0.734	0.01	+60 d	–
		SWC	0.291	0.394	0.14	+27 d	–

Figures

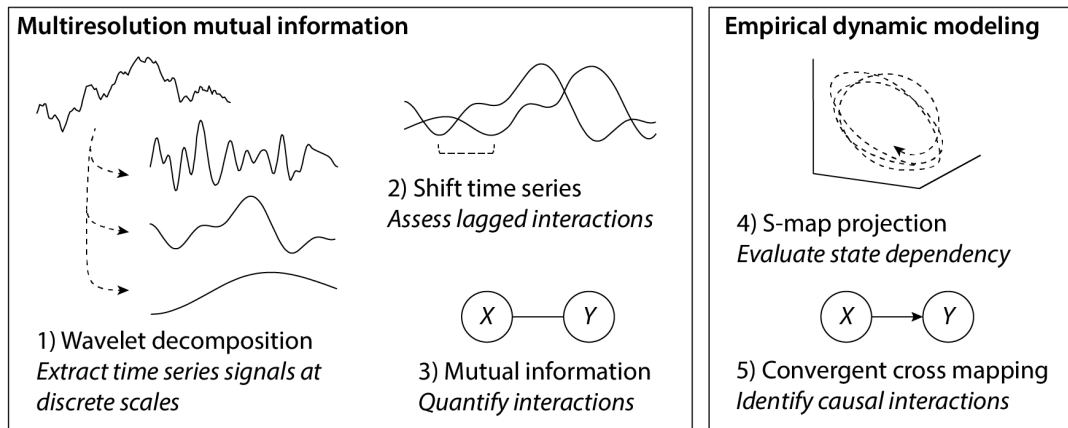


Figure 3.1. Summary of the analyses used to characterize biophysical drivers of CH₄ flux. Note that empirical dynamic modeling was applied to wavelet decomposed time series.

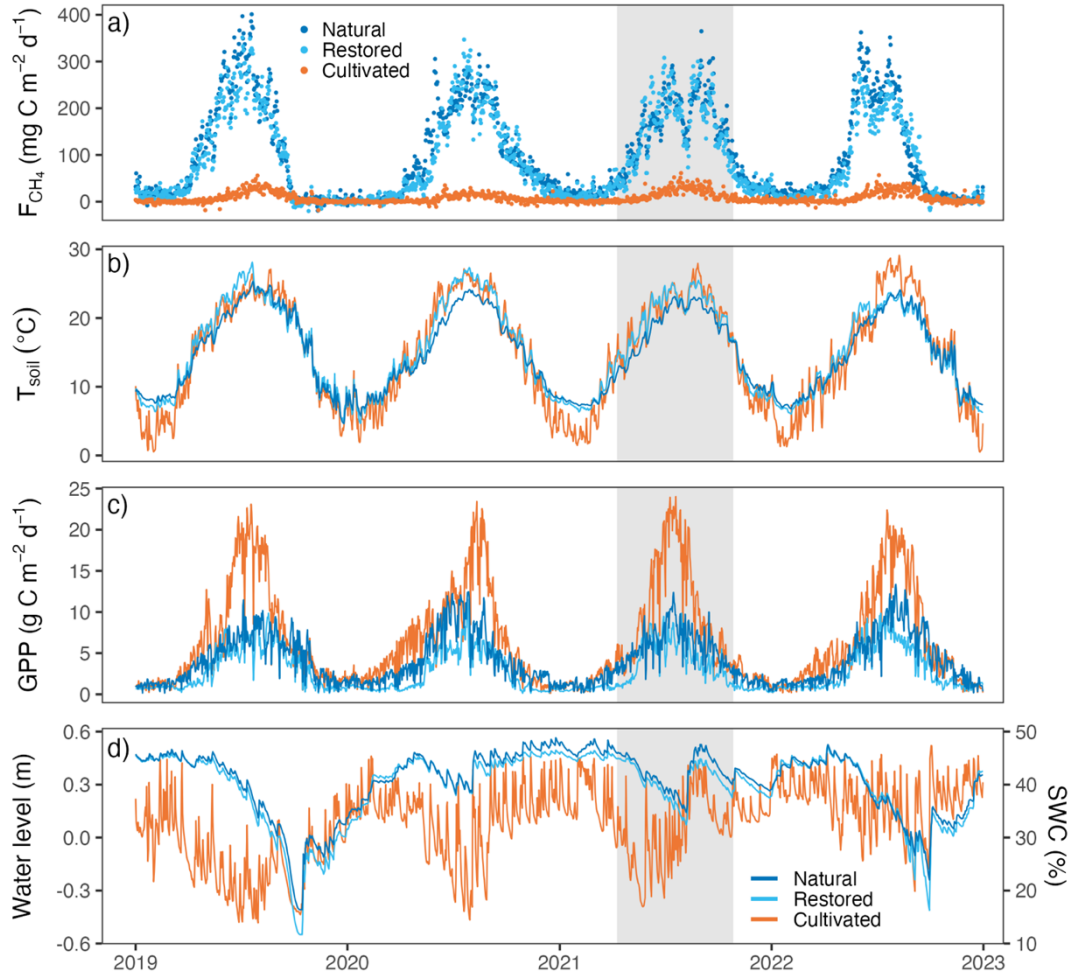


Figure 3.2. Time series of daily gap-filled a) CH_4 flux (F_{CH_4}), b) soil temperature (T_{soil}), c) gross primary productivity (GPP), and d) hydrologic variables in the natural wetland, restored wetland, and cultivated former wetland. Hydrology is represented by water level for wetland sites and soil water content (SWC) for the cultivated site. Fluxes F_{CH_4} and GPP are given in mass units of $\text{CH}_4\text{-C}$ and $\text{CO}_2\text{-C}$, respectively. The shaded area indicates the 2021 growing season (DOY 100–300), which was the focus for sub-seasonal analyses in this study.

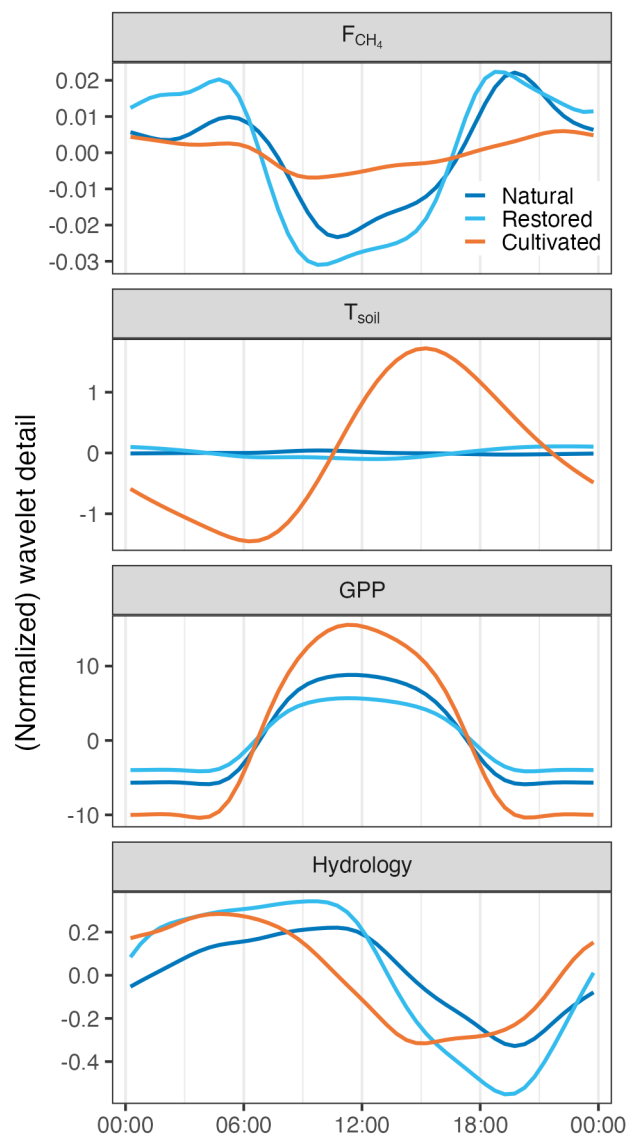


Figure 3.3. Diel cycles of CH_4 flux (F_{CH_4}), soil temperature (T_{soil}), gross primary productivity (GPP), and hydrologic variables in the 2021 growing season (DOY 100–300). Hydrology is represented by water level (WL) for the natural and restored wetlands and soil water content (SWC) for the cultivated site. Diel variation is shown as diel-scale wavelet detail, averaged by time of day. Wavelet detail was normalized by variable, and additionally by site for hydrologic variables to show WL and SWC on the same scale.

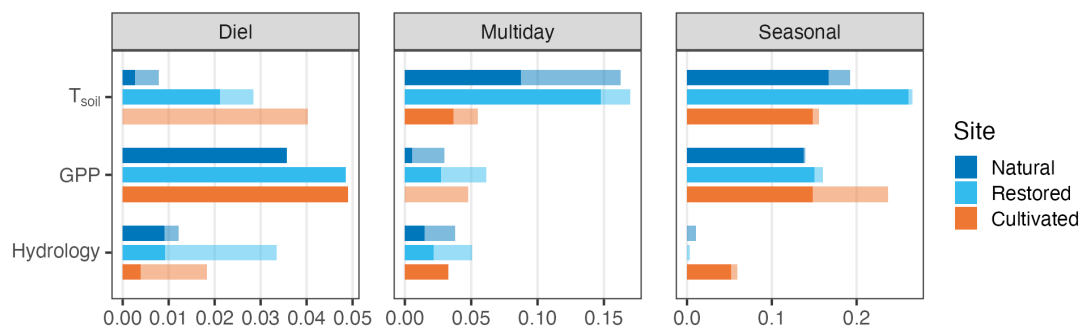


Figure 3.4. Mutual information (MI; i.e., statistical dependency) between CH_4 flux and biophysical variables at diel, multi-day, and seasonal time scales. Interactions at diel and multi-day scales were assessed during the 2021 growing season (DOY 100–300); seasonal scale encompasses all data from 2019 to 2022. Dark portions of bars are MI without time lag; lighter extensions are maximum lagged MI. Note different axis scales on each panel. T_{soil} = soil temperature; GPP = gross primary productivity.

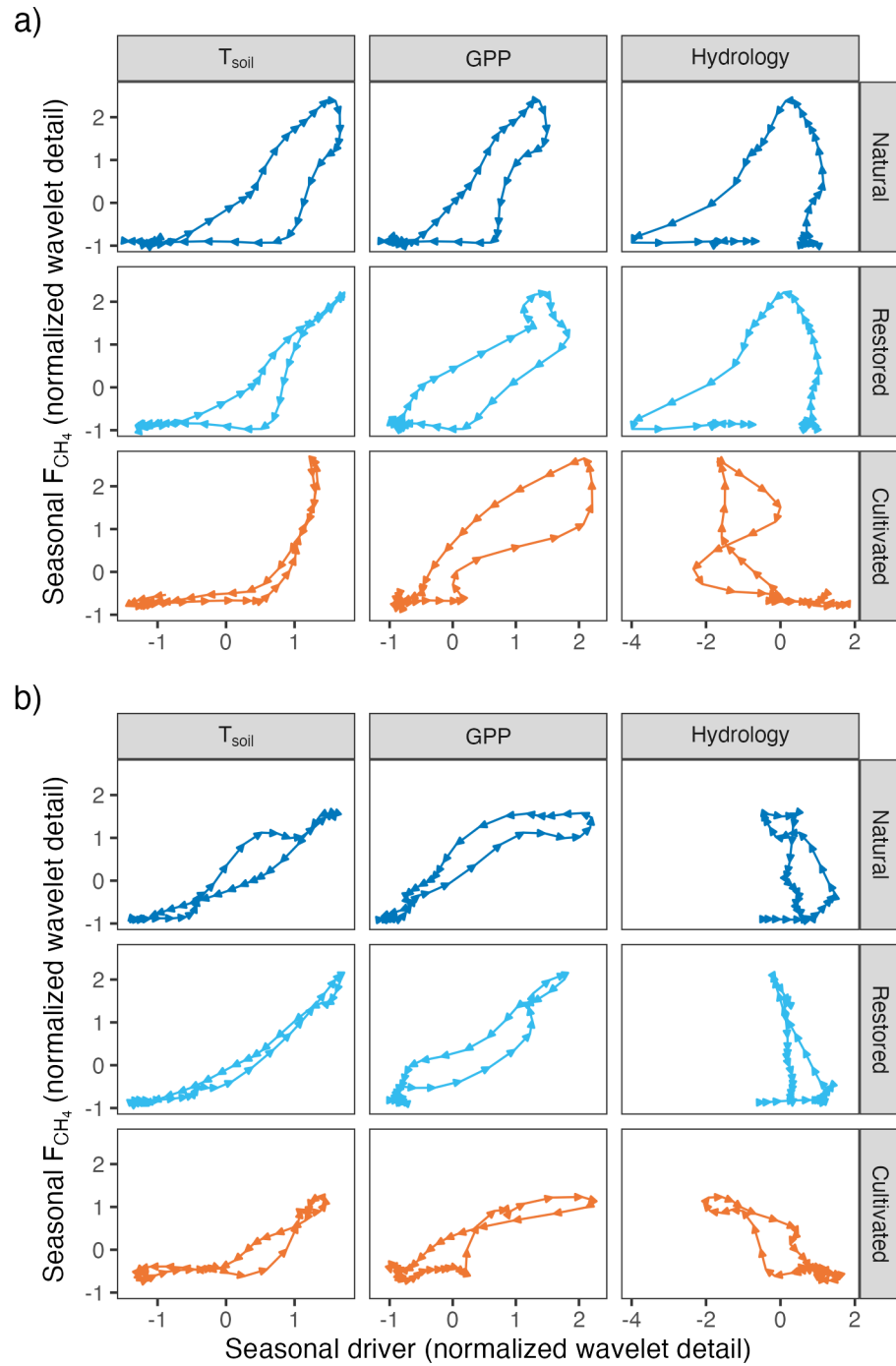


Figure 3.5. Seasonal hysteresis curves showing state dependency in relationships between CH_4 flux (F_{CH_4}) and soil temperature (T_{soil}), gross primary productivity (GPP), and hydrologic variables in the natural wetland, restored wetland, and cultivated former wetland. The exact shape of the hysteresis curves varied year-to-year; the a) 2019 (dry summer) and b) 2020 (wet summer) calendar years are shown here. Arrows point forward in time.

Supplementary materials

List of variables used to predict CH₄ flux in site-specific random forest regression:

Non-CH₄ turbulent fluxes

1. Net ecosystem CO₂ exchange (NEE)
2. Ecosystem respiration – partitioned from NEE using nighttime method
3. Ecosystem respiration – partitioned from NEE using daytime method
4. Gross primary productivity – partitioned from NEE using nighttime method
5. Gross primary productivity – partitioned from NEE using daytime method
6. Latent heat flux
7. Sensible heat flux

Environmental covariates (sensor)

8. Air temperature (Vaisala HMP155 humidity and temperature probe)
9. Incoming shortwave radiation (Kipp & Zonen CNR 4 net radiometer)
10. Wind speed (Gill Instruments WindMaster Pro)
11. Air pressure (LI-COR LI-7700 open path CH₄ analyzer)
12. Soil temperature (Stevens Hydra Probe II soil sensor)
13. Water table depth (Onset HOBO pressure transducer; wetland sites only)
14. Soil water content (Stevens Hydra Probe II soil sensor)
15. Soil heat flux (Hukseflux HFP01 heat flux sensor)
16. Outgoing shortwave radiation (Kipp & Zonen CNR 4 net radiometer)
17. Incoming & outgoing longwave radiation (Kipp & Zonen CNR 4 net radiometer)
18. Net radiation (Kipp & Zonen CNR 4 net radiometer)
19. Friction velocity (Gill Instruments WindMaster Pro)
20. Vapor pressure deficit (Vaisala HMP155 humidity and temperature probe)
21. Precipitation (Texas Instruments TR-525M tipping bucket rain gauge)
22. Relative humidity (Vaisala HMP155 humidity and temperature probe)
23. Photosynthetic photon flux density (LI-COR LI-190R quantum sensor)
24. Sine of wind direction (Gill Instruments WindMaster Pro)
25. Cosine of wind direction (Gill Instruments WindMaster Pro)

Fuzzy sets for time and annual cycles

26. Day of year
27. Sine of day of year
28. Cosine of day of year

Table S3.1. Annual climatic conditions and estimated greenhouse gas (GHG) budgets. Air temperature (T_{air}) and precipitation (P) are averaged across the sites. Flux units are $\text{g} [\text{GHG}]\text{-C m}^{-2} \text{y}^{-1}$. CO_2 balances were estimated as the difference between ecosystem respiration and gross primary productivity modeled using the “daytime” method (see main text for reference). Negative GHG balance indicates net uptake.

Year	T_{air} , °C	P, mm	Natural		Restored		Cultivated	
			CH_4	CO_2	CH_4	CO_2	CH_4	CO_2
2019	13.9	1134	37.0	-132	32.4	-100	2.78	-170
2020	14.4	1593	37.2	-310	33.4	-365	1.90	-38
2021	14.3	1306	38.7	-363	36.2	-315	3.72	-105
2022	13.6	1195	31.0	-138	26.3	-210	2.99	-79
Avg.	14.1	1307	36.0	-236	32.1	-248	2.85	-98

Table S3.2. Wavelet variance (% of total) of CH_4 flux at different time scales. Variance is shown for all data from 2019 to 2022, and for within the growing seasons (DOY 100–300) of these years. The hourly scale was not included in further analyses.

Site	All data				Growing season			
	Hour-ly	Diel	Multi-day	Season-al	Hour-ly	Diel	Multi-day	Season-al
Natural	7.39	6.55	4.76	81.3	12.0	10.7	7.37	70.0
Restored	9.53	9.86	5.32	75.3	14.6	15.4	7.56	62.4
Cultivated	36.0	31.1	7.12	25.8	38.2	35.3	7.99	18.5

Table S3.3. Multiresolution mutual information without lag and with lags of up to ± 12 h for diel interactions, ± 10 d for multi-day interactions, and ± 60 d for seasonal interactions.

Scale	Site	Driver	Without lag		Lagged		
			MI	<i>p</i> -value	Lag	MI	<i>p</i> -value
Diel	Natural	T _{soil}	0.003	0.13	-9 h	0.008	0.01
		GPP	0.036	0.01	0 h	0.036	0.01
		WL	0.009	0.01	-12 h	0.012	0.01
	Restored	T _{soil}	0.021	0.01	+11 h	0.029	0.01
		GPP	0.049	0.01	0 h	0.049	0.01
		WL	0.009	0.02	+7 h	0.034	0.01
	Cultivated	T _{soil}	-0.018	0.73	+4 h	0.040	0.01
		GPP	0.049	0.01	0 h	0.049	0.01
		SWC	0.004	0.07	-7 h	0.018	0.01
Multi-day	Natural	T _{soil}	0.088	0.01	+1.0 d	0.163	0.01
		GPP	0.006	0.31	-2.5 d	0.030	0.02
		WL	0.015	0.17	-6.0 d	0.038	0.02
	Restored	T _{soil}	0.148	0.01	+0.5 d	0.170	0.01
		GPP	0.027	0.05	-1.5 d	0.061	0.01
		WL	0.022	0.06	-6.5 d	0.051	0.01
	Cultivated	T _{soil}	0.036	0.01	+1.0 d	0.055	0.01
		GPP	-0.007	0.76	-1.0 d	0.048	0.01
		SWC	0.033	0.01	0 d	0.033	0.01
Seasonal	Natural	T _{soil}	0.167	0.01	+12 d	0.193	0.01
		GPP	0.138	0.05	-1 d	0.139	0.01
		WL	-0.077	0.97	-59 d	0.010	0.33
	Restored	T _{soil}	0.261	0.01	+2 d	0.266	0.01
		GPP	0.150	0.06	+4 d	0.160	0.06
		WL	-0.078	0.98	+60 d	0.003	0.43
	Cultivated	T _{soil}	0.148	0.03	-3 d	0.156	0.02
		GPP	0.148	0.07	-16 d	0.237	0.01
		SWC	0.052	0.14	-5 d	0.059	0.13

Table S3.4. Results of univariate empirical dynamic modeling of CH₄ flux. E = embedding dimension, θ = state dependency parameter, Δrho = increase in prediction skill from linear to nonlinear parameterization of S-map projection.

Scale	Site	E	θ	Δrho
Diel	Natural	3	3.5	5.34e ⁻³
	Restored	3	2.5	3.96e ⁻³
	Cultivated	3	3.5	7.20e ⁻³
Multi-day	Natural	5	2.0	3.68e ⁻⁴
	Restored	10	0.6	0.24e ⁻⁴
	Cultivated	4	0.1	0.01e ⁻⁴
Seasonal	Natural	5	1.5	5.41e ⁻⁵
	Restored	8	1.3	4.21e ⁻⁵
	Cultivated	6	1.0	1.92e ⁻⁵

Table S3.5. Results of convergent cross mapping (without time lag) for biophysical drivers and CH₄ flux. Cross-map skill (*rho*) is the strength of causation. corr is the magnitude of the linear correlation. Seasonal interactions were evaluated over first-differenced data from 2019 to 2022; diel and multi-day interactions are from the 2021 growing season (DOY 100–300). T_{soil} = soil temperature; GPP = gross primary productivity; WL = water level; SWC = soil water content.

Scale	Site	Driver	corr	<i>rho</i>	p-value
Diel	Natural	T _{soil}	0.117	0.127	0.01
		GPP	0.383	0.481	0.01
		WL	0.090	0.106	0.01
	Restored	T _{soil}	0.295	0.371	0.01
		GPP	0.434	0.580	0.01
		WL	0.154	0.178	0.02
	Cultivated	T _{soil}	0.097	0.544	0.01
		GPP	0.337	0.446	0.47
		SWC	0.015	0.120	0.01
Multi-day	Natural	T _{soil}	0.624	0.756	0.01
		GPP	0.119	0.075	0.06
		WL	0.043	-0.005	0.56
	Restored	T _{soil}	0.755	0.672	0.01
		GPP	0.426	0.443	0.01
		WL	0.062	0.069	0.07
	Cultivated	T _{soil}	0.382	0.297	0.01
		GPP	0.096	0.120	0.01
		SWC	0.236	0.293	0.01
Seasonal	Natural	T _{soil}	0.603	0.873	0.01
		GPP	0.608	0.647	1.00
		WL	0.216	0.340	0.01
	Restored	T _{soil}	0.737	0.856	0.67
		GPP	0.668	0.787	0.35
		WL	0.181	0.402	0.01
	Cultivated	T _{soil}	0.458	0.711	1.00
		GPP	0.641	0.634	1.00
		SWC	0.077	0.288	1.00

Table S3.6. Annual sustained global warming potential (SGWP) based on estimated CO₂ and CH₄ budgets (see Table S3.1). SGWP is given in g CO₂ eq. m⁻² y⁻¹ and calculated over 20, 100, and 500-y time horizons as in Neubauer & Megonigal (2015). Positive SGWP = net warming; negative SGWP = net cooling.

Year	Natural			Restored			Cultivated		
	20-y	100-y	500-y	20-y	100-y	500-y	20-y	100-y	500-y
2019	3419	1533	386	3010	1358	354	96.8	-44.9	-131
2020	3260	1363	211	2842	1138	103	144	47.4	-11.4
2021	3357	1381	179	3157	1312	191	252	61.9	-53.4
2022	2836	1256	295	2311	972	158	208	55.9	-36.7
Avg.	3218	1383	268	2830	1195	201	175	30.1	-58.1

Summary and conclusions

This dissertation examined variability in soil carbon storage and greenhouse gas emissions mid-Atlantic Coastal Plain wetlands.

In Chapter 1, I studied the variability of soil organic carbon (SOC) storage across a wetland landscape. I merged two datasets to estimate SOC stocks in 25 different wetlands, and in three different vegetation zones of heterogeneous wetlands. I conducted an analysis of fine-resolution hydrologic and remotely sensed topographic data to identify potential drivers of natural variability. I showed a wide range of SOC stocks among natural wetlands with similar vegetation and hydrogeomorphology, highlighting the inherent uncertainty in defining reference conditions for restored wetlands. I found that hydrology explains some variability in wetland SOC, but that hydrologic metrics beyond traditional ones like hydroperiod need to be considered, and that relative topography explains similar variability with more potential for upscaling. Based on my findings, I made recommendations to help guide restoration science on issues of baseline data, setting realistic targets, and accurate assessment.

In Chapter 2, I investigated how methane (CH_4) flux varies between vegetation patch types in a spatially heterogeneous wetland. I used a multi-scale approach with field sampling campaigns and footprint modeling of flux tower data. I developed a Bayesian model that produced robust estimates of patch-type fluxes, integrating data over three months and a broad wetland area. My field measurements revealed distinct flux distributions across patch types, suggesting that the mechanisms

regulating CH₄ flux are patch-specific. By extending my inference across the wetland, I found that patch types were likely different source of CH₄. These results support the view that patches organize the spatial variability in CH₄, and that for spatially heterogeneous wetlands, CH₄ may be best represented at the scale of patch types, rather than for entire wetlands.

In Chapter 3, I analyzed temporal variability in CH₄ flux and its relationships with biophysical drivers in a natural wetland, a restored wetland, and a cultivated former wetland. I compiled four years of continuous eddy covariance flux data as well as drivers soil temperature, gross primary productivity, and hydrologic variables from each site. I applied two emerging frameworks, multiresolution mutual information and empirical dynamic modeling, to describe both undirected and causal interactions between drivers and CH₄ flux. I found that interactions varied between sites and across time scales, but that the temporal dynamics of CH₄ flux in the restored wetland resembled those in the natural wetland. I hypothesized mechanisms that may have produced the observed patterns and relationships.

When considering the net climate impact of wetland restoration, the balance between CH₄ emissions and CO₂ uptake is of primary concern, but other components of the C cycle should not be overlooked. Hydrologic fluxes (i.e., runoff, groundwater flow, and temporary surface water connections) carry dissolved gases, dissolved organic matter, and particulate organic matter that can contribute significantly to wetland C budgets (Chu et al., 2015). In addition, greenhouse gas budgets are incomplete without accounting for nitrous oxide (N₂O) emissions. N₂O is produced by incomplete denitrification and is therefore most important in wetlands with flashy

hydrology or cultivated former wetlands where soils experience frequent redox fluctuations (Morse et al., 2012).

Most available evidence, including that presented in this dissertation, suggests that freshwater wetland restoration is not a near-term pathway to climate mitigation (Schuster et al., 2024). CH₄ emissions from wetlands are significant and growing—wetlands are thought to be primarily responsible for the recent increase in atmospheric CH₄ (Michel et al., 2024). Because the radiative effect of CH₄ emissions operates on a much shorter time scale than CO₂ uptake, the potential climate benefits of wetland restoration are likely to be realized long after the most damaging effects of climate change have occurred.

More generally, the framing of restoration as a "natural" or "nature-based climate solution" should be met with skepticism. This terminology has recently gained traction but has great potential to mislead and misdirect. Despite the promise of mitigating climate change through ecosystem management, the realistic impact of such measures is likely to be limited. For example, Schlesinger & Amundson (2019) estimated that enhancing carbon storage in agricultural soils would offset at most 5% of annual fossil fuel CO₂ emissions, and it is widely agreed that natural climate solutions must be part of a much broader strategy to address climate change. Therefore, “solution” is a careless use of language that at best distracts from the overriding need to preserve intact ecosystems and end the burning of fossil fuels, and at worst suggests that nature can be co-opted to sustain human activities with impunity.

Regardless of climate impacts, restoration remains important to regain other beneficial wetland functions and services such as nutrient removal (denitrification, phosphorus retention), flood control, and biodiversity. As restoration continues, practitioners need to be informed about the potential greenhouse gas consequences of their interventions. Studies have shown that flooding management may reduce CH₄ emissions (Chamberlain et al., 2016), and vegetation management may both increase CO₂ uptake (Valach et al., 2021) and reduce CH₄ emissions (Silvey et al., 2019).

On the Delmarva Peninsula, one restoration practice with potential greenhouse gas consequences is the preference for open-canopy emergent systems over the more naturally abundant forested wetlands. In Chapter 1, I presented similar ranges of SOC stocks in forested and emergent wetlands, but other studies have found higher SOC in forested than nonforested wetlands (e.g., Davila & Bohlen, 2021; Marín-Muñiz et al., 2014). Moreover, Hondula et al. (2021) reported average CH₄ emissions ranging from 4.56 to 35.6 mg CH₄-C m⁻² d⁻¹ for six natural forested Delmarva bays over one year of measurements. These averages translate to one-year CH₄ sources of 1.66 to 13.0 g m⁻², compared to 31.0–38.7 and 26.3–36.2 g m⁻², respectively, for the natural and restored emergent wetland I examined in Chapter 3. Biogeochemical differences such as lower soil temperatures, phenolic-rich litter inputs, lack of herbaceous vegetation, and more dynamic hydrologic conditions are all plausible in forested wetlands (compared to emergent wetlands) and could result in systematically lower CH₄ emissions. Emergent wetlands are favored as habitat for wildlife and rare plant species in the Delmarva region and elsewhere, but such a focus on biodiversity may involve a trade-off with climate mitigation services.

The research presented in this dissertation highlights the current uncertainty in the exact climate impacts of wetland restoration. Wetland ecosystem processes are inherently variable and context dependent, meaning that unexpected outcomes should be expected. As the interactions between land-use change and environmental variability take shape, restoration science should resist the temptation, and likely hubris, of precision. Management should be based on local knowledge and remain flexible, allowing restored wetlands to follow their unique trajectories. Credit should be earned, not assumed. Uncertainty should be recognized as a feature rather than a flaw; after all, natural variability in wetland C storage is rooted in the heterogeneity of landscapes, and spatial heterogeneity of patches is not just a challenge to modeling and estimating emissions, but a fundamental property of wetland gas exchange.

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