A Global Review of Wetland Biodiversity and Carbon Connections

Mel Baldino[1*], Jessica Triebswetter[1], Alejandra Echeverri[1], Iryna Dronova[1]

[1] University of California, Berkeley, Berkeley, CA 94720 USA
* Corresponding author: melbaldino@berkeley.edu
Department of Environmental Science, Policy, and Management
University of California, Berkeley
130 Mulford Hall, Room 222
Berkeley, CA 94720-3114

Abstract

As human actions have degraded global ecosystems over time, communities have often combated ecosystem function loss through restoration with a singular focus, falling on one side of the habitat and biodiversity protection or carbon sequestration dichotomy. Wetlands are no exception to this trend, and the large global push to protect and restore wetlands has widely ignored multiple-benefit practices. This scoping review aimed to determine whether this historic restoration dichotomy was also represented in studies of wetlands and to what extent the potential biodiversity and carbon synergy differs between taxonomic groups. Of the 106 studies included in this review, a majority did not investigate this synergy despite many studies reporting metrics of both biodiversity and carbon cycling. In studies that included synergy comparisons, floral diversity increased carbon sequestration overall while microbial diversity could increase or decrease carbon sequestration depending on which functional groups were present. We discuss limitations in metric selection, wetland types, restoration stage, and time scales that prevent current work from improving the ability for restored wetlands to support multiple benefits and take advantage of the synergy seen in other wetlands.

1. Introduction

Over two-thirds of natural ecosystems globally have been degraded or converted from native habitat to human-focused land cover over time (Suding, 2011). This land use change has prompted an era of restoration and management to reverse human impacts and reintroduce services and functions that were once supported by the historical ecosystems and regimes (Suding, 2011). A notable dichotomy prevails between restoration and conservation initiatives interested in habitat, biodiversity, and endangered species and projects promoting ecosystem functions such as carbon uptake and storage (Hallett et al., 2013; Shen et al., 2023; J. B. Zedler et al., 1998). Even though restoration and management may impact both carbon cycling and biodiversity of an ecosystem (Palomo et al., 2019), the goals and implementation of most projects still focus on isolated objectives even within the same regions. This disjointed approach to restoration fails to take advantage of the co-benefits supported by the ecosystem and to maximize the potential impact of any project. Current strategies remain divorced from truly holistic, multi-benefit focuses likely due to the lack of knowledge on the potential synergies among biodiversity and carbon goals.

This dichotomy has emerged over time due to shifting values and economic influences over land management. Historically, most restoration was tied directly to conservation of individual species to prevent extinction or enhance biodiversity of the entire local community or ecosystem (Moracho et al., 2025). Reactive land management attempted to preserve or restore habitat with the focus of prying individual species from the verge of extinction with mixed success (Senior et al., 2024). When carbon markets began to be established following the ratification of the Kyoto Protocol in 2005, cap-and-trade programs created direct economic benefits for restoring carbon sequestration to the land, and there was a boom in restoration focused on carbon goals (Calel, 2013; Edwards & Cerullo, 2024; Wedding et al., 2021). Since that transition, conservation has somewhat declined as a restoration focus despite an increasing number of species lost, and biodiversity is rarely considered in carbon-focused projects despite examples of biodiversity enhancement bolstering carbon goals in terrestrial ecosystems (Edwards & Cerullo, 2024; Palomo et al., 2019; Senior et al., 2024).

However, managers and agencies have not abandoned biodiversity-focused restoration all together, and there is a new focus on replacing species-based conservation with process-based restoration to ensure the protection of a variety of ecosystem functions and resilience along with biodiversity (Moracho et al., 2025). Despite this new push towards process-based restoration with multiple goals, we lack a robust understanding of how our current strategy of restoring and managing land for a single aspect of the ecosystem impacts other goals and to what extent diverse objectives can be met by a single effort to achieve a "win-win" outcome for both biodiversity and carbon, especially in wetlands (Hallett et al., 2013; Neugarten et al., 2025; Shen et al., 2023). Without accurate evaluations of management and restoration changes to services and functions provided by the target ecosystems, there is no way to adequately inform future land stewardship (Suding, 2011).

Wetland ecosystems are salient examples of this restoration and management dichotomy due to their current prominence in expanding restoration efforts and their capabilities to provide critical co-benefits simultaneously. Over 40% of restoration projects listed in the Global Restoration Network are in wetlands and coastal ecosystems despite wetlands extending across less than 9% of the Earth's surface (Hallett et al., 2013; Mitsch et al., 2023). This is likely motivated by the large losses of global wetlands - about 50% loss globally with some countries losing over 90% of their historical wetlands (Davidson, 2014; Mitsch et al., 2023). When wetlands are restored, management regimes have increasingly focused on blue carbon, the ability for wetlands to act as carbon sinks and reverse land subsidence (Wedding et al.,

2021). Through the interplay of wetland plant and microbial productivity in the unique anaerobic setting of flooded soils, carbon is sequestered at higher rates than seen in traditional forest ecosystems (Wedding et al., 2021), although the rates of sequestration are not uniform. Wetlands vary in their sequestration potential based on their type, characteristic vegetation present, and structure, generally ranging from 20-140 grams of carbon per meter squared per year (Mitsch et al., 2013), and the potential of each site to sequester and store carbon depends heavily on the species of vegetation present on the landscape, the structure of the landscape, and time since restoration (Means et al., 2016; Valach et al., 2021). Regardless of wetland type, their carbon storage relies highly on the dead biomass on the landscape that, when buried under waterlogged conditions, slowly decomposes (Valach et al., 2021). This burial allows for carbon to be stored for longer and for these sites to effectively reverse subsidence in areas experiencing land elevation loss over time (Valach et al., 2021). The ability of wetlands to provide such dual carbon benefits makes their restoration very appealing to governments and agencies looking to reach carbon capture goals in the near future (Valach et al., 2021; Wedding et al., 2021).

Besides greenhouse gas regulation, wetlands can provide a wide variety of other ecosystem functions, services, and nature's contributions to people that could be supported through carbon-focused management (Chaplin-Kramer et al., 2019; Mitsch et al., 2015). Wetlands improve water quality, mitigate flooding, protect and stabilize shorelines, and regulate local and regional climate (Mitsch et al., 2015, 2023; J. Zedler & Kercher, 2005). These ecosystems provide local communities with resources like timber, food, and water, which often are especially valuable to indigenous communities, along with cultural services such as ecotourism, recreation, and science (Mitsch et al., 2015; J. Zedler & Stevens, 2018). Wetland regulating, provisioning, and cultural services are supported or limited by basic functions and processes including nutrient cycling, decomposition, soil accretion, and providing nursery habitats to support biodiversity and trophic webs (Mandle et al., 2020; Mitsch et al., 2015). These ecosystem services provide a disproportionately large amount of economic value globally compared to other ecosystems, so there is a missed opportunity to increase ecosystem services and local value around wetlands when they are restored for just one goal (J. Zedler & Kercher, 2005).

The recent expansion of focus in restoration and management towards carbon, especially in wetlands, raises questions about whether biodiversity goals are being lost and whether there might be win-win solutions that support more than one of the many ecosystem services that wetlands can provide. While the relationships between biodiversity and carbon have been studied in many ecosystems, there have been fewer such studies in the context of restoration and especially in wetlands, where unique and dynamic conditions can make it difficult to generalize evidence across sites (Neugarten et al., 2025; J. B. Zedler et al., 1998). In this scoping review, we aimed (1) to explore whether this historical management dichotomy is being investigated in wetlands and to what extent the synergy between supporting carbon goals and increasing biodiversity have been recognized to date and (2) to assess if this synergy differs by taxonomic group of the biotic components included in biodiversity indicators in such studies.

DEFINITIONS BOX
Wetland: lands with saturated or flooded soils, flood-tolerant biota without the present of flood-intolerant biota, and buried plant matter that decomposes slower than the upland areas nearby
Restoration: actions that assist in the recovery of an ecosystem that is degraded, damaged, or destroyed (Holl, 2020)
Carbon-focused Restoration: restoration with goals of increasing carbon sequestration, decreasing

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methan and/or carbon dioxide release, impacting the carbon cycle, and/or reversing subsidence

Species-based Restoration: restoration focused on protecting one or a few key species from future extinction risks or bringing species back from the brink of extinction to prevent species loss

Process-based Restoration: restoration with goals of bolstering ecosystem functions as a way to protect communities on a landscape more generally (Moracho et al., 2025)

Active Restoration: restoration that includes human interventions after the initial disturbance that shapes the rate and trajectory of recovery (Holl, 2020)

Conservation: actions that protect wildlife and plants along with their habitat, with a focus on inherent value rather than the benefits humans derive from species

Management: maintenance and repair of ecosystems (which can include restoration) (Holl, 2020)

Ecosystem Function: ecosystem level processes that serve a function (Srivastava & Vellend, 2005)

Ecosystem Service: the benefit that human communities gain from an ecosystem (Zhang et al., 2022)

Nature's Contribution to People: quantifies the impact of individual ecosystem services based on the needs of the people that benefit from that service in a particular place (Chaplin-Kramer et al., 2019)

Biodiversity: variability among living organisms including within and between species variations and diversity of ecosystems (Holl, 2020)

Alpha Diversity: a measurement of biodiversity (taxonomic, functional, or phylogenetic) of one particular community

Beta Diversity: the difference between biodiversity (taxonomic, functional, or phylogenetic) in multiple communities, often the difference between regional species pools and local species pools

Taxonomic Diversity: measurement of the number and dominance of species in a community

Functional Diversity: the kind, range, and relative abundance of functional traits present in a community (Tilman, 2001; Díaz et al., 2007)

Phylogenetic Diversity: measurement of evolutionary and genetic information represented by a group of taxa (Faith, 1992)

## 2. Scoping Literature Review

2.1. Literature Selection

2.1.1. Search Criteria

Our scoping literature review included peer reviewed studies and dissertations published prior to February 2024. We conducted literature searches in Proquest, Thomson Reuters Web of Science, Google Scholar, and SCOPUS databases using topic keywords for wetlands, biodiversity, carbon sequestration, ecosystem services, and measured metrics (see **Synthesis Protocol**), which returned 1,000 papers published between 2000 and 2024. When duplicates were removed, we screened the abstracts, titles, and keywords of the remaining 646 papers to identify studies of biodiversity in wetlands. While carbon sequestration and ecosystem services were also included in the keywords, we were aiming to understand biodiversity literature specifically due to the overshadowing of biodiversity-focused projects by carbon-focused ones and determine how many studies measure other ecosystem functions and services in conjunction with biodiversity. For this reason, we did not reject papers that lacked mention of carbon cycling or sequestration as long as biodiversity was present. We excluded any review papers, gray literature, or other papers that did not fit our criteria. We retained papers in which the abstract, title, and keywords did not give enough information to determine if biodiversity was studied in wetlands. The full text assessment included 249 papers, although two were removed due to our inability to access the

documents for further review. Any papers that did not study and report metrics of biodiversity in wetlands were not included. Additionally, if papers only modeled biodiversity, they were removed. After the full text review, 106 papers were selected for extraction (**SI**). From the selected study, we extracted information about location, wetland type, taxa studied, biodiversity methods, carbon measurements, ecosystem services studied, carbon and biodiversity trends, and purpose of study.

2.1.2. Geographic and Technical Characteristics of Reviewed Wetland Studies

This pool included papers from six continents and spanned a variety of wetland ecosystems (**Figure 1**). North America (n=31) and Asia (n=30) had the largest number of studies, with North Carolina (n=5) and California (n=4) having the most of any state in North America and China (n=7) and Indonesia (n=5) having the most of any country in Asia. A majority of the papers were published in the last 10 years (2014 to 2024). The ecosystems most studied included mangrove forests (n=27), riparian or forested wetlands (n=18), salt marshes and saltwater tidal wetlands (n=18), and peatlands and moorlands (n=17). The least studied ecosystems (n=1) included saline-soda wetlands, karst, abandoned rice paddies, and lowland fens.
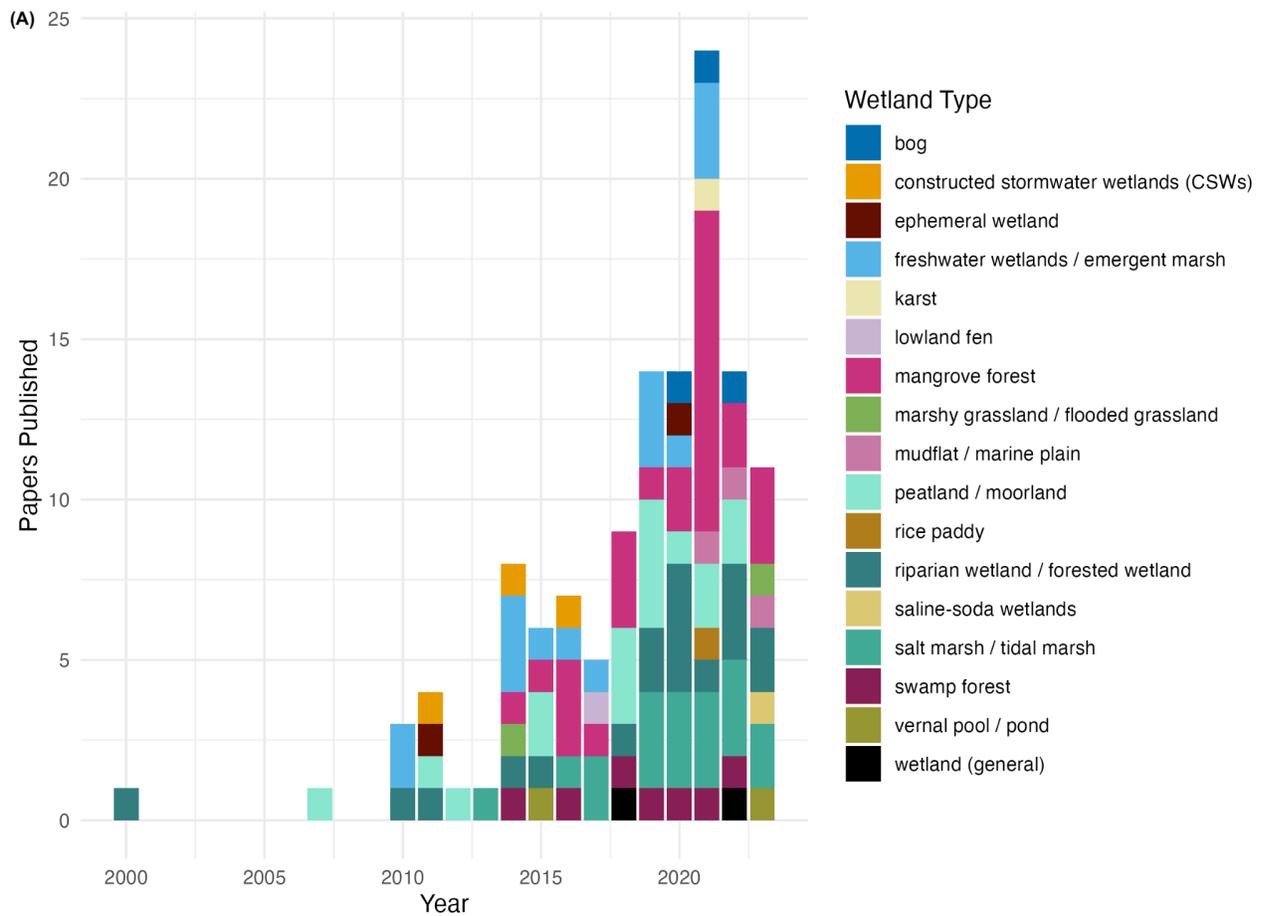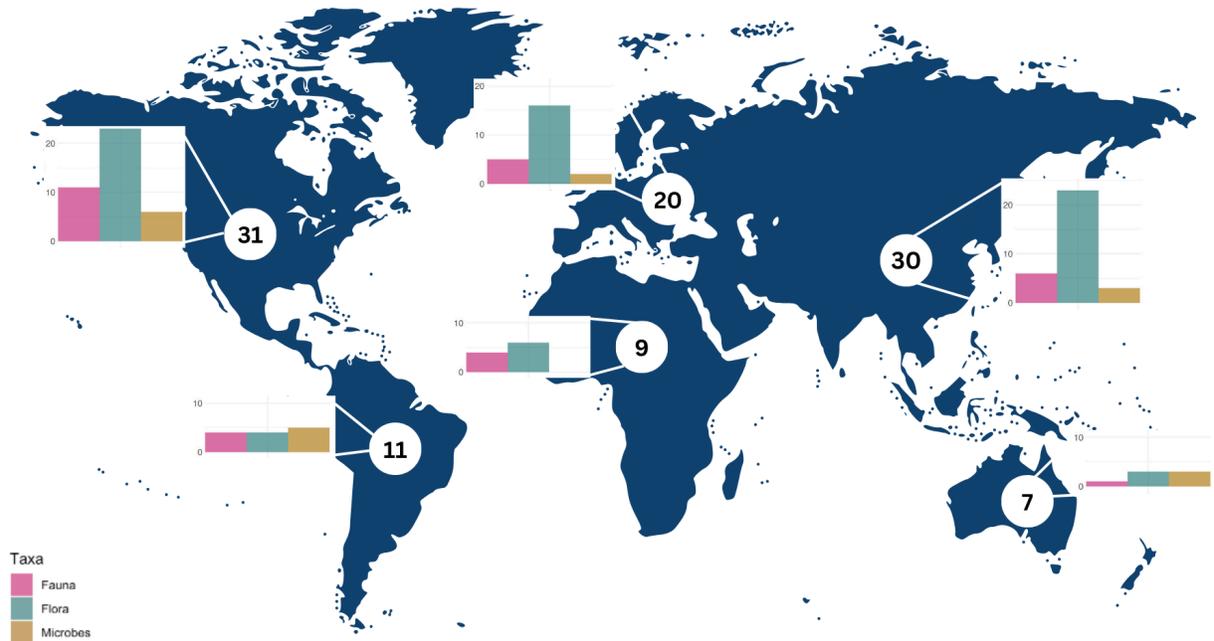
*Figure 1. **Summary of Study Characteristics.** a) Papers published per year separated by wetland type. Wetland type was either classified directly in the study or determined by searching other literature from the same location to find a classification. When wetland type could not be determined, it was labeled as "wetland (general)." Despite having no limitations on year of publication, papers that fit our criteria were exclusively published in or after 2000. b) Geographic representation of papers published and taxa represented in each study. Papers included in the literature pool studied wetlands on all continents except Antarctica with the most studies choosing wetlands in North America and Asia. Floral biodiversity was reported most often in all continents except for South America, which had slightly more microbial focused papers.*

To determine if there is a substantial amount of research exploring the restoration dichotomy or if studies focus on natural wetlands, we were interested in the types of land surveyed in wetland biodiversity studies. A majority of papers studied at least one site that was restored, managed, or extracted from (n=76) as opposed to papers that only studied "natural" wetlands without any major, recent human interference. However, many papers studied a multitude of land types, including papers that compared natural ecosystems to human influenced lands. Overall, there were 44 papers that studied natural ecosystems in some way. Non-natural sites included wetlands that were managed or protected (n=36), restored or created (n=29), degraded (n=10), and experimental (n=8). Land that was specifically managed for extractive uses such as logging or agriculture were also included (n=14). Because the number of papers including restored or created wetlands was so limited, we chose to include all wetland types and distinguish when there were trends in restored or created wetlands.

2.2. Measuring Biodiversity

Biodiversity was measured for three major taxa: flora (n=75), fauna (n=31), and microbial communities (n=18). The faunal groups represented included macroinvertebrates and insects (n=16), birds (n=9), amphibians (n=5), fish (n=4), phytoplankton and plankton (n=3), soil mesofauna (n=3), soil microfauna (n=2), mammals (n=1), epifauna (n=2), foraminifera (n=1), microphytobenthos (n=1), and

nekton (n=1). The highest reported biodiversity metrics overall included species richness (n=54), Shannon-Diversity Index (n=41), percentage cover (n=24), abundance (n=22), relative abundance (n=19), and evenness or Pielou's evenness (n=14) (**Figure 2**). Metrics used to categorize biodiversity were almost exclusively measuring alpha diversity (72 out of 73 reported metrics) with one reporting beta diversity. Reported metrics primarily focused on taxonomic diversity (n=56), with functional diversity (n=11) and phylogenetic diversity (n=4) being much less represented.

Species richness (n=41) was the most commonly reported biodiversity metric in papers that studied flora followed by the Shannon-Wiener Diversity Index (n=26), percent cover (n=24), Importance Value Index (n=10), and species composition (n=10). In papers that studied microbial communities, the most reported metrics were relative abundance (%) (n=9), abundance (n=6), the Shannon-Wiener Diversity Index (n=6), species richness (n=4), and OTU richness (n=3). Species richness (n=16) was the most commonly reported biodiversity metric in papers that studied fauna followed by abundance (n=15), the Shannon-Wiener Diversity Index (n=12), evenness/Pielou's evenness (n=7), and presence/absence (n=5).
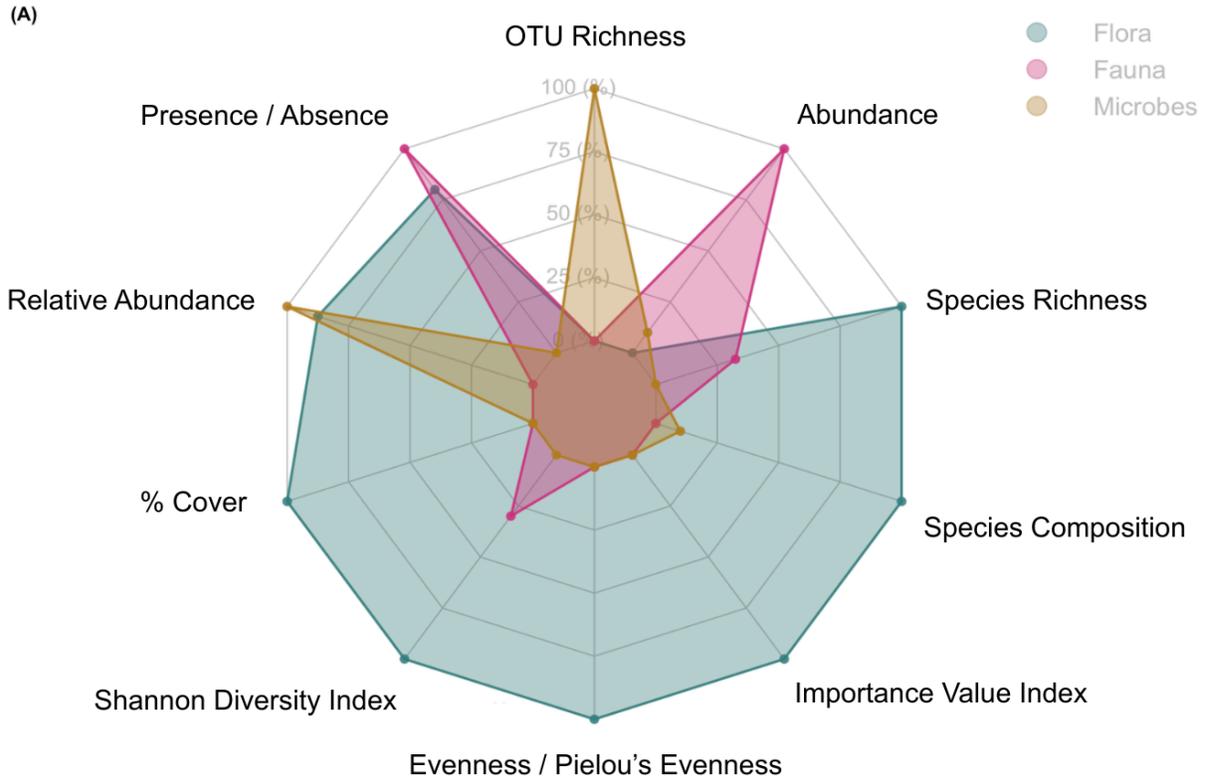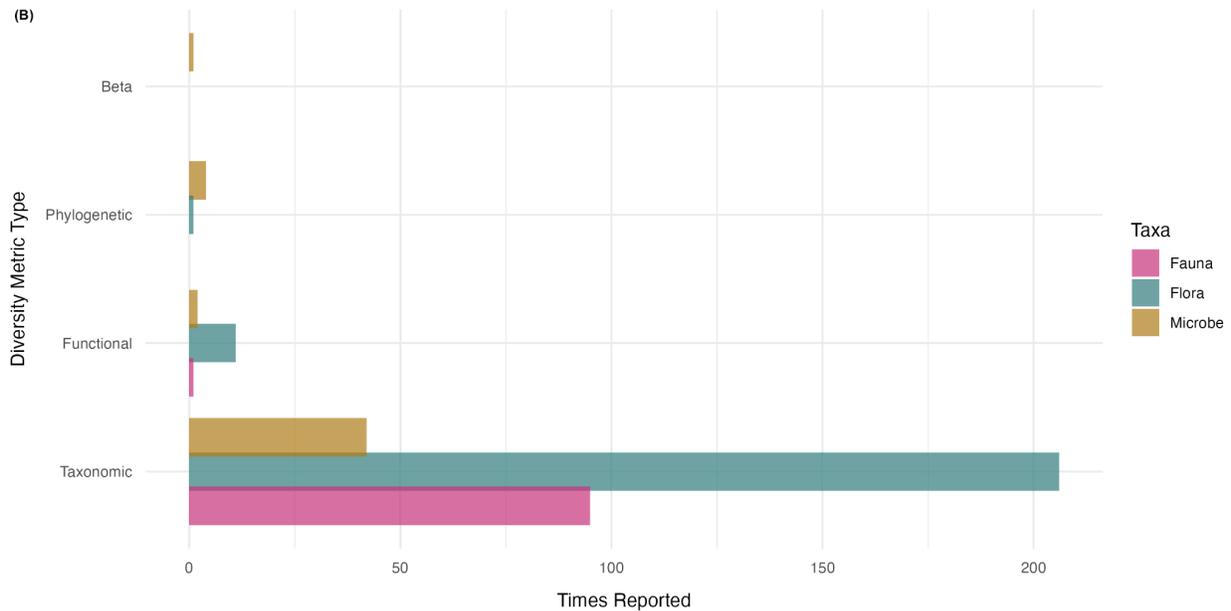
Figure 2. Reported Biodiversity Metrics. a) The top five biodiversity metrics for each taxa. Many popular metrics for vegetation biodiversity (percent cover, evenness, importance value index, species composition) are not reported for other taxa while Shannon Diversity Index and species richness are also popular in animal biodiversity papers. Microbial diversity reported relative abundance and OTU richness most frequently in addition to measures of functional diversity. b) Biodiversity metrics reported by diversity type (alpha (taxonomic, functional, phylogenetic) or beta). A disproportionate amount of papers rely on taxonomic diversity metrics and widely ignore functional, phylogenetic, and beta diversity metrics when studying biodiversity in wetlands.

2.3. Measuring Carbon

Wetland biodiversity studies reported carbon metrics in five major categories: soil, vegetation, water, microbes, and ecosystem (**Figure 3**). For all taxa, the most commonly reported carbon metrics reported were soil carbon stock (n=15), aboveground carbon stock (n=12), soil organic carbon stock (n=12), soil C:N ratio (n=11), and dissolved organic carbon (DOC) (n=9). Papers that studied floral biodiversity measured carbon from all five metric categories, and the most common metrics were aboveground carbon stock (n=12), soil carbon stock (n=10), soil organic carbon stock (n=7), dissolved organic carbon (DOC) (n=7), ecosystem carbon stock (n=6), and carbon sequestration rates (n=6). Papers that studied microbial biodiversity reported primarily soil carbon metrics and did not report any microbe specific carbon metrics. The most common metrics were soil C:N ratio (n=5), soil carbon stock (n=4), soil organic carbon stock (n=3), and soil carbon dioxide flux (n=3). Papers that studied faunal biodiversity reported carbon metrics in all categories except water with the most common metrics being soil C:N ratio (n=3), soil carbon stock (n=3), and soil organic carbon stock (n=3).

CARBON METRICS

SOIL

BELOWGROUND CARBON
MEAN SOIL CARBON STOCK
SOIL CARBON (%)
SOIL CARBON DENSITY
SOIL CARBON STOCK
SOIL C:N

SOIL C:P
SOIL CH4 FLUX
SOIL CO2 FLUX
SOIL CO (%)
SOIL ORGANIC CARBON STOCK

VEGETATION

ABOVEGROUND CARBON / NDVI
ABOVEGROUND ORGANIC CARBON
ABOVEGROUND CARBON STOCK
ABOVEGROUND VEGETATION CARBON STOCK
BELOWGROUND ROOT CARBON STOCK
BELOWGROUND VEGETATION CARBON STOCK
DOWNED WOODY DEBRIS CARBON STOCK
LIVE TREE CARBON STORAGE
ROOT BIOMASS CARBON STOCK
TOTAL LITTER AND VEGETATION CARBON STOCK
SHRUB-HERB CARBON STOCK

GROSS PRIMARY PRODUCTIVITY
LEAF C:N
LITTER CARBON STOCK
MACROPHYTE CARBON STOCK
MID-STORY CARBON STOCK
NET PRIMARY PRODUCTIVITY
ORGANIC CARBON
OVERSTORY ALIVE CARBON STOCK
OVERSTORY DEAD CARBON STOCK
RHIZOME MASS CARBON STOCK
UNDERSTORY CARBON STOCK
PLANT CARBON STOCK

WATER

BIODEGRADABLE DISSOLVED ORGANIC CARBON (BDOC)
CARBON INTRODUCED INTO WATER VIA DECOMPOSITION
DISSOLVED ORGANIC CARBON (DOC)
DISSOLVED INORGANIC CARBON (IC)
POREWATER DISSOLVED CARBON CONCENTRATION
WATER DISSOLVED CH4 AND CO2

MICROBES

AREAL CARBON DENSITY

MICROBIAL BIOMASS CARBON STOCK

ECOSYSTEM

CARBON ACCUMULATION
CARBON BURIAL RATE
CARBON SEQUESTRATION POTENTIAL
CARBON SEQUESTRATION RATE
CARBON SEQUESTRATION VALUE
CO2 SEQUESTRATION
ORGANIC CARBON SEQUESTRATION
FLUVIAL ORGANIC CARBON FLUX
TOTAL CARBON SEQUESTERED
TOTAL ORGANIC CARBON STOCK
NORMALIZED TOTAL CARBON INVENTORY
NET ECOSYSTEM PRODUCTIVITY

CH4 EMISSIONS
GAS FLUX
MEAN CO2-C EMISSIONS
NET ECOSYSTEM FLUX
TOTAL BIOMASS CARBON STOCK
TOTAL CARBON DENSITY
TOTAL CARBON STOCK
TOTAL CARBON (%)
TOTAL ORGANIC CARBON (%)
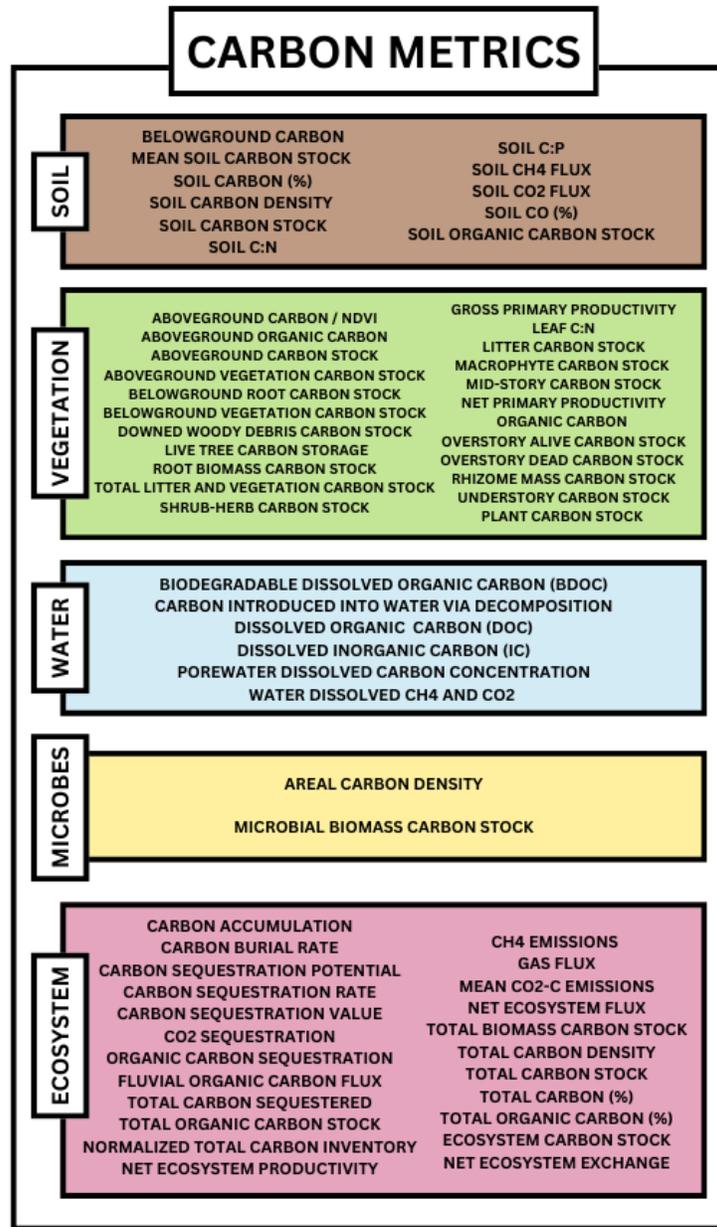ECOSYSTEM CARBON STOCK
NET ECOSYSTEM EXCHANGE

*Figure 3. Complete list of reported carbon metrics in the literature pool. Metrics were divided into which carbon pool they focused on, as reported in each paper: soil, vegetation, water, microbes, or total ecosystem. Vegetation and total ecosystem carbon pools represent the most unique metrics given the number of components that can be uniquely quantified in each. For information on how many times each metric was reported, see **SVI**.*

2.4. Comparing Biodiversity and Carbon

　　Of the 68 papers that reported carbon and biodiversity metrics, 38 looked for a connection between the two directly, either by statistically comparing the trends or by reporting site specific metrics of carbon and biodiversity and making claims about their connection in their discussion or synthesis (**SII**). In papers comparing floral biodiversity and carbon sequestration, papers reported a positive trend (n=11),

a negative trend (n=5), and instances where there was no significant trend (n=4). An additional 10 papers reported carbon by species or functional group rather than doing a holistic comparison between biodiversity and carbon. Only two papers compared faunal biodiversity with carbon metrics. Avian biodiversity had no significant connection to carbon sequestration and storage, while macro- and mesofauna biodiversity was only compared by functional group. In the eight papers that compared microbial biodiversity to carbon metrics, three reported negative trends between biodiversity and carbon metrics, while the remaining papers reported carbon by functional group. Five papers reported biodiversity metrics for multiple taxon where at least one was compared to carbon. There were positive trends observed between flora (n=4), fauna (n=3), and microbes (n=1) while there was only one negative trend reported between microbes and carbon.

When biodiversity and carbon metrics were directly compared in the literature, nearly all studies were motivated by a desire to understand the factors that regulate ecosystem services (**Table 1**). Floral and faunal focused papers often reported a goal of assessing the success of past restoration or management choices while microbe focused papers looked to inform future management decisions and quantify the impact of human action on the ecosystem. This split between floral and faunal biodiversity studies and microbial biodiversity studies extends to the types of wetlands studied. Floral and faunal focused studies mostly chose restored, created, managed, and protected wetlands. Microbe studies, which were less interested in restoration and more in understanding how humans have and will continue to impact the ecosystem, primarily focused on natural wetlands. When studies reported biodiversity metrics for multiple taxon and compared at least one to carbon measurements, they primarily studied restored or created wetlands and focused on understanding factors regulating ecosystem services, assessing past restoration success, and understanding ecosystem bundles or tradeoff assessments.

Table 1. *The reported purposes of study for all studies in the literature pool that directly compared carbon and biodiversity of vegetation (n=28), animals (n=2), or microbes (n=8). Studies with multiple taxa were not included in this table. Papers could have more than one purpose. Definitions of each purpose type can be found in the Supplemental Materials.*

Purpose of Study	Flora	Fauna	Microbes
Basic Science or Creating Baselines	6	0	2
Workflow For Monitoring or Modeling	2	0	1
Assessing Success of Past Restoration or Management	9	2	0
Directly Quantifying and Valuing Services	2	0	0
Informing Future Management Decisions	7	0	5
Quantify Impact of Human Action on Ecosystem	3	1	5
Ecosystem Bundle or Tradeoff Assessment	0	0	0
Understand Factors Regulating Ecosystem Services	22	2	8
Determine Ecosystem Service Potential	1	0	0

2.5. Additional Ecosystem Services and Project Motivations

Another major motivation behind this review was to understand what drove each study to include biodiversity in wetlands along with additional ecosystem functions or services like carbon sequestration and storage. A detailed explanation of these study purpose categories can be found in the **Supplemental Materials (SIII)**. The major categories include 1) basic science or creating baselines, 2) creating a workflow for monitoring or modeling, 3) assessing the success of past restoration or management, 4) directly quantifying and valuing services, 5) informing future management decisions, 6) quantifying the impact of human actions on an ecosystem, 7) assessing ecosystem bundles or tradeoffs, 8) understanding factors regulating ecosystem services, and 9) determining ecosystem service potential. Papers may have multiple listed purposes of study. The most frequently mentioned study purposes were to assess the success of past restoration (n=46), to understand factors regulating ecosystem services (n=42), and to inform future management (n=34).

In addition, we were interested in whether papers were exclusively looking at biodiversity and carbon or if they included additional ecosystem services. Regulating services, such as water quality, climate regulation, and pest control, were reported 53 times (**Table 2**). Provisioning services, which include wood production and food yield, were measured in 25 instances. Supporting services, such as nutrient cycling and soil quality, were reported 50 times. Science, education, entertainment, and other cultural services were reported 12 times.

Papers that studied flora reported metrics measuring water quality, chemistry, storage, and runoff most often (n=26), but they also included soil quality and nutrient cycling (n=20). Papers that studied microbes did not often report additional ecosystem services. Nutrient cycling and decomposition (n=7), soil quality and composition (n=5), and water quality and chemistry (n=3) were the only ecosystem services besides carbon productivity and biodiversity support reported. Papers that studied fauna reported metrics of water quality (n=8), nutrient cycling and decomposition (n=7), entertainment and recreation (n=5), and water storage (n=4) most frequently. The prevalence of water quality and nutrient cycling ecosystem services come from the papers studying soil macrofauna and mesofauna, macroinvertebrates, fish, and birds.

Table 2. Wetland ecosystem services that were reported in addition to those relating to carbon cycling and biodiversity in the literature pool. Any service that was measured and reported in a study was included, aggregated with similar services, and separated by taxa. Services were divided into the four service types as defined by the Millennium Ecosystem Assessment (Alcamo et al., 2003).

Service Type	Service	All Papers	Flora	Microbe	Fauna
Regulating	General Regulating Services	1	1	0	0
	Water Quality / Water Chemistry	17	13	3	8
	Water Storage / Surface Runoff Mitigation / Stormwater Retention / Flow Regulation	13	13	0	4
	Bioremediation / Pollutant Removal / Water Treatment	5	4	0	2
	Particulate Matter Concentration	1	1	0	1

Service Type	Service	All Papers	Flora	Microbe	Fauna
	Climate Regulation	3	2	0	2
	Microclimate Regulation	2	2	0	0
	Temperature Regulation	3	3	0	2
	Wind or Wave Resistance	1	0	0	1
	Erosion Resistance / Shoreline Stabilization	2	2	0	0
	Pest or Disease Control	1	1	0	0
	Pollination	1	1	0	0
	Seed Dispersal / Seed Bank / Seed Retention	3	3	0	0
Provisioning	General Provisioning Services	1	1	0	0
	Water Storage / Surface Runoff Mitigation / Stormwater Retention / Flow Regulation	13	13	0	4
	Litterfall / Woody Debris Production	5	5	0	1
	Wood Production	2	2	0	0
	Crop / Food Yield / Livestock Raising	4	4	0	2
Supporting	General Supporting Services	1	1	0	0
	Soil Quality / Soil Composition / Soil Chemistry	18	10	5	3
	Soil Accumulation	5	5	0	0
	Nutrient Cycling / Nitrogen Fixing / Denitrification / Decomposition	22	10	7	7
	Nursery Habitat / Quality Habitat	4	3	0	2
Cultural	General Cultural Services	3	3	0	2
	Science / Education	3	2	0	3
	Leisure / Entertainment / Recreation	5	3	0	5
	Employment	1	1	0	0

3. Discussion

3.1 Lack of Comparison between Biodiversity and Carbon

      Overall, despite the general recognition of various co-benefits in wetland restoration, the explicit attention to the synergy between biodiversity and ecosystem function remains nascent. In the reviewed literature, nearly half of the papers that studied biodiversity and carbon did not assess their statistical relationship at all even when reporting indicators for both. Instead, papers focused on assessing the success of past restoration and management, directly quantifying and valuing ecosystem services, and informing future management. Only four papers reported an interest in understanding factors that impact the ecosystem's ability to provide regulating services, which can exemplify the synergy (Bacar et al., 2023; Marrs et al., 2007; Moore & Hunt, 2012; Oertli et al., 2023). Further, a vast majority of studies did not choose their taxon because of its potential connection with or the effect on carbon cycling, likely due to the fact that their primary focus was not on either. Rather, these studies looked at the differences between restored and degraded wetlands, the impacts of salinity or human actions like logging or removal of invasive species, the benefits of payment for ecosystem services, or how ecosystem services change in different stages of succession (Chuvochina et al., 2021; Gonzalez Mateu, 2019; Huang et al., 2018; Mitsch et al., 2014; Murdiyarso et al., 2021; Nóbrega et al., 2020; Ritson et al., 2019; Theuerkauf et al., 2017). Often, biodiversity that was reported actually was not connected to the main ecosystem service of interest like nitrogen cycling or flood mitigation, and instead, these papers look more frequently to determine explicit relationships between threats to a wetland ecosystem's biodiversity than how to bolster those same ecosystems to support a variety of ecosystem services despite their interest in informing future management. Thus, despite the obvious relevance of biodiversity-ecosystem function synergies to many processes and questions pursued by wetland restoration, the win-win potential of synergies is yet to be explicitly explored and incorporated in restoration visions.

      The evidence of this potential can be seen in the studies which recognize the significance of species and their functional traits in regulating ecosystem processes in specific contexts, even if they do not statistically compare biodiversity to carbon at the site level. For example, among the studies that compared vegetation biodiversity and carbon **(SII)**, there was an elevated interest in mangrove forests, and a majority of those studies chose to study mangroves specifically because of their ability to sequester and hold carbon. The purpose of these studies was to understand factors that regulate ecosystem services and to create baselines of carbon stocks in mangrove forests which require accurate forest inventories of species to calculate biomass using allometric equations. Yet, in many of these studies, the reporting of species carbon stocks is a byproduct of the calculation they are after, which is the ecosystem or forest level carbon stock or sequestration potential. This reflects that even when carbon and biodiversity are reported together and compared, often it is as a secondary or peripheral goal. Outside of wetlands, there is a large body of literature that highlights the connection between plant diversity and carbon sequestration (Hooper et al., 2005), which could provide an important scientific basis for considering such synergies in restoration efforts directly. An important question persists - whether remaining uncertainties, knowledge gaps, and known challenges such as the cost and effort to sample with enough power to statistically compare multiple functions and services are perceived as barriers to studying synergy as a primary goal and what can be done to overcome such barriers.

      Despite the importance of food web relationships at the aquatic-terrestrial interfaces (e.g., Belaire et al., 2022; Junk et al., 2006), animal biodiversity has been largely neglected when studies look towards biodiversity and carbon synergies. Even in the two papers that did directly compare both (Dybala et al., 2019; Sterzyńska et al., 2015), neither picked their taxon due to a connection to carbon cycling or

provided any mechanisms or explanations for the connection or lack thereof between their faunal populations and carbon. This also suggests that to date, in restored and managed wetlands, animal biodiversity-carbon synergies are still mostly secondary to other research foci such as quantifying human impact on the ecosystem (Dybala et al., 2019; Sterzyńska et al., 2015). More generally, biodiversity-function studies outside of carbon specific research have not commonly included animals outside of those in aquatic trophic webs, so there may be insufficient theory or foundations for researchers to form hypotheses specifically on the connection between carbon and faunal biodiversity, especially across aquatic-terrestrial domains (e.g., Dahlin et al., 2021). Nevertheless, the attention to this gap seems to be growing (Edwards & Cerullo 2024), and one study in our pool explicitly justified their motivation by the concern that carbon markets will encourage restoration at the expense of biodiversity (Dybala et al., 2019), indicating that treating synergy as a peripheral goal may not be enough to justify the protection of communities in restored wetlands moving forward.

3.2 Synergy between Biodiversity and Carbon

When the synergy between biodiversity and carbon in wetlands has been studied, the trends observed differ by land management type, purpose of study, and taxa likely due to the different mechanisms that potentially drive biodiversity-carbon synergy in wetlands. While not discussed in-depth in the reviewed studies, such mechanisms, as suggested both by our literature pool and by prior wetland research, provide the basis for a stronger emphasis on such synergies in restoration projects. Based on the research to date, mechanisms fall into two major categories: mechanisms that connect vegetation structure and functions with plant and faunal diversity and mechanisms that connect microbial diversity and carbon cycling.

3.2.1 Mechanisms behind Floral and Faunal Diversity and Carbon Cycling Synergy

Wetland vegetation contributes to carbon goals of restoration by sequestering carbon as patches expand, as well as storing carbon in live vegetation and contributing to peat formation after burial of dead biomass in oxygen-limited flooded settings (Bai et al., 2021; Valach et al., 2021). Though less extensively studied than terrestrial systems (Cardinale et al., 2011; Kollmann et al., 2016), these wetland functions have also shown evidence of positive couplings with biodiversity, especially plant diversity (Doherty & Zedler, 2018). This synergy has been similarly attributed to selection effects, ecological niche partitioning, and functional redundancy leading to enhanced above- and/or belowground biomass, resource acquisition and retention (e.g., Bouchard et al., 2007; Engelhardt & Ritchie, 2001; Ford et al., 2016; Van Zuidam et al., 2019), and transfer of carbon and nutrients to consumer trophic levels (e.g., Belaire et al., 2022; Junk et al., 2006). Sometimes these outcomes are associated with common and dominant plant species (e.g., Junk et al., 2006; Liu & Li, 2026; Pasion et al., 2021) but other times rely on diversity to take advantage of multiple niches to achieve highest productivity (Díaz & Cabido, 2001). Over time since restoration, changes may occur both in the relative importance of contributing ecological mechanisms (Fitzgerald et al., 2021) and in the strength of the diversity-function association, particularly with removal of management controls like weeding (Doherty et al., 2011).

Ultimately, biodiversity-function synergies may also enhance the availability, quality, and heterogeneity of wetland habitats and trophic relationships thus facilitating taxonomic and functional diversity of consumers (e.g., Belaire et al., 2022; Qiu et al., 2024). Given that the latter include mobile species, it becomes critical to consider such synergies across different landscape scales, where they may respond to wetland surface composition, configuration, and properties of the embedding matrix. At the

local scale, for instance, it is critical to consider vertical structure and 3-dimensional configuration of vegetation canopies which affect transfer of solar radiation and on-site microclimate and ultimately vegetation recruitment, survival, and productivity (e.g., Dronova et al., 2021; Williams et al., 2017). In addition, avian functional diversity has been known to increase with diversity in total vegetation and canopy specific vegetation structure in a variety of ecosystems, including wetlands (Sweeney et al., 2025). Ecotonal heterogeneity along topographic and hydrological gradients may enable coexistence of plant species with diverse tolerance to shade which together maximize the efficiency of light utilization, enhancing carbon sequestration and storage, and produce vertical structural diversity of habitat (Belaire et al., 2022; Kinnoumè et al., 2024; Williams et al., 2017).

At the site level, wetland surfaces are often patchy mosaics of vegetation, open water, and exposed substrates, which together shape a variety of animal habitats supporting different species, food guilds, and complex trophic webs (Belaire et al., 2022; Qiu et al., 2024). In such a heterogeneous context, edges of vegetation patches become important interfaces for sediment and nutrient retention, nursery habitat for fish and macroinvertebrates, and nesting areas for birds (e.g., Beck et al., 2001; Elliott et al., 2020). Yet, edges may also strongly contribute to primary productivity when they receive more light and less dead biomass-build-up than denser patch interiors (Dronova et al., 2021; Matthes et al., 2014). Further, common zonality of wetland vegetation along elevation-inundation gradients may also support biodiversity and complementary functions of both plants and animals (Shikuzawa et al., 2024) and enhanced ecosystem productivity as well as longer-term stability and resilience to disturbance (Carvalho et al., 2013; Jiang et al., 2012).

3.2.2 Mechanisms behind Microbial Diversity and Carbon Cycling Synergy

Due to direct effects of the microbial community on processes governing carbon and energy fluxes, the latter has a direct relationship with their diversity - in the words of Finlay et al. 1997, "microbial diversity is a part of ecosystem function". Indeed, microbial communities contribute to the carbon cycle in a variety of ways depending on which functional groups are represented in the soil (Arias‑Ortiz et al., 2021; Finlay et al., 1997). In flooded wetland soils, methanogens release methane while methanotrophic bacteria consume it (Gougoulias et al., 2014). Microbes decomposing organic matter release carbon dioxide as some bacteria participate in carbon dioxide fixation (Gougoulias et al., 2014). Other microbial connections to the carbon cycle mentioned in our literature pool include chemoheterotrophy, fermentation, iron and methane oxidation, nitrification and denitrification, carbon mineralization, sulfate reduction, and carbon degradation (**SIV**). The connection between microbe diversity and carbon becomes important in carbon sequestration focused restoration as these projects aim to limit the net loss of carbon (CO_2 and CH_4) and require their wetlands to become net carbon sinks in order to participate in the carbon markets (e.g., Arias‑Ortiz et al., 2021; Matthes et al., 2014).

As a result of the complexity of microbial communities, studies that compare soil microbe diversity to carbon often focus more closely on functional diversity that can be directly tied to services of interest (Li et al., 2022; McDaniel et al., 2021; Pozo-Solar et al., 2023; Santini et al., 2019; Thomas et al., 2019a). The management of microbial gas fluxes does not solely focus on promoting methanotrophic organisms while limiting methanogens because the communities and gas flux changes with soil depth, salinity, heat, pH, and seasonality. More generally, microbial diversity responds to a variety of factors beyond carbon cycling per se, such as seasonal environmental changes (Finlay et al., 1997; Pozo-Solar et al., 2023), hydrological fluctuations which can promote diversity (Thomson et al., 2022), extreme

conditions favoring unique extremophiles, and the source and properties of wetland substrate (Li et al., 2022; Santini et al., 2019; Thomas et al., 2019).

Outside of these conditions, restoration plan design choices can also impact carbon cycling in soils. In restored salt marshes, sediment may be placed across the ecosystem to fight sea level rise and increase resilience of the vegetation. However, this addition of sand can decrease bacterial diversity while replacing native species specialized in iron oxidation and heterotrophy that increase carbon dioxide release in the wetland (Thomas et al., 2019). As future restoration and management efforts attempt to limit carbon release and increase carbon sequestration in wetlands, we must directly consider the impacts of soil characteristics, temperature, water conditions, and sediment addition or our efforts may have the reverse effect.

3.2.3 Caution in the Interpretation of Synergies

Interpreting biodiversity and carbon synergies requires caution in several respects. First, based on the research to date, the effects of biodiversity on carbon cycling-related ecosystem functions seem to be more evident and better understood than the "reverse" effects of such functions on biodiversity. While greater diversity of certain taxa, especially plants, help increase carbon uptake and storage, diversity of plants, animals, and microorganisms also depends on a number of other factors, including hydrological flow regimes, time since restoration, management interventions, and dispersal and transfer of nutrients between wetlands (Belaire et al., 2022; Davidson et al., 2012; Doherty et al., 2011; Fitzgerald et al., 2021; Qiu et al., 2024; Shikuzawa et al., 2024).

Second and related to this, not all wetland systems supporting high biodiversity are characterized by high carbon storage and sequestration. Across various global biomes, some wetland environments have severe limiting factors (such as low nutrient status), yet support unique assemblages of plants and associated animals, as well as microbial communities, including endemic species (Bedford & Godwin, 2003; Junk et al., 2006; Olde Venterink et al., 2003). Further, special feedbacks between plant adaptations and microbial functions in such systems may enable efficient nutrient transport to the upper trophic levels despite nutrient limitations, supporting abundant fauna (Junk et al., 2006; Yule & Gomez, 2009). Conversely, natural or anthropogenically induced amelioration, such as increased nutrient supply or eutrophication, may disrupt these feedbacks and threaten these wetlands' diversity, facilitating invasive species (Bedford & Godwin, 2003; Olde Venterink et al., 2003). Invasions may also occur when initial post-restoration management ends, effectively weakening biodiversity levels and effects on ecosystem functions even if the latter is maintained by the invader (Doherty et al., 2011; Doherty & Zedler, 2018).

Restoration efforts thus must carefully consider ecological properties of a target wetland system to assess whether mechanisms promoting desired levels of productivity are feasible in light of the local ecological community. It is also critical to understand the broader landscape context, in which diverse but low-productivity systems can be pivotal contributors to regional beta-diversity and ecological refugia. Therefore, it is vital that restoration goals are set within the context of the wetland type, contribution to the carbon cycle, and behavior of the species that inhabit the land to avoid forcing synergy into locations that are not fit to amplify this connection.

3.3 Limitations in Synergy Research and Future Opportunities

There are major gaps in synergy research for all taxonomic groups. Faunal biodiversity was underrepresented with only two studies directly connecting its indicators to carbon metrics (Dybala et al., 2019; Sterzyńska et al., 2015). Research into the synergy between microbial biodiversity and carbon

sequestration in wetlands is highly site specific and often neglect timescales relevant to wetland restoration. Despite the important and complex nature of trophic relationships stemming from biodiversity-function synergies in wetlands, there has been limited investigation into these dynamics (Kollmann et al. 2016).

Regardless of taxa, measurements of biodiversity in wetlands are highly skewed towards taxonomic diversity, with a notable lack of inclusion of indicators of functional and phylogenetic diversity **(SV)**. This imbalance is not unexpected, as historically, taxonomic diversity metrics have been favored for their ease of measurement and speed (Cassol et al., 2025; Moreno et al., 2006**).** This emphasis has been hindering our ability to understand the connection between biodiversity and ecosystem functions such as carbon sequestration and may promote the increase in species number without any understanding of the gaps in function or genetic diversity in wetlands (Luck et al., 2012; Tobias et al., 2025). In order to adequately monitor and manage carbon and biodiversity in future wetlands, focus needs to be shifted onto intentional comparisons between carbon and community structure (as described above), comprehensive studies of functional and phylogenetic diversity, and projects that highlight restoration relevant topics and timelines.

3.3.1 Expanding Biodiversity Metrics

Functional diversity (FD) has emerged as the critical mechanistic link between biodiversity and ecosystem functioning (Cadotte et al., 2011), shifting the focus from taxonomic identity to organismal performance. There is now broad consensus within community ecology that FD provides a more robust prediction of ecosystem functioning than taxonomic richness alone, as it accounts for the unequal contribution of species to specific ecological processes (Díaz & Cabido, 2001; Naeem & Wright, 2003; Petchey & Gaston, 2006; Tilman et al., 1997). Understanding FD in restored wetlands is vital additionally to amplify resilience of the ecosystem to future disturbances by being able to increase functional redundancy and take advantage of the "insurance hypothesis" (Díaz & Cabido, 2001; Loreau, 2000). The literature we surveyed did not acknowledge this connection between FD and ecosystem function production, as less than half of the floral studies compared functional diversity to carbon metrics. If future wetland management and restoration strategies aim to create wetlands with co-benefits, there needs to be a higher value placed on monitoring and supporting FD, specifically by studying traits related to the impacts of environmental change on a species as well as the way species can change their surrounding environment (Luck et al., 2012).

Phylogenetic diversity (PD) provides a measurement of evolutionary and genetic diversity in an ecosystem (Faith, 1992). Historically, phylogenetic diversity has been proposed as a strong surrogate for functional diversity, under the assumption that ecologically relevant traits are phylogenetically conserved (Cadotte et al., 2008; Cavender‑Bares et al., 2009). However, more recent meta-analyses challenge the universality of this proxy, advising instead to use PD as a measure of the evolutionary and genetic information protected through restoration and as a method of investigating what drives community composition (Mazel et al., 2018; Tucker et al., 2017). While phylogenetic metrics remain valuable, contemporary research suggests they should be treated as complementary to, rather than strictly interchangeable with, direct measures of functional diversity. Within our species pool, PD was only reported in papers published after 2020, indicating a relatively recent acknowledgement of this value (Andras et al., 2020; Nóbrega et al., 2020; Thomson et al., 2022**).** Measuring phylogenetic diversity in wetlands is critical to connect local processes on a shorter timescale to global processes that occur on evolutionary timescales, which is vital to understand in wetlands to properly restore communities that can

support processes of interest, such as carbon sequestration, and understand how those communities may be shaped as development progresses (Cavender‑Bares et al., 2009; Faith, 1992). In addition, phylogenetic patterns shift with scale and can be used to better understand wetland diversity at a landscape level (Cavender‑Bares et al., 2009; Graham & Fine, 2008).

Outside of expanding alpha diversity metrics for individual wetland sites, beta diversity, or the measurement of dissimilarity between different sites, can be advantageous when we want to utilize restoration at the landscape level to protect biodiversity by understanding community overlap and species turnover (Baselga, 2010; Rolls et al., 2023; Swenson, 2011; Yang et al., 2022). While biodiversity increasing in a singular site is valuable in itself, the homogenization of wetlands near each other limits the resilience of the landscape to change and can minimize the ecosystem services provided on a larger scale (Rolls et al., 2023). At the regional management level, measuring beta diversity can assess large scale restoration and inform future project planning, allowing scientists and management agencies to target locations to focus funds and time on while understanding diversity at a large scale.

3.3.2 Research on Relevant Timescales

Succession and development of wetland ecosystems after restoration is often difficult to predict, happening on unique timelines very dependent on restoration methodology, active interventions, and the goals we set for the ecosystem (Cronk & Fennessy, 2016; Lanceman et al., 2022; Spieles, 2022; Suding, 2011). This perspective is especially relevant when looking to measure restoration success based on ecosystem functions or community structure that can change throughout these stages of development. In the literature pool, studies of vegetation diversity in relation to carbon cycling occurred across a variety of timelines from initial restoration to many years post-disturbance (e.g. Murdiyarso et al., 2021 sampled every five years after disturbance for 25 years) while microbial studies focused on short time scales (e.g. Thomas et al., 2019 only sampled bacterial communities five months after restoration). This is especially concerning as microbial communities experience rapid turnover and wetlands experience slow changes in soil, water, and vegetation as they progress from their initial disturbance. This dynamic change may be difficult to measure if soils are not monitored seasonally, which is not an issue with vegetation as we can identify plants even after they have died. If the future of restoration pivots more towards process-based goals of maximizing ecosystem function, we will require short-term studies and long-term studies to understand the ways wetlands and microbial communities cycle through seasons as carbon sources and sinks over time and whether we need to interfere at any point to promote the creation of the long-term carbon sink. Managers need to provide wetlands and microbial communities time to establish while also performing frequent checks of the status.

3.3.3 Research Design with Restoration Management Implications

Future research can serve to inform wetland restoration that amplifies the benefits of biodiversity and carbon synergy, achieving multiple benefits from singular actions, only if that research is designed to fill restoration-relevant gaps. Primarily, as discussed above, studies need to directly quantify the synergy across wetland types and at different stages of time since disturbance. Despite being the most common type of wetland, accounting for about 60% total wetland area (Mitsch et al., 2023), bogs and fens were only included in four studies in this review, and restored wetland sites were only investigated in a third of the papers, where the goals of the site restoration were often not connected to the purpose of the study. Future efforts need to extend past short-term sampling to long-term systematic monitoring in order to

determine whether restoration efforts fail to capitalize on the synergy or if we haven't given the site enough time to establish the relationship.

Establishing research projects that comprehensively monitor wetlands in conjunction with local land managers provides the most direct opportunity to holistically understand restoration success and plan future management interventions. When possible, it will be advantageous to further explore connections between competing restoration goals and the impact of outside pressures that managers are concerned about, such as invasion of non-native species that may amplify carbon while reducing biodiversity. If the necessary methods for holistic monitoring, such as calculating phylogenetic diversity or accurately estimating dissolved organic carbon, are too time consuming to learn or are excluded due to their difficulty, we should facilitate collaborations between biogeochemists and ecologists with the appropriate expertise. If possible, this connectivity across fields should be used to enhance monitoring blueprints by establishing clear, instructive methods that can be reproduced in other wetlands.

4. Conclusion

Our scoping review reveals that studies of biodiversity in wetlands including the potential carbon and biodiversity synergy that can be promoted in wetlands are largely absent in the literature, mimicking the current restoration dichotomy that highlights singular goals of increasing biodiversity or carbon sequestration rather than amplifying multiple benefits at once. There are a variety of mechanisms that can support this synergy like microbial functional group connections to the carbon cycle and diverse vegetation structure increasing carbon sequestration and animal diversity, but current research has been narrow in time scale, limited in biodiversity metric selection, and unequally distributed between natural and restored wetland types. Studies that did investigate biodiversity and carbon synergy illuminated a variety of limiting factors that could impact the extent that restored wetlands can support such functions including vegetation structure, soil inundation, climate, and restoration practices. To maximize the impact of future wetland restoration efforts and achieve multi-benefit goals, it is critical for research to directly study taxonomic, functional, and phylogenetic diversity in tandem with carbon storage, sequestration, and cycling across restored wetland types and relevant timeframes.

References

Alcamo, J., Bennett, E. M., & Millennium Ecosystem Assessment (Program) (Eds.). (2003). *Ecosystems and human well-being: A framework for assessment*. Island Press.

Andras, J. P., Rodriguez-Reillo, W. G., Truchon, A., Blanchard, J. L., Pierce, E. A., & Ballantine, K. A. (2020). Rewilding the small stuff: The effect of ecological restoration on prokaryotic communities of peatland soils. *FEMS Microbiology Ecology*, *96*(10), fiaa144. https://doi.org/10.1093/femsec/fiaa144

Arias‑Ortiz, A., Oikawa, P. Y., Carlin, J., Masqué, P., Shahan, J., Kanneg, S., Paytan, A., & Baldocchi, D. D. (2021). Tidal and Nontidal Marsh Restoration: A Trade‑Off Between Carbon Sequestration, Methane Emissions, and Soil Accretion. *Journal of Geophysical Research: Biogeosciences*, *126*(12), e2021JG006573. https://doi.org/10.1029/2021JG006573

Bacar, F. F., Lisboa, S. N., & Sitoe, A. (2023). The Mangrove Forest of Quirimbas National Park Reveals High Carbon Stock Than Previously Estimated in Southern Africa. *Wetlands*, *43*(6), 60. https://doi.org/10.1007/s13157-023-01707-1

Baselga, A. (2010). Partitioning the turnover and nestedness components of beta diversity. *Global Ecology and Biogeography*, *19*(1), 134–143. https://doi.org/10.1111/j.1466-8238.2009.00490.x

Beck, M. W., Heck, K. L., Able, K. W., Childers, D. L., Eggleston, D. B., Gillanders, B. M., Halpern, B., Hays, C. G., Hoshino, K., Minello, T. J., Orth, R. J., Sheridan, P. F., & Weinstein, M. P. (2001). The Identification, Conservation, and Management of Estuarine and Marine Nurseries for Fish and Invertebrates. *BioScience*, *51*(8), 633. https://doi.org/10.1641/0006-3568(2001)051%255B0633:TICAMO%255D2.0.CO;2

Belaire, J. A., Higgins, C., Zoll, D., Lieberknecht, K., Bixler, R. P., Neff, J. L., Keitt, T. H., & Jha, S. (2022). Fine-scale monitoring and mapping of biodiversity and ecosystem services reveals multiple synergies and few tradeoffs in urban green space management. *Science of The Total Environment*, *849*, 157801. https://doi.org/10.1016/j.scitotenv.2022.157801

Bouchard, V., Frey, S. D., Gilbert, J. M., & Reed, S. E. (2007). EFFECTS OF MACROPHYTE FUNCTIONAL GROUP RICHNESS ON EMERGENT FRESHWATER WETLAND FUNCTIONS. *Ecology*, *88*(11), 2903–2914. https://doi.org/10.1890/06-1144.1

Cadotte, M. W., Cardinale, B. J., & Oakley, T. H. (2008). Evolutionary history and the effect of biodiversity on plant productivity. *Proceedings of the National Academy of Sciences*, *105*(44), 17012–17017. https://doi.org/10.1073/pnas.0805962105

Cadotte, M. W., Carscadden, K., & Mirotchnick, N. (2011). Beyond species: Functional diversity and the maintenance of ecological processes and services. *Journal of Applied Ecology*, *48*(5), 1079–1087. https://doi.org/10.1111/j.1365-2664.2011.02048.x

Calel, R. (2013). Carbon markets: A historical overview. *WIREs Climate Change*, *4*(2), 107–119. https://doi.org/10.1002/wcc.208

Cassol, I., Ibañez, M., & Bustamante, J. P. (2025). Key features and guidelines for the application of microbial alpha diversity metrics. *Scientific Reports*, *15*(1), 622. https://doi.org/10.1038/s41598-024-77864-y

Cavender‑Bares, J., Kozak, K. H., Fine, P. V. A., & Kembel, S. W. (2009). The merging of community ecology and phylogenetic biology. *Ecology Letters*, *12*(7), 693–715. https://doi.org/10.1111/j.1461-0248.2009.01314.x

Chaplin-Kramer, R., Sharp, R. P., Weil, C., Bennett, E. M., Pascual, U., Arkema, K. K., Brauman, K. A., Bryant, B. P., Guerry, A. D., Haddad, N. M., Hamann, M., Hamel, P., Johnson, J. A., Mandle, L.,

Pereira, H. M., Polasky, S., Ruckelshaus, M., Shaw, M. R., Silver, J. M., … Daily, G. C. (2019). Global modeling of nature's contributions to people. *Science*, *366*(6462), 255–258. https://doi.org/10.1126/science.aaw3372

Chuvochina, M., Adame, M. F., Guyot, A., Lovelock, C., Lockington, D., Gamboa-Cutz, J. N., & Dennis, P. G. (2021). Drivers of bacterial diversity along a natural transect from freshwater to saline subtropical wetlands. *Science of The Total Environment*, *759*, 143455. https://doi.org/10.1016/j.scitotenv.2020.143455

Cronk, J. K., & Fennessy, M. S. (2016). *Wetland Plants: Biology and Ecology* (0 ed.). CRC Press. https://doi.org/10.1201/9781420032925

Dahlin, K. M., Zarnetske, P. L., Read, Q. D., Twardochleb, L. A., Kamoske, A. G., Cheruvelil, K. S., & Soranno, P. A. (2021). Linking Terrestrial and Aquatic Biodiversity to Ecosystem Function Across Scales, Trophic Levels, and Realms. *Frontiers in Environmental Science*, *9*, 692401. https://doi.org/10.3389/fenvs.2021.692401

Davidson, N. C. (2014). How much wetland has the world lost? Long-term and recent trends in global wetland area. *Marine and Freshwater Research*, *65*(10), 934. https://doi.org/10.1071/MF14173

Díaz, S., & Cabido, M. (2001). Vive la différence: Plant functional diversity matters to ecosystem processes. *Trends in Ecology & Evolution*, *16*(11), 646–655. https://doi.org/10.1016/S0169-5347(01)02283-2

Dronova, I., Taddeo, S., Hemes, K. S., Knox, S. H., Valach, A., Oikawa, P. Y., Kasak, K., & Baldocchi, D. D. (2021). Remotely sensed phenological heterogeneity of restored wetlands: Linking vegetation structure and function. *Agricultural and Forest Meteorology*, *296*, 108215. https://doi.org/10.1016/j.agrformet.2020.108215

Dybala, K. E., Steger, K., Walsh, R. G., Smart, D. R., Gardali, T., & Seavy, N. E. (2019). Optimizing carbon storage and biodiversity co‑benefits in reforested riparian zones. *Journal of Applied Ecology*, *56*(2), 343–353. https://doi.org/10.1111/1365-2664.13272

Edwards, D. P., & Cerullo, G. R. (2024). Biodiversity is central for restoration. *Current Biology*, *34*(9), R371–R379. https://doi.org/10.1016/j.cub.2024.02.032

Elliott, L. H., Igl, L. D., & Johnson, D. H. (2020). The relative importance of wetland area versus habitat heterogeneity for promoting species richness and abundance of wetland birds in the Prairie Pothole Region, USA. *The Condor*, *122*(1), duz060. https://doi.org/10.1093/condor/duz060

Engelhardt, K. A. M., & Ritchie, M. E. (2001). Effects of macrophyte species richness on wetland ecosystem functioning and services. *Nature*, *411*(6838), 687–689. https://doi.org/10.1038/35079573

Faith, D. P. (1992). Conservation evaluation and phylogenetic diversity. *Biological Conservation*, *61*(1), 1–10. https://doi.org/10.1016/0006-3207(92)91201-3

Ford, H., Garbutt, A., Ladd, C., Malarkey, J., & Skov, M. W. (2016). Soil stabilization linked to plant diversity and environmental context in coastal wetlands. *Journal of Vegetation Science*, *27*(2), 259–268. https://doi.org/10.1111/jvs.12367

Gonzalez Mateu, M. (2019). *Anthropogenic disturbance alters plant and microbial communities in tidal freshwater wetlands in the Chesapeake Bay, USA*. Digital Repository at the University of Maryland. https://doi.org/10.13016/NK3P-GDAT

Graham, C. H., & Fine, P. V. A. (2008). Phylogenetic beta diversity: Linking ecological and evolutionary processes across space in time. *Ecology Letters*, *11*(12), 1265–1277. https://doi.org/10.1111/j.1461-0248.2008.01256.x

Hallett, L. M., Diver, S., Eitzel, M. V., Olson, J. J., Ramage, B. S., Sardinas, H., Statman‑Weil, Z., & Suding, K. N. (2013). Do We Practice What We Preach? Goal Setting for Ecological Restoration. *Restoration Ecology*, *21*(3), 312–319. https://doi.org/10.1111/rec.12007

Holl, K. (2020). *Primer of Ecological Restoration*. Island Press.

Hooper, D. U., Chapin, F. S., Ewel, J. J., Hector, A., Inchausti, P., Lavorel, S., Lawton, J. H., Lodge, D. M., Loreau, M., Naeem, S., Schmid, B., Setälä, H., Symstad, A. J., Vandermeer, J., & Wardle, D. A. (2005). EFFECTS OF BIODIVERSITY ON ECOSYSTEM FUNCTIONING: A CONSENSUS OF CURRENT KNOWLEDGE. *Ecological Monographs*, *75*(1), 3–35. https://doi.org/10.1890/04-0922

Huang, L., Shao, Q., Liu, J., & Lu, Q. (2018). Improving ecological conservation and restoration through payment for ecosystem services in Northeastern Tibetan Plateau, China. *Ecosystem Services*, *31*, 181–193. https://doi.org/10.1016/j.ecoser.2018.04.005

Junk, W. J., Brown, M., Campbell, I. C., Finlayson, M., Gopal, B., Ramberg, L., & Warner, B. G. (2006). The comparative biodiversity of seven globally important wetlands: A synthesis. *Aquatic Sciences*, *68*(3), 400–414. https://doi.org/10.1007/s00027-006-0856-z

Lanceman, D., Sadat-Noori, M., Gaston, T., Drummond, C., & Glamore, W. (2022). Blue carbon ecosystem monitoring using remote sensing reveals wetland restoration pathways. *Frontiers in Environmental Science*, *10*, 924221. https://doi.org/10.3389/fenvs.2022.924221

Li, W., Luo, M., Shi, R., Feng, D., Yang, Z., Chen, H., & Hu, B. (2022). Variations in bacterial and archaeal community structure and diversity along the soil profiles of a peatland in Southwest China. *Environmental Science and Pollution Research International*, *29*(2), 2276–2286. (2559674336; 34365597). https://doi.org/10.1007/s11356-021-15774-6

Liu, X., & Li, S. (2026). Biodiversity-ecosystem functioning relationship under water level regulation: Wetland plant biomass is more strongly related to functional redundancy than functional diversity. *Water Biology and Security*, *5*(1), 100416. https://doi.org/10.1016/j.watbs.2025.100416

Loreau, M. (2000). Biodiversity and ecosystem functioning: Recent theoretical advances. *Oikos*, *91*(1), 3–17. https://doi.org/10.1034/j.1600-0706.2000.910101.x

Luck, G. W., Lavorel, S., McIntyre, S., & Lumb, K. (2012). Improving the application of vertebrate trait‑based frameworks to the study of ecosystem services. *Journal of Animal Ecology*, *81*(5), 1065–1076. https://doi.org/10.1111/j.1365-2656.2012.01974.x

Mandle, L., Shields-Estrada, A., Chaplin-Kramer, R., Mitchell, M. G. E., Bremer, L. L., Gourevitch, J. D., Hawthorne, P., Johnson, J. A., Robinson, B. E., Smith, J. R., Sonter, L. J., Verutes, G. M., Vogl, A. L., Daily, G. C., & Ricketts, T. H. (2020). Increasing decision relevance of ecosystem service science. *Nature Sustainability*, *4*(2), 161–169. https://doi.org/10.1038/s41893-020-00625-y

Marrs, R. H., Galtress, K., Tong, C., Cox, E. S., Blackbird, S. J., Heyes, T. J., Pakeman, R. J., & Le Duc, M. G. (2007). Competing conservation goals, biodiversity or ecosystem services: Element losses and species recruitment in a managed moorland-bracken model system. *JOURNAL OF ENVIRONMENTAL MANAGEMENT*, *85*(4), 1034–1047. (WOS:000251038100025). https://doi.org/10.1016/j.jenvman.2006.11.011

Matthes, J. H., Sturtevant, C., Verfaillie, J., Knox, S., & Baldocchi, D. (2014). Parsing the variability in CH_4 flux at a spatially heterogeneous wetland: Integrating multiple eddy covariance towers with high‑resolution flux footprint analysis. *Journal of Geophysical Research: Biogeosciences*, *119*(7), 1322–1339. https://doi.org/10.1002/2014JG002642

Mazel, F., Pennell, M. W., Cadotte, M. W., Diaz, S., Dalla Riva, G. V., Grenyer, R., Leprieur, F., Mooers, A. O., Mouillot, D., Tucker, C. M., & Pearse, W. D. (2018). Prioritizing phylogenetic diversity captures functional diversity unreliably. *Nature Communications*, *9*(1), 2888. https://doi.org/10.1038/s41467-018-05126-3

McDaniel, M. D., Hernandez, M., Dumont, M. G., Ingram, L. J., & Adams, M. A. (2021). Disproportionate CH4 Sink Strength from an Endemic, Sub-Alpine Australian Soil Microbial Community. *MICROORGANISMS*, *9*(3). (WOS:000633907300001). https://doi.org/10.3390/microorganisms9030606

Mitsch, W. J., Bernal, B., & Hernandez, M. E. (2015). Ecosystem services of wetlands. *International Journal of Biodiversity Science, Ecosystem Services & Management*, *11*(1), 1–4. https://doi.org/10.1080/21513732.2015.1006250

Mitsch, W. J., Gosselink, J. G., Anderson, C. J., & Fennessy, M. S. (2023). *Wetlands* (Sixth edition). Wiley.

Mitsch, W. J., Zhang, L., Waletzko, E., & Bernal, B. (2014). Validation of the ecosystem services of created wetlands: Two decades of plant succession, nutrient retention, and carbon sequestration in experimental riverine marshes. *Ecological Engineering*, *72*, 11–24. https://doi.org/10.1016/j.ecoleng.2014.09.108

Moore, T. L. C., & Hunt, W. F. (2012). Ecosystem service provision by stormwater wetlands and ponds – A means for evaluation? *Water Research*, *46*(20), 6811–6823. https://doi.org/10.1016/j.watres.2011.11.026

Moracho, E., Normand, S., & Ordonez, A. (2025). Rebuilding ecological networks: A multi-scale approach to global restoration. *Biological Conservation*, *312*, 111477. https://doi.org/10.1016/j.biocon.2025.111477

Murdiyarso, D., Sasmito, S. D., Sillanpää, M., MacKenzie, R., & Gaveau, D. (2021). Mangrove selective logging sustains biomass carbon recovery, soil carbon, and sediment. *Scientific Reports*, *11*(1), 12325. https://doi.org/10.1038/s41598-021-91502-x

Naeem, S., & Wright, J. P. (2003). Disentangling biodiversity effects on ecosystem functioning: Deriving solutions to a seemingly insurmountable problem. *Ecology Letters*, *6*(6), 567–579. https://doi.org/10.1046/j.1461-0248.2003.00471.x

Neugarten, R. A., Davis, C. L., Duran, G., & Rodewald, A. D. (2025). Co-benefits of nature for birds, people, and climate in the United States. *Ecosystem Services*, *73*, 101733. https://doi.org/10.1016/j.ecoser.2025.101733

Nóbrega, R. L. B., Ziembowicz, T., Torres, G. N., Guzha, A. C., Amorim, R. S. S., Cardoso, D., Johnson, M. S., Santos, T. G., Couto, E., & Gerold, G. (2020). Ecosystem services of a functionally diverse riparian zone in the Amazon–Cerrado agricultural frontier. *Global Ecology and Conservation*, *21*, e00819. https://doi.org/10.1016/j.gecco.2019.e00819

Oertli, B., Decrey, M., Demierre, E., Fahy, J. C., Gallinelli, P., Vasco, F., & Ilg, C. (2023). Ornamental ponds as Nature-based Solutions to implement in cities. *Science of The Total Environment*, *888*, 164300. https://doi.org/10.1016/j.scitotenv.2023.164300

Palomo, I., Dujardin, Y., Midler, E., Robin, M., Sanz, M. J., & Pascual, U. (2019). Modeling trade-offs across carbon sequestration, biodiversity conservation, and equity in the distribution of global REDD+ funds. *Proceedings of the National Academy of Sciences*, *116*(45), 22645–22650. https://doi.org/10.1073/pnas.1908683116

Pasion, B. O., Barrias, C. Dp., Asuncion, M. P., Angadol, A. H., Pabiling, R. R., Pasion, A., Braulio, A. A., & Baysa, A. M. (2021). Assessing tree diversity and carbon density of a riparian zone within a protected area in southern Philippines. *Journal of Asia-Pacific Biodiversity*, *14*(1), 78–86. https://doi.org/10.1016/j.japb.2020.10.006

Petchey, O. L., & Gaston, K. J. (2006). Functional diversity: Back to basics and looking forward. *Ecology Letters*, *9*(6), 741–758. https://doi.org/10.1111/j.1461-0248.2006.00924.x

Pozo-Solar, F., Cornejo-D'Ottone, M., Orellana, R., Acuna, C., Rivera, C., Aguilar-Munoz, P., Lavergne, C., & Molina, V. (2023). Microbial and Biogeochemical Shifts in a Highly Anthropogenically Impacted Estuary ("El Sauce" Valparaiso). *WATER*, *15*(6). (WOS:000959878200001). https://doi.org/10.3390/w15061251

Qiu, J., Zhang, Y., & Ma, J. (2024). Wetland habitats supporting waterbird diversity: Conservation perspective on biodiversity-ecosystem functioning relationship. *Journal of Environmental Management*, *357*, 120663. https://doi.org/10.1016/j.jenvman.2024.120663

Ritson, J. P., Croft, J. K., Clark, J. M., Brazier, R. E., Templeton, M. R., Smith, D., & Graham, N. J. D. (2019). Sources of dissolved organic carbon (DOC) in a mixed land use catchment (Exe, UK). *Science of The Total Environment*, *666*, 165–175. https://doi.org/10.1016/j.scitotenv.2019.02.228

Rolls, R. J., Deane, D. C., Johnson, S. E., Heino, J., Anderson, M. J., & Ellingsen, K. E. (2023). Biotic homogenisation and differentiation as directional change in beta diversity: Synthesising driver–response relationships to develop conceptual models across ecosystems. *Biological Reviews*, *98*(4), 1388–1423. https://doi.org/10.1111/brv.12958

Santini, N. S., Lovelock, C. E., Quan Hua, Zawadzki, A., Mazumder, D., Mercer, T. R., Muñoz-Rojas, M., Hardwick, S. A., Bindu Swapna Madala, Cornwell, W., Thomas, T., Marzinelli, E. M., Adam, P., Paul, S., & Vergés, A. (2019). Natural and Regenerated Saltmarshes Exhibit Similar Soil and Belowground Organic Carbon Stocks, Root Production and Soil Respiration. *Ecosystems*, *22*(8), 1803–1822. (2206828125). https://doi.org/10.1007/s10021-019-00373-x

Senior, R. A., Bagwyn, R., Leng, D., Killion, A. K., Jetz, W., & Wilcove, D. S. (2024). Global shortfalls in documented actions to conserve biodiversity. *Nature*, *630*(8016), 387–391. https://doi.org/10.1038/s41586-024-07498-7

Shen, Z., Tian, Y., Yao, Y., Jiang, W., Dong, J., Huang, X., Wu, X., Farooq, T. H., & Yan, W. (2023). Ecological restoration research progress and prospects: A bibliometric analysis. *Ecological Indicators*, *155*, 110968. https://doi.org/10.1016/j.ecolind.2023.110968

Spieles, D. J. (2022). Wetland Construction, Restoration, and Integration: A Comparative Review. *Land*, *11*(4), 554. https://doi.org/10.3390/land11040554

Srivastava, D. S., & Vellend, M. (2005). Biodiversity-Ecosystem Function Research: Is It Relevant to Conservation? *Annual Review of Ecology, Evolution, and Systematics*, *36*(1), 267–294. https://doi.org/10.1146/annurev.ecolsys.36.102003.152636

Sterzyńska, M., Pižl, V., Tajovský, K., Stelmaszczyk, M., & Okruszko, T. (2015). Soil Fauna of Peat-Forming Wetlands in a Natural River Floodplain. *Wetlands*, *35*(4), 815–829. https://doi.org/10.1007/s13157-015-0672-0

Suding, K. N. (2011). Toward an Era of Restoration in Ecology: Successes, Failures, and Opportunities Ahead. *Annual Review of Ecology, Evolution, and Systematics*, *42*(1), 465–487. https://doi.org/10.1146/annurev-ecolsys-102710-145115

Swenson, N. G. (2011). Phylogenetic Beta Diversity Metrics, Trait Evolution and Inferring the Functional Beta Diversity of Communities. *PLoS ONE*, *6*(6), e21264. https://doi.org/10.1371/journal.pone.0021264

Theuerkauf, S. J., Puckett, B. J., Theuerkauf, K. W., Theuerkauf, E. J., & Eggleston, D. B. (2017). Density-dependent role of an invasive marsh grass, Phragmites australis, on ecosystem service provision. *PLOS ONE*, *12*(2), e0173007. https://doi.org/10.1371/journal.pone.0173007

Thomas, F., Morris, J. T., Wigand, C., & Sievert, S. M. (2019a). Short-term effect of simulated salt marsh restoration by sand-amendment on sediment bacterial communities. *PLOS ONE*, *14*(4). (WOS:000466131200021). https://doi.org/10.1371/journal.pone.0215767

Thomas, F., Morris, J. T., Wigand, C., & Sievert, S. M. (2019b). Short-term effect of simulated salt marsh restoration by sand-amendment on sediment bacterial communities. *PLOS ONE*, *14*(4), e0215767. https://doi.org/10.1371/journal.pone.0215767

Thomson, T., Ellis, J. I., Fusi, M., Prinz, N., Bennett-Smith, M. F., Aylagas, E., Carvalho, S., & Jones, B. H. (2022). The Right Place at the Right Time: Seasonal Variation of Bacterial Communities in Arid Avicennia marina Soils in the Red Sea Is Specific to Its Position in the Intertidal. *Frontiers in Ecology and Evolution*, *10*, 845611. https://doi.org/10.3389/fevo.2022.845611

Tilman, D., Knops, J., Wedin, D., Reich, P., Ritchie, M., & Siemann, E. (1997). The Influence of Functional Diversity and Composition on Ecosystem Processes. *Science*, *277*(5330), 1300–1302. https://doi.org/10.1126/science.277.5330.1300

Tobias, J. A., Bullock, J. M., Dicks, L. V., Forester, B. R., & Razgour, O. (2025). Biodiversity conservation requires integration of species-centric and process-based strategies. *Proceedings of the National Academy of Sciences*, *122*(31), e2410936122. https://doi.org/10.1073/pnas.2410936122

Tucker, C. M., Cadotte, M. W., Carvalho, S. B., Davies, T. J., Ferrier, S., Fritz, S. A., Grenyer, R., Helmus, M. R., Jin, L. S., Mooers, A. O., Pavoine, S., Purschke, O., Redding, D. W., Rosauer, D. F., Winter, M., & Mazel, F. (2017). A guide to phylogenetic metrics for conservation, community ecology and macroecology. *Biological Reviews*, *92*(2), 698–715. https://doi.org/10.1111/brv.12252

Valach, A. C., Kasak, K., Hemes, K. S., Szutu, D., Verfaillie, J., & Baldocchi, D. D. (2021). Carbon Flux Trajectories and Site Conditions from Restored Impounded Marshes in the Sacramento‑San Joaquin Delta. In K. W. Krauss, Z. Zhu, & C. L. Stagg (Eds.), *Geophysical Monograph Series* (1st ed., pp. 247–271). Wiley. https://doi.org/10.1002/9781119639305.ch13

Van Zuidam, J. P., Van Leeuwen, C. H. A., Bakker, E. S., Verhoeven, J. T. A., Ijff, S., Peeters, E. T. H. M., Van Zuidam, B. G., & Soons, M. B. (2019). Plant functional diversity and nutrient availability can improve restoration of floating fens via facilitation, complementarity and selection effects. *Journal of Applied Ecology*, *56*(1), 235–245. https://doi.org/10.1111/1365-2664.13256

Wedding, L. M., Moritsch, M., Verutes, G., Arkema, K., Hartge, E., Reiblich, J., Douglass, J., Taylor, S., & Strong, A. L. (2021). Incorporating blue carbon sequestration benefits into sub-national climate policies. *Global Environmental Change*, *69*, 102206. https://doi.org/10.1016/j.gloenvcha.2020.102206

Williams, L. J., Paquette, A., Cavender-Bares, J., Messier, C., & Reich, P. B. (2017). Spatial complementarity in tree crowns explains overyielding in species mixtures. *Nature Ecology & Evolution*, *1*(4), 0063. https://doi.org/10.1038/s41559-016-0063

Yang, F., Liu, Z., Yang, G., & Feng, G. (2022). Dominated Taxonomic and Phylogenetic Turnover but Functional Nestedness of Wetland Bird Beta Diversity in North China. *Land*, *11*(7), 1090. https://doi.org/10.3390/land11071090

Zedler, J. B., Fellows, M. Q., & Trnka, S. (1998). Wastelands to Wetlands: Links Between Habitat Protection and Ecosystem Science. In M. L. Pace & P. M. Groffman (Eds.), *Successes, Limitations, and Frontiers in Ecosystem Science* (pp. 69–112). Springer New York. https://doi.org/10.1007/978-1-4612-1724-4_4

Zedler, J., & Kercher, S. (2005). WETLAND RESOURCES: Status, Trends, Ecosystem Services, and Restorability. *Annual Review of Environment and Resources*, *30*(1), 39–74. https://doi.org/10.1146/annurev.energy.30.050504.144248

Zedler, J., & Stevens, M. (2018). Western and Traditional Ecological Knowledge in Ecocultural Restoration. *San Francisco Estuary and Watershed Science*, *16*(3). https://doi.org/10.15447/sfews.2018v16iss3art2

Zhang, C., Li, J., & Zhou, Z. (2022). Ecosystem service cascade: Concept, review, application and prospect. *Ecological Indicators*, *137*, 108766. https://doi.org/10.1016/j.ecolind.2022.108766