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REVIEW PAPER

Using Plant Functional Traits to Inform Wetland Restoration

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Abstract

Plant functional trait frameworks have been increasingly used to understand plant community dynamics, linkages between plants and ecosystem function, and have recently been applied to inform species selection for restoration of many ecosystem types. Yet, despite rapid development in this field over the past decade, the use of plant functional trait frameworks in the context of wetland restoration remains limited. Ambitious wetland restoration goals, and previous difficulties to meet them, underscore the need for continued refinement of science-backed restoration approaches for present and future conditions. Plant functional traits are one approach that deserves additional attention and scientific inquiry to inform restoration in wetlands. We conducted a systematic review of the peer-reviewed literature (published 2000 to 2020) addressing plant functional traits in wetland restoration. Here, we summarize that body of literature and identify factors limiting the inclusion of plant functional trait frameworks in wetland restoration. We emphasize the need for consensus on terminology and trait selection in this field, provide definitive guidelines for moving this field forward for both researchers and practitioners, identify key plant functional traits to inform specific restoration goals, and highlight case studies exemplary of this approach in wetland restoration. A plant functional trait framework has the potential to inform and improve restoration of the world's wetlands by making important linkages between traits, desired ecosystem functions, and restoration trajectories. However, the use of this approach requires further development and that both research and practice reach a consensus on which traits are most critical to measure.

Keywords Plant functional traits · Plant height · Restoration · Seed mass · Specific leaf area · Trait-based framework · Wetlands

Introduction

Conservation and restoration of the world's wetland ecosystems have grown over the past few decades, as evidenced by the recent United Nation's declaration of a Decade on Ecosystem Restoration (Cadier et al. 2020; United Nations 2023). Further, substantial wetland-specific goals were established for the 172 countries that ratified the Ramsar Convention, the most signification international treaty for wetlands protection (Ramsar Convention on Wetlands 2021). This increasing appreciation for wetland ecosystem functions and services position the practice of wetland restoration for greater advancement over the coming years (Jisha and Puthur 2021), particularly for re-establishment of native wetland plant communities which underlie many of the functions and services wetlands provide. Despite an overwhelming understanding of the urgency for wetland restoration, restoration remains particularly challenging in wetlands, partially due to lack of understanding of site-specific ecosystem processes and interactions between vegetation and the physical environment (Li et al. 2018).

Plant species composition and structure-based indicators (e.g., composition, structural complexity, heterogeneity) characterize ecosystem health and function and can serve as indicators of ecological processes (Lindenmayer et al. 2000; Sterk et al. 2016). Wetland plant communities are influenced by multiple interactive drivers such as flooding regimes, and dynamic physical, chemical, and biological attributes, in addition to anthropogenic drivers experienced by any ecosystem (e.g., climate change, pollution, land conversion, etc.) (Galatowitsch 2018). In wetlands, these

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environmental extremes (e.g., for hydrology, salinity) can be beyond the tolerance thresholds of sensitive early life stages of vegetation thereby limiting establishment. Furthermore, as downstream systems, wetlands often face disproportionate degradation from upstream influences such as nutrient loading, sediment supply, and propagules of invasive species (Zedler and Kercher 2004), which can undermine efforts to re-establish diverse, productive native plant communities. Underdeveloped or untested revegetation approaches and limited consensus on wetland restoration success criteria further complicate the ability to prescribe restoration actions (Zhao et al. 2016; Kettenring and Tarsa 2020). Even well-planned wetland restoration projects may still be plagued by low survivorship of seeds and vegetation transplants due to site environmental variability and high mortality rates inherent to early plant life stages (Wodehouse and Rayment 2019; Pearce 2022).

The 'successful' restoration of wetland ecosystem structure, function, and services remains a challenge that will require creative approaches to meet ambitious goals set to combat global biodiversity and climate crises (Suding 2011). One such creative approach is to advance the characterization of restoring wetland plant communities beyond vague metrics such as pre-degradation species composition (Engst et al. 2016) or areal cover (Yando et al. 2021). Instead, characterizing the plant composition by more informative metrics (e.g., growth strategy, energy allocation, stress tolerance thresholds, etc.) may aid the field of wetland restoration to design projects that are more successful under present and future conditions. Incorporating plant functional traits as a tool for restoration species selection and characterization of site function may be one such tool to improve wetland restoration.

Over the past few decades, the use of plant functional traits has grown as ecologists, ecophysiologists, and evolutionary biologists strive to explain and predict complex patterns in plant species performance and community dynamics in a variety of ecosystems (Lavorel and Garnier 2002; Funk et al. 2017). Although the term 'trait' has been applied to a variety of ecological scales, from the individual to the community level, here we refer to a plant functional trait using the definition provided by Violle et al. (2007): "a [plant functional] trait is any morphological, physiological, or phenological feature measurable at the individual level, from the cell to the whole-organism level, without reference to the environment or any other level of organization." Plant functional traits are thus measurable attributes that serve as a proxy for the individual's fitness, performance, or how the individual interacts with its environment (McGill et al. 2006). Consequently, these functional traits can serve as a type of common currency between species or ecosystems that allow for expanded capacity to make comparisons as well as apply and test ecological principles.

Plant functional traits contain a suite of information about a species' or individual's evolution, physiology, and ecology and are therefore informative to a variety of basic science and applied questions. Traits have been operationalized in several contexts in a variety of ecosystems. For example, plant functional traits have often served as a proxy for species diversity, from a functional perspective instead of taxonomic. Community-weighted means of trait values can be used to characterize community diversity and ecosystem properties via quantification of distribution of trait values among species (e.g., functional diversity; Petchey and Gaston 2006; Shipley et al. 2006). Traits have also been used to describe species composition dynamics along environmental gradients and understand biogeographic variation among taxa as traits may be more reflective of distribution and ecological sorting than evolution and genetics (Losos 1996; Reich et al. 2003). For example, Merritt et al. (2010) used a suite of plant functional traits to create non-phylogenetic groupings of plant species relative to components of hydrologic condition to inform management of environmental flows. One major breakthrough in recent years has been the use of plant functional traits (and community weighted means analyses) to understand correlations between trait variation and ecosystem function. Plant traits have been operationalized to understand underlying causes of productivity (Roscher et al. 2012), carbon sequestration and storage (Bu et al. 2019), habitat quality (Kossmann 2005), biodiversity (Fry et al. 2014), and ecosystem response to climate change (Bjorkman et al. 2018). A review by Green et al. (2022) emphasized the potential for using trait-based approaches as a tool for understanding community assembly and function under changing global conditions. Their review (of 865 studies) emphasized that although the majority of trait-based work has been conducted on terrestrial plant morphology, there remains much potential to expand employment of this framework. We propose plant functional traits are equally informative for improving restoration, specifically for wetlands.

A recent review by Carlucci et al. (2020) assessed the inclusion of both plant functional traits and evaluation of ecosystem services in restoration targets for tropical ecosystems. Their review found that papers which specifically presented a trait-based framework to address ecosystem restoration were limited (only 10 of 265 studies) compared to overall studies on forest restoration and regeneration. Importantly, they recommended several focus areas to improve the inclusion and operationalization of trait-based approaches in restoration; specifically: 1) focusing on measuring key functional traits linked to priority plant-based restoration goals, and 2) using trait-based frameworks to select sets of native species for areas that will be subject to restoration to help achieve ecosystem service restoration goals. Here we provide a systematic review of existing literature that specifically addresses plant functional traits in wetland restoration science with the goal of summarizing the state of knowledge in this field and addressing the priorities indicated by Carlucci et al. (2020).

Through this review of literature, we sought to understand how research to date has incorporated the use of plant functional traits in restoration science, what traits are most informative and valuable, and the context in which traits are applied to understand function. Our work identifies the following key aspects of this growing body of literature: 1) trends among geographic location, wetland types, and dominant species/growth forms in which traits are used to inform wetland restoration, 2) the most commonly measured and traits most responsive to ecological drivers, 3) trends in methodological approaches to these studies, and 4) whether studies were conducted in actual restoration scenarios as opposed to strict experiments. Finally, we provide recommendations for future research in this field with the goal of directing both future scientific inquiry and enhancing the use of plant functional traits in wetland restoration practice.

Materials and Methods

We conducted a systematic review of literature (i.e., a systematic search for and appraisal and synthesis of research evidence, see: Grant and Booth (2009)) using Web of Science. In February 2021, we searched for all English language peer-reviewed journal articles published between 2000 and 2020 using the topic (TS) search terms: plant trait* AND restoration AND wetland*. The twenty-year time frame for the search was selected to capture the most recent and relevant literature, and comparisons with longer time frames resulted in minimal additional studies. This search was the most targeted approach for this topic and revealed 99 publications, of which 85 were selected as appropriate and applicable for inclusion of analysis after review of all titles and abstracts (Supplementary Table 1). For comparison, a WoS search for 'plant trait*' using the same guidelines provided 62,550 results, a search for "plant trait* AND restoration' revealed 1617 results, and "plant trait* AND wetland*" revealed 704 results. Articles that were excluded from our analysis either did not explicitly address functional traits in plant species (e.g., measured functional traits in animal taxa within restored wetlands), were not conducted in wetlands (e.g., were conducted in lakes), or had no focus or context in restoration (e.g., briefly mentioned habitat restoration but did not link restoration to the study results). Consequently, the selected literature captured a wide variety of wetland types, plant traits, and research in active and passive restoration sites as well as research with broader impacts for restoration. As with any literature search, there are publications that could have met the search criteria but were not identified by the systematic search. However, the unbiased selection of such a breadth of papers allowed us to still draw strong conclusions. The 85 publications selected from our narrowed search were characterized using a systematic mapping review (Cooper 2016) in which we extracted both data from the research and information about the paper itself (full detailed descriptions of extracted data are explained in Supplementary Table 2). All extracted data were originally recorded using the author's terminology verbatim. Measured traits, wetland habitat type, and growth form terminology were later standardized and grouped for commonality among publications. For example, 'freshwater wetland' and 'freshwater marsh' were combined as 'freshwater wetland'. The location of each study (latitude and longitude) was directly extracted from each publication or derived from the provided location information. Locations and the frequency of studies per country were mapped using ArcGIS software (Esri. ArcGIS and ArcMap). Summary statistics of all extracted data were analyzed in R Studio (RStudio Team 2020) using the tidyverse package (v 1.3.0, Wickham et al. 2019). Summaries included frequency analyses of all extracted data categories, number of publications per year, proportion of plant growth forms represented in different wetland types, frequency each plant functional trait was measured in overall selected publications, frequency of occurrence of key words in each publication, and frequency of plant traits represented across difference wetland types.

Results

State of the Science

Since 2000, the number of publications that address plant traits in wetland restoration has been increasing moderately, however, the total number of publications are still relatively limited (<10 publications per year; Fig. 1). Although all these studies mention the term 'restoration' and many are purposely intended to inform wetland restoration, only a small fraction of publications were actually conducted within restoration sites (Fig. 1). The remaining studies were either conducted in a controlled greenhouse setting or in the field (either observational or experimental), but not at a site that was actively being restored as determined by a full review of each study's methodology. Studies on this topic are geographically spread throughout the globe, with a disproportionate number of studies conducted in the United States, China, and the Netherlands (Fig. 1). More studies that measure plant traits in the context of wetland restoration may exist worldwide, but were not revealed by our search, perhaps due to differences in terminology or being in non-English publications. Common themes revealed by the frequency of keywords of these selected 85 publications

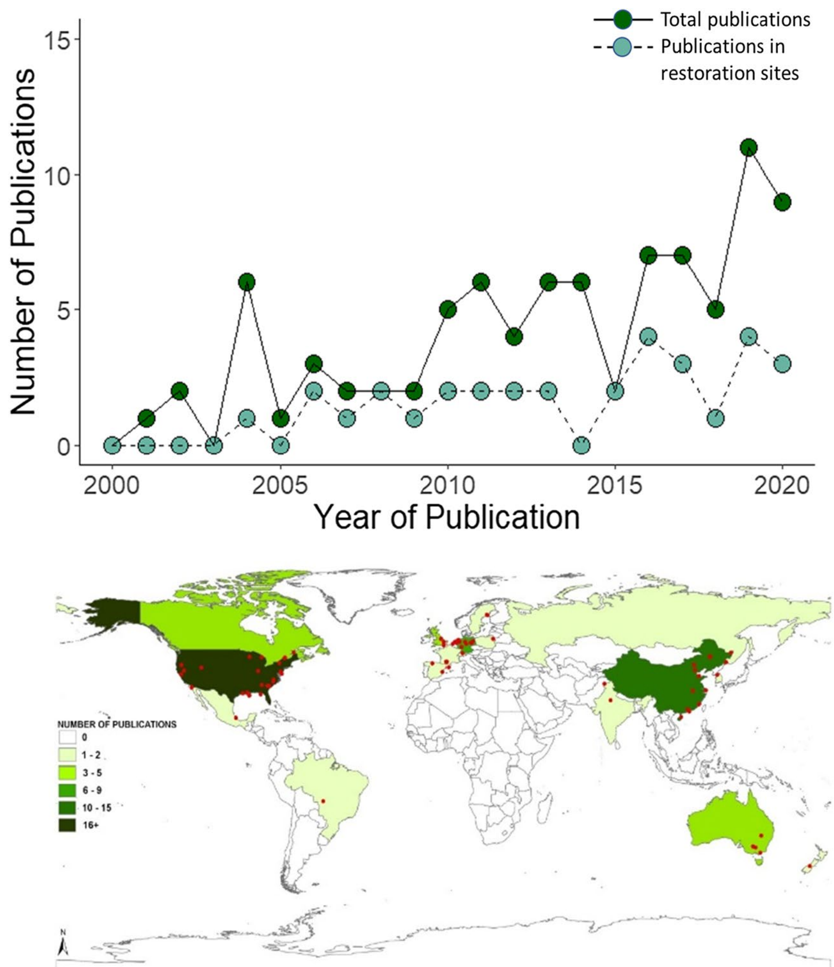

Fig. 1 Quantity and origin of publications identified by the search terms. Top figure: number of publications by year (dark green, solid line) compared to publications featuring studies conducted at a restoration site (light green, dashed line). Bottom figure: Map of the location of studies addressing plant functional traits in wetland restoration identified by our search terms. Red points represent the geographic location of each study, whereas shading color of country distinguishes overall number of publications per country

included, predictably, wetland restoration (23) and plant functional traits (14), but also invasion resistance (16), seed bank (6), hydrochory (6), biodiversity (5), and climate change (4), indicating that the use of plant functional traits in wetland restoration tends to focus on early life stages (germinating seeds) with a purpose of informing invasive species management or climate change response and resilience.

Representation of Traits

To improve the use of plant functional traits in research and restoration, some have proposed that botanical sub-disciplines need to convene around a select number of standardized traits that are consistently measured to aid with comparison-making (Ackerly 2009). Our review revealed a total of 182 different plant functional traits that were measured in the selected studies (Supplementary Table 3), but only 44 of these traits were measured in more than one study. Metrics that clearly characterized community level metrics (e.g., species diversity, cover) were removed from the trait list and instead recorded as 'community properties', but all publications measured other qualifying functional traits as well. Some traits (Ellenberg value and niche breadth) do not meet Violle et al.'s (2007) definition of plant functional trait but were included in this review because multiple publications used these measurements to describe an individual species, rather than community. Traits such as plant height, specific leaf area (SLA), seed mass, and total aboveground biomass were the most commonly measured traits (Fig. 2). A limited number of studies clearly identified the most important/informative trait measured, but of the studies that did, seed mass, plant height, SLA, tissue nitrogen (N), dispersal vector, native status, and life stage emerged as the traits most frequently identified as informative.

Most papers we reviewed (57) used traits to characterize an ecosystem, whereas fewer studies (28) measured traits as a response variable to some kind of driver (e.g., flooding duration). The majority of studies (51) measured and compared traits within plant communities (addressing 10 or more species), whereas the remaining studies focused on one or a few particular species. Riparian wetlands, freshwater wetlands, and fens were the most commonly studied wetland habitat types, with graminoids and forbs/herbs the most prevalent growth forms overall (Fig. 3). Graminoids

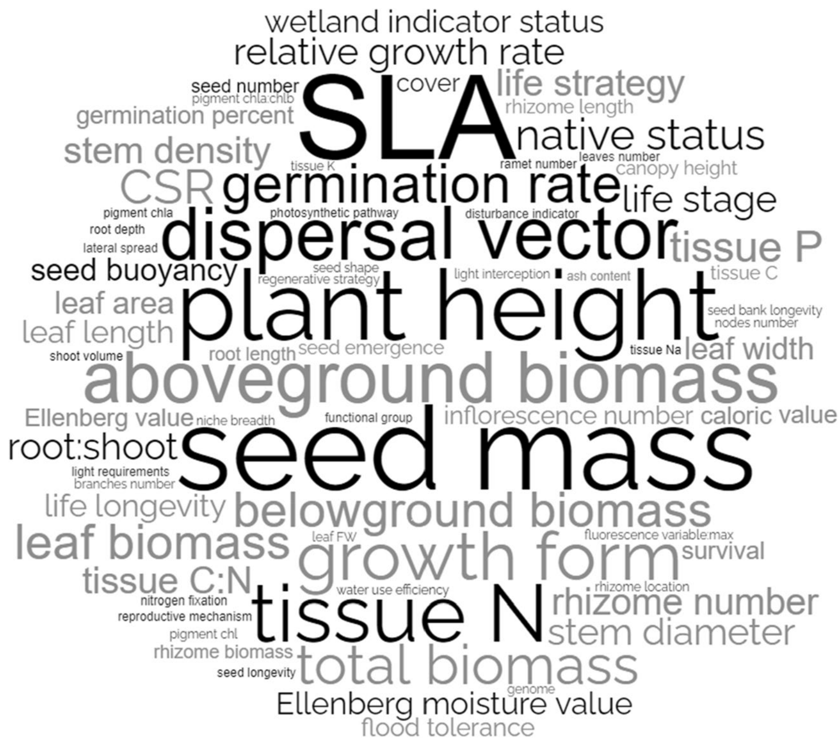

Fig. 2 Word cloud representing the frequency of which individual plant functional traits were measured in publications analyzed in this review. Only traits that occurred in two or more of the 85 publications analyzed are presented. Word size corresponds with frequency. The full list of traits are in Supplementary Table 3. Abbreviations: C = carbon; chl = chlorophyll; CSR = competitor, stress tolerator, or ruderal species classification; FW = fresh weight; K = potassium; N = nitrogen; Na = sodium; P = phosphorus; SLA = specific leaf area

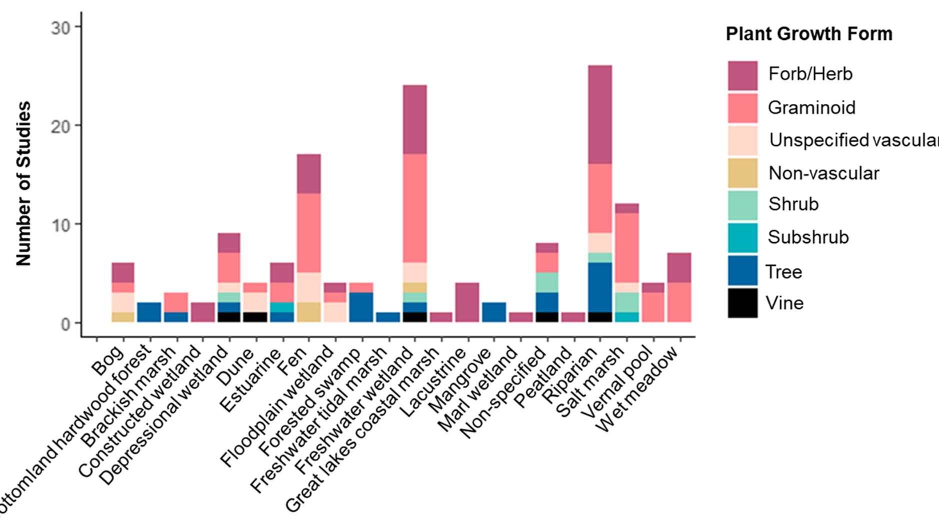

Fig. 3 Representation of wetland types and plant growth forms in studies addressing plant functional traits in wetland restoration. If a single study (publication) included multiple wetland types or growth forms, each combination is represented, thus resulting in a greater number of represented work than the number of papers analyzed

and forbs/herbs were the most commonly measured plant growth forms in most wetland types, with the exception of bottomland hardwood forests, forested swamps, freshwater tidal marsh, and mangroves, which were dominated by trees. Commonly measured species/genera included (in order of frequency) *Spartina alterniflora* (smooth cordgrass, now *Sporobulus alterniflorus* (Loisel) P.M. Peterson & Saarela), *Phragmites australis* (common reed or phragmites), *Carex* spp. (sedges), *Juncus* spp. (rushes), *Scirpus* spp. (bulrushes), *Sarracenia* spp. (pitcher plants), and *Typha* spp. (cattails). These genera may be heavily represented in research as they serve as foundational species (*Spartina alterniflora, Typha* spp.), or are concerns for invasive species management (*Spartina alterniflora* and *Phragmites australis*) or conservation (*Sarracenia* spp.). Representation of individual traits differed depending on wetland type and growth form of vegetation measured (Fig. 4). Common simple traits, such as plant height, SLA, biomass, and seed traits, were relatively ubiquitous across wetland types. Traits that characterized abiotic stress tolerance (i.e., flooding stress tolerance, water use efficiency, acidity tolerance, Young's bending modulus) were most prevalent in salt marshes, freshwater wetlands,

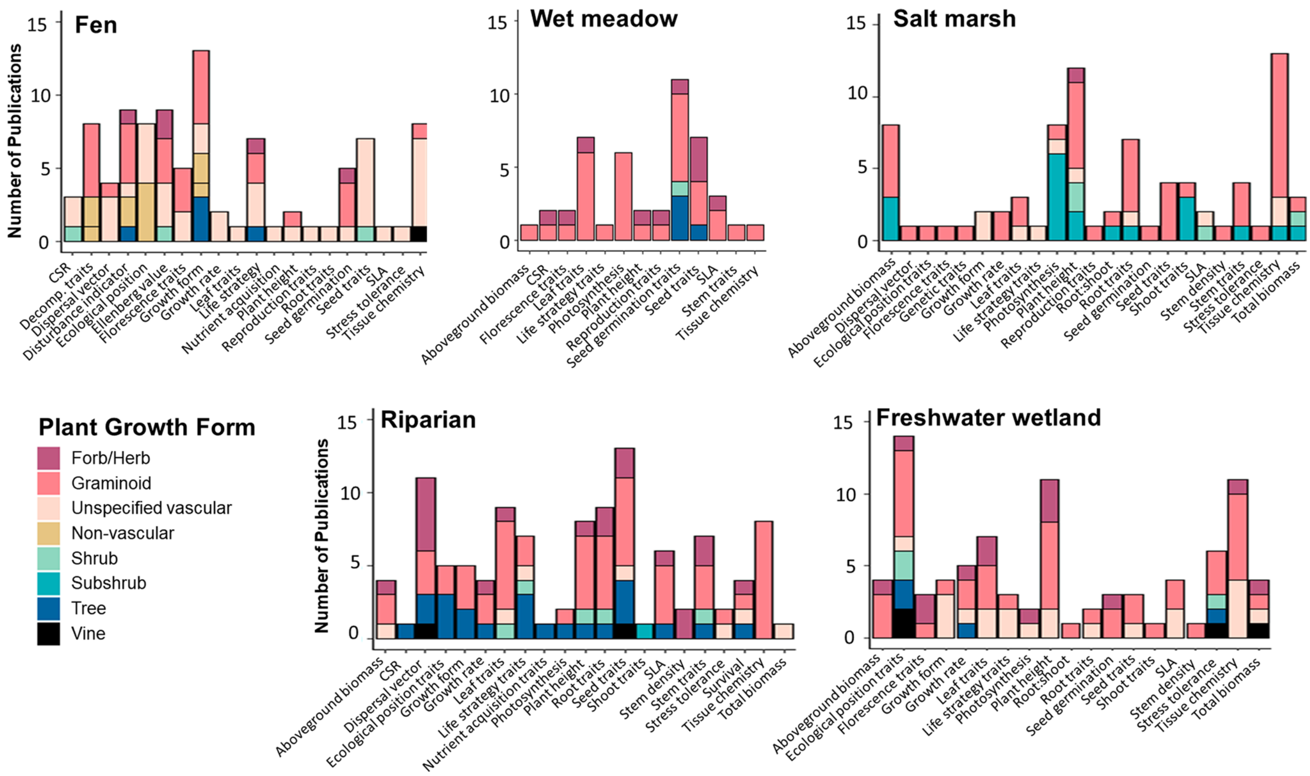

Fig. 4 Representation of plant functional traits (bars) across plant growth forms (color) in the five most frequently researched wetland types (graph). If a single study included multiple wetland types, growth forms, or traits, each combination is represented. Abbreviations: CSR = competitor, stress tolerator, ruderal species, Decomp. = decomposition, SLA = specific leaf area. Some traits have been grouped into categories for simplicity. A full list of traits can be found in Supplementary Table 3

and riparian wetlands. Traits that are more difficult to measure, such as photosynthesis, tissue chemistry, and genetics, were most well represented in salt marshes.

Study Design and Spatial/Temporal Scales

We extracted information on study design, longevity, and data acquisition approaches to determine any similarities among studies. Study design varied among the selected papers, with 32 field-based observational studies, 18 field-based manipulated experiments, 11 field-based natural experiments, and 22 controlled experiments conducted in a greenhouse, growth chamber, or mesocosm. The remaining few studies were conducted using remote sensing, meta-analysis, or an undefined approach. The spatial scale of these studies, defined by the grain (smallest resolution of the data collected) and extent (largest scale at which analysis is applied) of the research, showed consistency among design. The grain of the majority of studies (64) occurred at the level of the individual, 15 at the plot level, six at the population/community level, and the remaining not defined. The extent of these studies was far more variable, with 16 at the patch/plot level, 44 at the population/community level, 3 at metapopulation, 19 at regional level, and 1 at the global level. Three studies did not extend beyond the individual.

The temporal duration of each study was characterized to understand if plant functional traits are used to understand ecosystem change over time, an element relevant to restoration goals and ecosystem trajectories. The majority of these studies were conducted in less than one year's time or did not include any temporal component. The reviewed papers included a total of 14 longitudinal studies lasting more than one year, and 11 studies used a chronosequence. The longest longitudinal study spanned 12 years, whereas most studies incorporating a chronosequence included a temporal component of more than 20 years, with several studies including chronosequences representing 50 to 70 + years. A total of 21 studies specifically mentioned the phrase 'succession' in the context of their research, indicating a focus on longer temporal scales and ecosystem development.

Discussion

Our review of two decades of literature shows that the employment of plant functional traits to inform wetland restoration has been practiced across five continents and in nearly every wetland type, though representation of traits differed by wetland type and their dominant growth form. The collective findings of this review, and several exemplary publications (Table 1), demonstrate the application of a trait-based approach to achieve wetland restoration goals, such as rapid revegetation, invasive species resistance, and climate resilience. However, many studies draw implications to restoration as an afterthought, not the main focus of the study. We identified several shortcomings in this field (e.g., consistency in terminology and selection of traits and

Table 1 Example list of priority wetland restoration goals, ecological features and functions needed to meet said goal, recommended informative plant functional traits, and examples of how those functional traits link to goals with exemplary case studies. Priority wetland restoration goals were identified first, followed by selection of informative plant functional traits and identification of case studies. Abbreviations: *C* Carbon; *C:N* Carbon to nitrogen ratio; *CSR* Competitor, stress tolerator, ruderal species; *SLA* Specific leaf area; *WUE* Water use efficiency

Wetland restoration goal	Pertinent ecosystem feature/function	Recommended plant functional trait	Reasoning and exemplary case studies
Habitat quality	Vegetation structure Forage quality	Plant maximum height Spines/pubescence SLA Tissue C:N	Traits on plant size provide context for habitat structure and complexity. Plant defenses, SLA, and C:N indicate plant nutritional quality, palatability, and serve as a proxy for resource availability (Wong et al. 2010; Sivakoff et al. 2016)
Carbon sequestration and storage	Carbon flux dynamics Carbon sequestration rates Carbon storage rates	Tissue C Total Biomass Photosynthetic assimilation of carbon	Tissue C and biomass provide quantification of atmospheric carbon uptake (sequestration), carbon storage in plant material, and carbon deposition belowground. Photosynthesis quantifies the atmosphere to plant carbon fluxes (Cui et al. 2005; Means et al. 2016)
Invasion resistance	Fitness Spread Biodiversity	SLA CSR type Seed production Seed mass Dispersal vector Lateral tillering (asexual reproduction)	SLA, CSR type, and reproduction capacity provide information on species life strategies, ecological interactions with other species, as well as rates and processes driving reproduction and revegetation (Byun et al. 2013)
Climate resilience	Drought tolerance Inundation tolerance Salinity thresholds	SLA Water use efficiency Flooding and drought tolerance Seed dormancy	SLA serves as a proxy for resource availability, whereas water use efficiency, climatic tolerance, and seed dormancy indicate species' stress thresholds and future resilience (Bonin and Zedler 2008; Garssen et al. 2014; Markus-Michalczyk et al. 2019; Green and Miller 2019; Zhang et al. 2019a, b; Li et al. 2018)
Improvement of water quality	Nutrient uptake Heavy metal uptake	Tissue C:N Tissue elemental content Total biomass Plant maximum height	Tissue chemistry and biomass production indicate plant efficiency with uptake and assimilation of elemental nutrients/metals (Pan et al. 2020)
Rapid and lasting revegetation	Plant survival Vegetation spread Plant sustainability	Growth rate Germination rate Germination percentage Dispersal vectors Lateral tillering (asexual reproduction) Seed longevity/germination	Growth rates and reproduction strategies indicate the speed and rates of revegetation (Battaglia et al. 2004; Van Dijk et al. 2007)

necessity to work in restoration spaces) that will need to be addressed as the use of plant functional traits continues to develop. We provide several recommendations for improving the operationalization of this approach specifically for wetland restoration.

A Consensus on Terminology and Measured Traits

The literature available on plant functional traits in wetland restoration is growing, but remains relatively limited, both in the number of publications as well as the geographic extent of where studies occur. There may be an abundance of plant trait data collected in the context of wetland ecology and/or informing wetland restoration, but the use of explicit functional trait terminology is not prevalent in this field of study and thereby limits the results of a formal search. As a field, we must find consensus on both terminology and measured traits to connect this gap. Community- and population-level metrics (e.g., species cover, species diversity, etc.), while valuable, should not be considered plant functional traits as these are not attributes of the individual. One potential issue limiting the adoption and use of plant functional traits in wetland restoration literature is the lack of a common understanding of the definition of a plant functional trait. We define plant functional traits as aspects that characterize an individual; however, several selected studies identified population/community-level metrics as plant functional traits. For example, of the total 85 papers, 12 considered plant cover as a trait, 3 used species abundance/density, and 1 used genetic diversity (all were excluded from our analyses). These metrics may be informative criteria, but as these metrics occur at the population or community level, calling them traits is a misnomer.

Furthermore, empirical research and restoration monitoring efforts alike have long been collecting measurements from individuals across a variety of species and wetland types, but perhaps not identifying them as functional traits in publications, making it more difficult to coalesce as a field. Along with the increased use of functional traits as a tool has been the emergence of publicly available plant functional trait data bases (e.g., TRY database). The success of these databases, and the ability to extend the use of plant functional traits to understanding larger scale processes, depends on the identification and mass measurement of key functional traits across species and geographic regions (Wang et al. 2018). Seed mass, plant height, and SLA are three of the most commonly measured traits, regardless of ecosystem, as these succinctly characterize plant form and function (Moles 2018). Our review of literature identified that these traits are also commonly measured in wetland systems. These traits provide information about the vigor, health, and dispersal capacities of individuals and thus we recommend inclusion of measuring these metrics whenever feasible (Moles 2018; Table 1). Our systematic review also found that the most measured traits tend to be simple and cost-effective metrics. The inclusion of more complex traits (e.g., genome space length, photosynthetic assimilation of carbon) is certainly present in research literature, but whether these traits are feasible to measure (i.e., cost effective) and informative for restoration goals is unclear. The selection of traits, and utility of traits on restoration success, is partly determined by the environmental context of a restoration site, and is therefore unique to distinct ecosystem types (Balazs et al. 2020). Through standardizing selection of traits to be measured in wetlands, we will be able to better compare across various wetland types and conditions. The creation of a restoration-focused trait database, or addition to existing databases, consisting of traits measured in both empirical research and restoration monitoring efforts would make strides in improving the accessibility and use of traits to inform wetland restoration as well as closing the research-practice gap.

Research Should be Conducted in Restoration Spaces

The inclusion of plant functional traits in restoration ecology in peer-reviewed literature (for a variety of ecosystems) has increased over recent years (Funk et al. 2017). However, the increasing application of a functional trait framework has not necessarily translated to practice. Merchant et al. (2022) partially attribute this disparity to a communication gap between research and practice, but also differing foci of restoration goals (e.g., increasing biodiversity) that do not necessitate the measuring of traits, ineffectiveness of applying trait-based theoretical frameworks to practice, and impracticalities of including trait-based approaches in restoration. Many barriers exist that make the adoption of trait-based approaches in restoration practice difficult, but perhaps the onus should instead be on plant functional trait researchers to actually work in restoration sites, as has been recommended by others (Bell et al. 1997). In the context of wetland restoration, only a small portion of peer-reviewed research papers addressing plant functional traits involve true restoration sites. Many authors working in this space may be guilty of glossing over the broader application of the research to restoration without making it at the forefront of their work. We mention this not as a criticism of authors trying to connect basic and applied science, but rather to encourage more to work in actual restoration spaces. The scale at which plant functional traits are applied to wetland restoration is consistently limited to smaller spatial resolutions. This is not a surprising result as traits are measured at the individual scale, but scaling up findings to address questions relevant to larger spatial scales is encouraged. For example, can seed traits predict climate resilience across a biome? Finally, it has been well-recognized that the process of ecosystem recover following restoration takes time (Moreno-Mateos et al. 2020). Unfortunately, funding (or researcher life-spans) can rarely support research efforts at time-scales relevant to restoration. Changes in traits over longer time spans represents a knowledge gap that may partially be remedied by greater inclusion of chronosequences or longitudinal studies.

Specify Which Plant Functional Traits are Most Informative for Wetland Restoration Goals

Plant functional traits reflect eco-evolutionary responses to environmental conditions (Lavorel et al. 2007) and have been widely operationalized to make comparisons between traits and environmental thresholds, climate, and ecosystem function (Fonseca et al. 2000; Dong et al. 2016). Recently, restoration practitioners and researchers are recognizing the potential for functional traits to inform achievement of restoration outcomes (Clark et al. 2012; Laughlin 2014). For example, plant functional traits have been used to understand drought tolerance and interspecific competition dynamics in planning grassland and dryland restoration in a changing climate (Balachowski and Volaire 2018; Balazs et al. 2020). In tropical forests, traits have been used to inform species selection for restoration plantings (Ostertag et al. 2015; Charles 2018). For wetland restoration in particular, traits that relate to priority restoration goals should be prioritized and further explored through quantitative empirical research. Goals of wetland restoration are multifaceted, and the traits measured to inform these goals may differ by the objective. For example, SLA or leaf construction cost can provide information about community structuring as well as habitat suitability, as high-SLA species tend to be distributed in more resource-rich portions of the gradient compared with low-SLA species (Jung et al. 2010). Correlations between SLA and ecosystem level resource availability can serve as a proxy for determining whether ecosystem function and trajectories are on track. Examples from other ecosystems have shown contradicting evidence regarding whether low SLA relates to poor invasion resistance (Drenovsky and James 2010) or improved invasion resistance (Conti et al. 2018). Further study on the role of SLA in invasion resistance in wetlands is needed as restoring invasion resistant wetlands is a common goal (Byun et al. 2023).

Whenever possible we encourage the inclusion of longer time frames, either through longitudinal studies or chronosequence, to better connect plant functional traits with processes of ecological succession or ecosystem development inherent to wetland restoration. Wetland restoration efforts often include various human-mediated environmental changes (e.g., hydrologic engineering, species introduction, invasive species removal) intended to set the ecosystem down a particular path of succession toward a desired end point. However, differences in climate, species composition, abiotic characteristics, or simply discontinued land management, may cause that path to deviate from the restoration's intended destination. Functional traits, rather than species, have been lauded for their ability to identify mechanisms of succession (Kahmen and Poschlod 2004; Raevel et al. 2012). Understanding the mechanisms that drive succession may, in turn, aid with mitigating loss of biodiversity and ecosystem function (Chai et al. 2016). As these are key goals of most restoration goals, plant functional traits are therefore a useful tool for helping wetland restoration efforts meet ecosystem trajectories and goals. We provide an example list of plant functional traits that may be informative for specific goals for wetland restoration with descriptions of the mechanistic relationship of each trait to the restoration goal and an exemplary study (Table 1). This is not an exhaustive list of goals nor traits, but rather frequently measured, or most pertinent, traits for each goal. We also acknowledge that hyper focus on some traits may detract from attention on potentially more informative traits that should be explored. Nevertheless, we offer this table as a starting place for future development and consensus among wetland restoration researchers and practitioners.

The restoration of the world's wetlands remains a challenging undertaking that will require creative and explorative scientific approaches, as well as inner- and interdisciplinary communication and consensus. Taking a plant functional trait perspective on wetland restoration has potential to make important linkages between traits and desired ecosystem functions and trajectories. To maximize the use of this approach, it is important that the fields of research and practice reach a consensus on both terminology and which traits are most critical to measure.

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Data Availability The datasets analyzed during the review are available from the corresponding author on reasonable request.

Declarations

Competing Interests The authors have no relevant financial or non-financial interests to disclose.

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