General plant strategies and functions in wetlands: global trait-based analyses

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潘应骥

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PhD Thesis at Leiden University, The Netherlands

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‘Simplex sigillum veri’

‘Simplicity is the sign of truth’

Herman Boerhaave (1668–1738)

Contents

Chapter 1

General introduction

1.1 Wetland ecosystems

Wetlands are globally important ecosystems, which include various habitat types that depend on a variety of water regimes and nutrient supply features. As defined by the RAMSAR convention: “wetlands are areas of marsh, fen, peatland or water, whether natural or artificial, permanent or temporary, with water that is static or flowing, fresh, brackish or salt, including areas of marine water the depth of which at low tide does not exceed six meters” (Ramsar Convention Secretariat, 2016). Along this spectrum, bogs occur at long waterlogging periods and oligotrophic conditions, and floodplains and swamps stay at short waterlogging periods and eutrophic conditions, while shallow lakes are usually permanently inundated but at any nutrient conditions. The diverse wetland types at the global scale provide a natural laboratory to examine and extend established ecological theories (Moor *et al.*, 2017).

Wetlands support many kinds of life, including our human beings. Humans have managed and exploited wetlands for more than 8,000 years to harvest fish, waterfowl, fur-bearing animals and timber (McInnes, 2011; Mitsch & Gosselink, 2015). Nowadays, wetland ecosystems provide up to 40% of global renewable ecosystem services while covering less than 3% of the globe’s surface (Costanza *et al.*, 1998; Zedler & Kercher, 2005). The ecosystem services provided by wetlands mainly include water purification, flood abatement, biodiversity support and carbon sequestration (Zedler & Kercher, 2005; Couwenberg *et al.*, 2010; Moor *et al.*, 2017).

The special role of wetland ecosystems in providing more and different ecosystem services than most other terrestrial ecosystems is related to their unique hydrological and soil conditions. Under water-saturated conditions, soil oxygen will be quickly depleted, which has profound impacts on the biogeochemical processes in wetland substrates and associated ecosystem functions. For example, wetlands improve water quality mainly through the microbial denitrification process and plants uptake. Both ammonium and nitrate can be directly taken up by wetland plants, removing nitrogen from the system. Nitrification of ammonium (NH_4^+) to nitrate (NO_3^-) occurs in the oxic rhizosphere of wetland plants. Then, the formed nitrogen can diffuse to the deeper anoxic sediments to be reduced to N_2 gas (denitrification) (Reddy *et al.*, 1989). The lack of oxygen impedes the decomposition processes in wetlands, which makes wetlands an important global carbon sink. Peatlands alone, as one of the typical wetland ecosystems, contain 500 to 700 billion tons of carbon (this equals to the total amount of atmospheric carbon) (Page & Baird, 2016).

In contrast to various positive ecosystem services provided, wetlands are also the main global source of two important greenhouse gases (GHG): methane (CH_4) and nitrous oxide (N_2O). Natural wetlands are considered as the main drivers of global inter annual variability of CH_4 emission (Stocker *et al.*, 2013). For the decade of 2000-2009, natural wetlands emitted 177×10^{12} to $284\ \times10^{12}$ g methane (CH_4) per year, accounting for 32% of the total global methane emissions (Kirschke *et al.*, 2013). The release of CH_4 may counteract wetlands' positive role in GHG mitigation through carbon sequestration when considering the greater infrared absorptivity of CH_4 relative to CO_2 (Whiting & Chanton, 2001; Liu & Greaver, 2009). N_2O is released if the soil condition is not strictly anoxic during the denitrification processes (Schlesinger, 2009) and N_2O emissions increase by on average two folds through anthropogenic nitrogen enrichment (Liu & Greaver, 2009).

Hydrology is also the main driver of the plant community composition in wetlands (Mitsch & Gosselink, 2015; Silvertown *et al.*, 2015). The waterlogged/submerged conditions of wetlands lead to a much lower gas diffusion rate (around 10,000 times slower than in atmosphere). Below the water surface, oxygen is quickly depleted to a reduced or weakly reduced environment. The degree of oxygen deficit in wetland substrates therefore largely depends on the duration of flooding event. The lack of oxygen as an electron acceptor directly impedes the aerobic respiration metabolism of plants and other organisms in the substrate. As a consequence, some plants may undergo cellular energy deficits, because the replacement of aerobic respiration by fermentation yields only 2 instead of 32 ATP units from each unit of glucose. When oxygen in the substrate has been depleted, alternative electron acceptors will be used in biogeochemical processes along the well-established dynamics of the redox sequence. Following oxygen, the alternative electron acceptors in the sequence are nitrate, manganese, iron, sulphate and carbon (Ponnamperuma, 1972). The utilization of alternative electron acceptors can result in the production of reduced chemical matter, such as ferrous iron and sulphide (Singer & Havill, 1993) and low-weight monocarboxylic acids (e.g. acetic, propionic, butyric and hexanoic acids) (Armstrong & Armstrong, 2001; Pezeshki, 2001). Those chemical compounds are often phytotoxic to wetland plants. In addition, the return to oxic conditions after flooding does not necessarily mean salvation from the adverse situation for the oxygen-depleted wetland plants tissues. When at low oxygen conditions and upon re-aeration, accumulated electrons at electron transport chain in the mitochondria are donated to O_2, which produces reactive oxygen species (ROS) (Colmer & Voesenek, 2009). The accumulation of reactive oxygen species can cause damage to cellular macromolecules and membranes (Yordanova *et al.*, 2004; Bailey-Serres & Voesenek, 2008; Colmer & Voesenek, 2009). The above-mentioned adverse conditions form major challenges for plants to survive and prosper in wetland habitats. As a consequence, wetlands contain plant communities that are unique to these ecosystems.

1.2 Adaptations of plants to wetland conditions

To survive in the anoxic wetland environment with the abundant phytotoxic compounds and the lack of oxygen, plants have developed special ecophysiological adaptive strategies. For example, the development of spongy tissue (i.e. aerenchyma tissue) that forms spaces or air channels in the leaves, stems and roots can facilitate internal oxygen transportation from leaves/stems to roots and ameliorate the oxygen shortage in the rhizosphere (Visser *et al.*, 2000b; Mcdonald *et al.*, 2001; Colmer, 2003b). Oxygen can also be released to the rooting substrate through root radial oxygen loss (ROL). This process improves the oxygen content in the rhizosphere and induces detoxification of soil-borne phytotoxins such as ferrous iron and sulphide (Armstrong & Armstrong, 2001). To avoid excessive oxygen loss before it reaches the root tip, wetland plants developed ROL barriers to reduce diffusion of precious oxygen to the rhizosphere (Armstrong *et al.*, 2000; Colmer, 2003a). Shoot elongation under submergence allows leaves to access atmospheric oxygen. Varied root/shoot ratios of different plant species allow the optimal balance between gas transport capacity (as an oxygen source) and root oxygen consumption (as an oxygen sink) in different habitats (Van Bodegom et al., 2005; Jung et al., 2009). For plants undergoing long-term submerged conditions of low HCO_3-/CO_2 concentrations and low light intensity, underwater photosynthesis is an important process to allow for continued growth and survival (Mommer & Visser, 2005; Pedersen *et al.*, 2006, 2016; Colmer *et al.*, 2011). Adaptive traits involved in maintaining an optimal underwater photosynthetic rate include gas film formation (Colmer & Pedersen, 2008), modified leaf morphological structure to become thinner, narrower leaves with reduced cuticles, and rearranged chloroplasts closer to the epidermis (Voesenek *et al.*, 2006; Konnerup & Pedersen, 2017).

1.3 Trait-based approaches in ecology

To quantitatively study the response and effect of plants to their ambient abiotic environments, trait-based approaches apply the concept of plant functional traits to present plants' performance (such as growth, reproduction and survival) and strategies (such as adaptation and resources management) across organizational and spatial scales (Violle *et al.*, 2007; Shipley *et al.*, 2016). Trait-based ecology is promising in synthesising, integrating, and predicting general patterns in ecological niche, community assembly and ecosystem functioning (Violle & Jiang, 2009; van Bodegom *et al.*, 2012; Shipley *et al.*, 2016). The trait-based approaches advance over the traditional plant functional types (PFTs) by a better capability of capturing the variation/acclimation of individual plants along the environmental gradient.

Trait-based approaches have been widely applied to study a variety of ecosystem types at different spatial scales, such as the prediction of community assembly in forests, grasslands and shallow lakes (Shipley *et al.*, 2006; Ackerly & Cornwell, 2007; Pan *et al.*, 2017), and the modelling of global vegetation distribution maps (van Bodegom *et al.*, 2014). One important component of trait-based ecology is the generation of global leaf economics spectrum (LES) (Wright *et al.*, 2004). The LES provides convincing evidence of a consistent and continuous relationship among the so-called leaf economics traits, reflecting a gradient of slow (conservative) to fast (acquisitive) strategies in terms of investment and use of nutrients and other resources (Reich *et al.*, 1997; Shipley *et al.*, 2016; Funk *et al.*, 2017). This spectrum seems to represent an important axis of variation in plant strategies.

In the meantime, many global plant trait databases have been established through the compilation of trait data contributed from different countries and regions (e.g. Kleyer et al. 2008, Kattge et al. 2011, Forbes et al. 2018). This has systematically increased the accessibility of plant trait data over wide scales (Kattge *et al.*, 2011) and provided a promising basis for understanding various ecological questions from species to ecosystem levels (McGill *et al.*, 2006; Diaz *et al.*, 2016).

1.4 Trait-based wetland ecology

Despite the significant progress that have been achieved in trait-based ecology in many different ecosystems, there are still barriers towards a trait-based wetland ecology (Moor et al. 2017). On the one hand, the majority of trait-based studies have focused on terrestrial ecosystems, such as forests and grasslands. Most of the trait studies in wetlands have only concentrated on comparisons of trait expression within the local species pool under laboratory conditions (Pedersen *et al.*, 2011; Colmer *et al.*, 2013). This makes it difficult to understand the wetland plant strategies and functioning at a broader scale in the context of functional ecology. On the other hand, the unique hydrological regimes and the consequent environmental conditions in wetlands (as discussed in section 1.1) make it difficult to directly apply the ecological theories and concepts from other ecosystems to wetlands. For example, the leaf economics spectrum may be deformed if the cost of adaptation to wetland conditions is expensive from a resource utilization perspective (Kirk, 2003). Therefore, it requires special attention to both commonly measured traits (such as leaf nitrogen, specific leaf area and photosynthetic rate) and those unique wetland adaptive traits (such as root porosity, root/shoot ratio, radial oxygen loss and shoot elongation) when applying trait-based approaches to wetlands.

Important wetland plant functional traits include, but not limited to, wetland plant ecophysiological adaptive traits, leaf economics traits and size-related traits. Those wetland plant traits do not only play a critical role in the survival and prosperity of plants in wetland conditions, but also have important effects on the wetland ecosystem functioning (Engelhardt, 2006; Alldred & Baines, 2016; Moor *et al.*, 2017). For example, some wetland adaptive traits can help to transport oxygen to the rhizosphere to relieve the oxygen shortage in the substrate and allows plants to endure the flooding events. Leaf economics traits reflect resources acquisition and allocation strategies of the plants and considerably correspond to habitat fertility. Size-related traits are a proxy for competition and reproduction capacity. Considering the various ecological roles that different groups of traits play, it is imperative to apply trait-based approaches to wetlands for a better understanding of plant strategies, ecological niches, community assembly and ecosystem functioning in wetlands.

One example of how different wetland plant traits affect ecosystem functioning can be found in the complex interactions between wetland plants and methane emission (Ding *et al.*, 2005). On the one hand, plants can facilitate the methane emission through transporting the methane through the aerenchyma tissue (known as the chimney effect) and providing carbon sources through aboveground and belowground litter (Laanbroek, 2010; Bhullar *et al.*, 2013a). Conversely, plants can inhibit methane production by transporting oxygen to the rhizosphere, inhibiting the activity of methanogens, and oxidizing produced methane to carbon dioxide (Segers, 1998; Bhullar *et al.*, 2013a; Bridgham *et al.*, 2013). The application of trait-based approaches is promising to quantify these complex processes in wetlands through wetland plant functional traits (Sutton-Grier & Megonigal, 2011).

To fill the knowledge gaps and explore the ecological theories in wetlands, one powerful solution is the compilation of a wetland plant trait data to quantitatively understand the wetland plant strategies and functioning on the regional to global scale (Kattge *et al.*, 2011; Pan *et al.*, 2019). When compiling a wetland plant trait database, we should keep in mind that in addition to the traditionally studied plant functional traits, the important wetland adaptive traits should also be taken into consideration for their unique but fundamental roles in helping plants to survive in wetlands and affecting wetland ecosystem functioning.

1.5 Research aims and questions

The aim of this research is to develop trait-based approaches that enhance our understanding of general wetland plant strategies on a global scale. In this thesis, the following questions will be addressed (see also Figure 1.1 for a conceptual scheme of the thesis):

1. What are the general potential drivers for wetland adaptive traits? (Chapter 2)
2. What is the global leaf economics spectrum (LES) in wetlands? (Chapter 3)
3. How can we integrate both wetland adaptive traits and leaf economics traits for a better understanding of functional wetland ecology? (Chapter 4)
4. What are general plant strategies in wetlands? (Chapter 5)

To answer these questions, an original wetland plant trait database has been compiled for this study. The wetland plant trait data were compiled through systematic searches in Web of Science and Google Scholar for wetland plant ecophysiological adaptive traits, leaf economics traits and size-related traits. The references presented in important reviews that focused on the ecophysiological studies of how wetland plants adapt to flooding conditions published in the past 15 years were also checked for traits records. In addition, enquiries were sent around our network of colleagues working on the ecophysiology of wetland plants for recommendations for possible literature that may have been missed. Finally, several unpublished data sources along with contributions from our network were added. In total, around 8000 observations of more than 1200 species from over 200 references were included. Besides the functional trait data, the available plant species information that presents the characteristics and habitat information, such as life form, Ellenberg moisture indicator, as well as details of the habitat including habitat type, hydrological regime and geographic reference (coordinates) was recorded.

1.6 Thesis content

The wetland plant trait database compiled for the purpose of this thesis enables, for the first time, the quantitative analysis of the wetland plants strategies on a global scale. For instance, we can test the potential drivers for wetland plant traits by analysing the correlations between wetland plant traits and their environmental factors. We can also examine whether the global leaf economics spectrum exists in wetlands by analysing the trait-trait relationships between wetland plant leaf economics traits. Last but not the least, we can understand the wetland plant strategies by analysing the relationships between wetland adaptive traits and leaf economics traits to see whether facilitations or trade-offs occur among different groups of traits.

The conceptual scheme of trait-based relations in wetlands with links to each chapter is shown in Figure 1.1

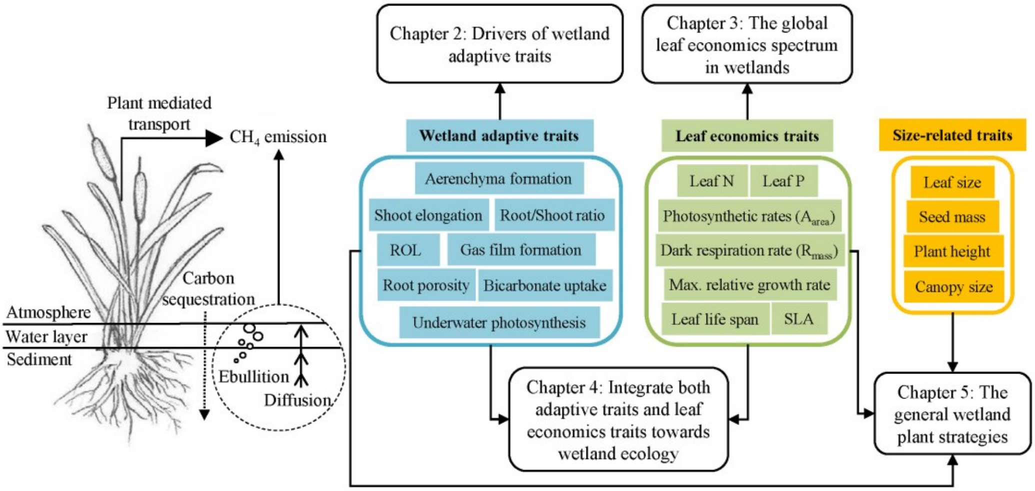

Figure 1.1 Conceptual scheme of the topics of chapters 2, 3, 4 and 5, and the plant functional traits involved with a brief illustration on how a wetland plant affects ecosystem functioning.

The principal content of each chapter is as follows:

Chapter 1: General introduction

This chapter provides a general introduction on wetland ecosystems, wetland adaptive strategies and trait-based approaches in wetland ecology. The major research questions and outline of the thesis are outlined.

Chapter 2: Drivers of plant traits that allow survival in wetlands

This chapter explores the potential driving factors of three important wetland adaptive traits (root porosity, root/shoot ratio and underwater photosynthetic rate) at a broader scale beyond the local species pool. The results show that in addition to bioclimatic variables (temperature and precipitation), each adaptive trait is also influenced by different driving factors (hydrological regime, habitat type and life form), which indicates a variety of driving mechanisms affecting the expression of different adaptive traits.

Chapter 3: The leaf economics spectrum revisited: global trait patterns in wetlands

The leaf economics spectrum (LES) reflects a gradient of slow (conservative) to fast (acquisitive) strategies in terms of investment and use of nutrients and other resources. However, whether and how the LES exists in wetlands at the global scale is still unclear. Based on a large wetland plant trait database, this chapter reveals a shifted LES in wetlands compared to other non-wetland terrestrial habitats, reflecting the special strategies of wetland plants in coping with resources. Wetland plants tend to hold a fast-return strategy with a relatively low respiration rate due to their unique leaf structure and plant functioning. This analysis provides a first step to bringing trait-based approaches to wetland ecology.

Chapter 4: Are ecophysiological adaptive traits decoupled from leaf economics traits in wetlands?

This chapter continues to advance trait-based approaches in wetland ecology, by incorporating both wetland adaptive traits and LES traits. First, it carefully reviews their distinct but important ecological roles and effects on ecosystem functioning, such as methane emission and denitrification processes. Moreover, this chapter addresses the importance of combing the two suites of traits within wetland ecology by understanding their trait-trait relations. Based on an exploratory analysis, it reveals that trait-trait relationships between wetland adaptive traits and LES traits are largely decoupled (i.e. are orthogonal in trait space), which provides an important premise for understanding the wetland plant strategies as well as the wetland ecosystem functioning from a trait-based perspective.

Chapter 5: What are general plant strategies in wetlands?

While trait-based approaches have provided critical insights in general plant functioning, we lack a comprehensive quantitative view on the role of adaptations to stressful habitats in plant strategies. This chapter uses the newly compiled wetland plant trait dataset, to explore adaptive strategies to wetlands in relation to other plant strategy components. As LES traits and size-related traits are considered as two major (but decoupled) trait axes representing the strategies for growth and resources competition in terrestrial ecosystems, this chapter evaluates the relationships between three key traits indicative of adaptations to wetland conditions (root porosity, root/shoot ratio, shoot elongation) vs. leaf economics traits and size-related traits on a global scale. The chapter reveals that the adaptive traits are largely independent of the other two dominant trait axes, and adaptive traits themselves are largely independent of each other. The pattern indicates that there are multiple mechanisms involved in plant adaptive strategies to deal with the multi-faceted wetland conditions, which include waterlogging, submergence and a range of nutrient conditions.

Chapter 6: General discussion

This chapter synthesizes the principal findings of this research project. It emphasizes the significance of bringing the trait-based approaches to wetland ecology to understand wetland plant strategies, wetland ecosystem functioning and ecosystem management. Based on the findings of previous chapters, this chapter discusses the implications for future ecosystem management.

Chapter 2

Drivers of plant traits that allow survival in wetlands

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Abstract

- Plants have developed a suite of traits to survive the anaerobic and anoxic soil conditions in wetlands. Previous studies on wetland plant adaptive traits have focused mainly on physiological aspects under experimental conditions, or compared the trait expression of the local species pool. Thus, a comprehensive analysis of potential factors driving wetland plant adaptive traits under natural environmental conditions is still missing.
- In this study, we analysed three important wetland adaptive traits, i.e. root porosity, root/shoot ratio and underwater photosynthetic rate, to explore driving factors using a newly compiled dataset of wetland plants. Based on 21 studies at 38 sites across different biomes, we found that root porosity was affected by an interaction of temperature and hydrological regime; root/shoot ratio was affected by temperature, precipitation and habitat type; and underwater photosynthetic rate was affected by precipitation and life form. This suggests that a variety of driving mechanisms affect the expression of different adaptive traits.
- The quantitative relationships we observed between the adaptive traits and their driving factors will be a useful reference for future global methane and denitrification modelling studies. Our results also stress that besides the traditionally emphasized hydrological driving factors, other factors at several spatial scales should also be taken into consideration in the context of future functional wetland ecology.

2.1 Introduction

Wetland ecosystems are of global importance for their provisioning of ecosystem services such as flood abatement, habitat provision, water purification and carbon sequestration at the regional and global scale (Zedler & Kercher, 2005). Among the variety of global wetland ecosystems (Ramsar Convention Secretariat, 2013), peat-forming wetlands (including bogs, fens and swamps) alone are considered to store more than half the amount of carbon present in the atmosphere (Page & Baird, 2016). At the same time, wetlands are the dominant single global methane emission source, contributing some 20% to 40% of global methane emissions (Ringeval *et al.*, 2010). To help understand these wetland functions, plant functional traits can be used to link the environmental conditions and species composition to the ecosystem processes (Moor *et al.*, 2017). Unravelling these interlinkages at a global scale is essential to inform ecological modelling, such as dynamic global vegetation models, to improve our predictions on important processes such as global wetland methane emissions (Wania *et al.*, 2013; Miller *et al.*, 2016).

Wetland ecosystems are distinguished from other (non-wetland) terrestrial ecosystems by their unique hydrological and anoxic soil conditions and associated biogeochemical processes. To survive in wetlands, plants need to deal with the lack of oxygen in the rooting substrate to avoid cellular energy-deficits, and the potential accumulation of phytotoxic compounds. Oxygen-depletion in tissues can also lead to an accumulation of reactive oxygen species (ROS) upon return to aerobic conditions after flooding, causing damage of cellular macromolecules and membranes (Yordanova *et al.*, 2004; Bailey-Serres & Voesenek, 2008; Colmer & Voesenek, 2009). In the rhizosphere, the lack of oxygen as an electron acceptor results in the production of toxic chemical matter such as ferrous iron and sulphide (Singer & Havill, 1993) and low-weight monocarboxylic acids (e.g. acetic, propionic, butyric and hexanoic acids) which impair plant root function (Armstrong & Armstrong, 2001; Pezeshki, 2001). There are also environmental stressors that are specific to a certain wetland type, such as salinity in saline wetlands (Flowers & Colmer, 2008). In this study, we focus on generalities that apply to all wetlands.

To cope with these adverse conditions, wetland plants have developed a suite of adaptive traits (Voesenek *et al.*, 2006; Winkel *et al.*, 2016; Pan *et al.*, 2019). Examples include: enhanced shoot and root porosity (aerenchyma formation) to facilitate internal oxygen transportation, ameliorate oxygen concentration in the root zone and aid (root) respiration and oxidation (Visser *et al.*, 2000b; Mcdonald *et al.*, 2001; Colmer, 2003b); shoot elongation to allow leaves to access atmospheric oxygen; decreased root/shoot ratios to create a better balance between gas transport capacity (oxygen source) and root oxygen consumption (oxygen sink) (van Bodegom *et al.*, 2005; Jung *et al.*, 2009); and a root radial oxygen loss (ROL) barrier to reduce diffusion of precious oxygen to the rhizosphere (Armstrong *et al.*, 2000; Colmer, 2003a). Underwater photosynthesis is an important process for growth and long-term persistence of wetland plants under submerged conditions, which create low HCO_3^-/CO_2 concentrations and low light intensity (Mommer & Visser, 2005; Pedersen *et al.*, 2006, 2016; Colmer *et al.*, 2011). Adaptive traits involved in maintaining an optimal underwater photosynthetic rate include gas film formation (Colmer & Pedersen, 2008), changed leaf morphological structure to become thinner, narrower, with reduced cuticles, and rearranged chloroplasts closer to the epidermis (Voesenek *et al.*, 2006; Konnerup & Pedersen, 2017).

The expression of wetland adaptive traits is likely determined by bioclimatic variables, hydrological regime, habitat type and plant life form. Bioclimatic variables (e.g. precipitation, temperature) may affect fundamental eco-physiological processes such as enzymatic activities and transpiration rates (Moles *et al.*, 2014) that may also be important in wetlands. However, these driving forces may be different than that in terrestrial systems, for example in relation to the general lack of water-limitation in wetlands compared with terrestrial plants. The hydrological regime, i.e. both the duration and depth of the water table (e.g. waterlogged or submerged), has a direct impact on wetland conditions and plant performance, and is recognized as an important factor. However, its importance in comparison to other drivers, such as habitat type or bioclimatic variables is unknown. Habitat type (e.g. marsh or floodplain) may drive the adaptive traits, for example through specific soil biochemistry, flooding depth (Voesenek *et al.*, 2004) or competition/facilitation of the local plant community (Maestre *et al.*, 2009; Luo *et al.*, 2010). Plant life form (such as sedge, grass, floating-leaved) in turn reflects plant morphological characteristics and life history strategies, and therefore might constrain the upper and lower range of adaptive traits. Our understanding of driving factors is further hampered by the often complex interactions among driving forces of plant functional traits in wetlands (Moor *et al.*, 2017). For instance, while the temperature in shallow waterbodies can fluctuate markedly, affecting the rate of underwater photosynthesis of tropical seagrass (Pedersen *et al.*, 2016), that of deeper waterbodies is much more stable even with strong changes in the surrounding air temperature (Colmer *et al.*, 2011). Likewise, the impact of a low redox potential on the need for aerenchyma tissues may reduce at low temperatures when respiration and thus oxygen demand is low.

The mechanisms through which such adaptive traits help plants adapt to wetland habitats, especially under flooded conditions, have been carefully studied in eco-physiological experiments (as reviewed in Colmer & Voesenek, 2009; Voesenek & Bailey-Serres, 2015). However, there is no analysis on the potentially generic driving factors of these plant traits in wetlands under natural environmental conditions. Despite their dominant ecological role in enhancing wetland plants’ survival, those wetland adaptive traits are not yet included in the global plant functional trait databases, such as the TRY database (Kattge *et al.*, 2011), while we consider this essential for comprehensive analyses within the functional ecology context. Most studies so far have focused on the molecular and physiological regulation of specific traits in a limited comparison of species or genotypes (e.g. Winkel *et al.*, 2013; Konnerup & Pedersen, 2017). Comparative experiments or field studies have concentrated on comparisons of trait expression within the local species pool (Pedersen *et al.*, 2011; Colmer *et al.*, 2013). To our knowledge, no study exists relating the expression of these traits to driving factors or to different wetland types on regional to global scales. Such understanding on the potential drivers of wetland adaptive traits comprises a fundamental step in applying trait-based approaches to wetland ecology.

In this research, we hypothesize that a) bioclimatic variables, hydrological regime, habitat type and plant life form, including their interactions, are potential key driving factors for wetland adaptive traits; b) since wetland adaptive traits all respond and adapt to the adverse wetland conditions, we expect that the driving factors for different wetland adaptive traits are similar. We aim to assess and evaluate the importance of these driving factors in determining wetland adaptive traits. Using a newly compiled wetland plant adaptive trait dataset, our paper is the first exploration of various potential driving factors for three key wetland plant adaptive traits (root porosity, root/shoot ratio and underwater photosynthetic rate) that represent key plant strategies in response to adverse wetland conditions (including anoxia, flooding and submergence). As a fundamental step towards understanding the wetland plants' adaptive strategies, our results should reveal a new perspective on the driving factors for wetland adaptive traits in the broad context of functional ecology, and provide a benchmark for modelling and predicting wetland plant species distributions and their impacts on ecosystem functioning.

2.2 Materials and Methods

2.2.1 Data compilation

We compiled a dataset of wetland plant adaptive traits, defining wetlands and wetland plants according to the Ramsar Convention (Ramsar Convention Secretariat, 2013), which includes plant species inhabiting aquatic systems (e.g. rivers and lakes) as well as those non-wetland terrestrial plants that inhabit temporarily/permanently flooded areas. The wetland plant adaptive trait dataset was compiled from a systematic search in Web of Science and Google Scholar (last updated on the 5th June 2018). The literature search included permutations of the following keywords: wetland plants, marsh plant, bog plant, isoetid, aquatic plants, macrophytes, submerged plants, floating-leaved plants, emergent plants, root porosity, root/shoot ratio and underwater photosynthesis. We also drew on references presented in several important reviews that focused on the eco-physiological studies of how wetland plants adapt to flooding conditions published in the past 15 years (e.g. Voesenek *et al.*, 2006; Bailey-Serres & Voesenek, 2008; Voesenek & Bailey-Serres, 2015). Finally, we added several of our own unpublished data sources, along with others within our network.

For the current analysis, we selected those studies that i) measured plants occurring in wetlands with sufficient information for us to consistently classify the habitat types and the hydrological regime(s) (drained, waterlogged or submerged); ii) were measured using field-collected specimens, thus we did not include data on plants from greenhouse experiments; and iii) provided accurate location information (with coordinates). We then compiled data from the selected studies that included quantitative measurements of three intensively studied wetland plant adaptive traits (root porosity (%), root/shoot ratio and the rate of underwater photosynthesis (mol m^{-2} s^{-1})). We are aware that there are many other important wetland adaptive traits, such as root radial oxygen loss (ROL), ethanol metabolism, and tolerance of reduced metal ions. However, the data available for these traits either were measurements in greenhouse/laboratory settings or were available only in a qualitative form, which was not suitable for this quantitative analysis. In total, 598 trait records from 21 studies at 38 different study sites were analysed. For root porosity, the data comprised 198 measurements of 103 unique species in 13 studies at 25 different sites; root/shoot ratio data contained 321 measurements on 12 unique species, described in 6 studies at 7 different sites; the 79 underwater photosynthetic rate measurements on 27 unique species were contained in 3 studies at 8 different sites. Location of the sampling sites in a global map were shown in Appendix 2A Fig. 2S1.

We included bioclimatic variables, hydrological regime, habitat type and the plant life form (see Table 2.1) as potential drivers for the above selected wetland plant adaptive traits. We could not include other abiotic variables, such as redox potential, due to a limited data availability and inconsistent measurement methods. Nevertheless, we believe that the variables we included, such as the hydrological regime, act as a good proxy for redox potential and oxygen depletion. We did not include soil variables in our analysis either. Local soil conditions in wetlands strongly deviate from those in nearby non-wetland terrestrial systems (organic matter content as an example) that is represented in available global soil databases. Also, the soil information provided in the original publications was inconsistent and insufficiently detailed to be included in our analyses.

For our analyses, we classified hydrological regime as drained, waterlogged or submerged (as defined by Sasidharan *et al.*, 2017), as provided in the original study. While this provides baseline information on local (hydrological and fertility) wetland conditions, additional insights can be obtained from a classification into specific wetland habitat types. Based on the guidance of the Ramsar Convention (Ramsar Convention Secretariat, 2013) and the definitions by the Environmental Protection Agency (EPA, https://www.epa.gov/wetlands/classification-and-types-wetlands#marshes), we grouped wetland habitats into eleven categories (Appendix 2B). Studies selected for the current paper encompassed eight habitat types (Table 2.1). We grouped the life form of plants into seven categories (Table 2.1). We acquired bioclimatic variables at the global scale with an accuracy of 2.5 minutes (WorldClim Version 2.0, http://www.worldclim.org/) (Fick & Hijmans, 2017). These bioclimatic variables represent 19 climate attributes of ecological importance, in terms of annual means, seasonality and extreme or limiting climate factors. To determine the major axes of variation in all bioclimatic variables and to minimize the effect of inter-correlations, we ran a principal component analysis (PCA), and took the scores of the first two axes of the PCA to represent the climatic conditions. The PCA surface and axis scores reveal that the first and second axes (explained 51.8% and 25.8% of total variance, respectively) are mainly related to temperature and precipitation, respectively (Appendix 2A Fig. 2S2). Therefore, below we will refer these axes as *temperature* and *precipitation*, respectively. Our data points represent most of the global bioclimatic space, illustrated by an overlay of the sampling points onto the PCA surface (Appendix 2A Fig. 2S3).

Table 2.1 The explanatory variables in the model as driving factors for wetland adaptation traits.

Explanatory variables	Continuous/Categories
Bioclimatic variables	*temperature; precipitation*
Hydrological regime	*drained; waterlogged; submerged*
Habitat type	*fens; permanent forested wetlands; mangrove swamps; marshes; permanent brackish/saline non-forested wetlands; rivers and lakes; temporary brackish/saline non-forested wetlands; temporary non-forested wetlands*
Plant life form	*emergent; floating-leaved; grass; isoetid; sedge; shrub/tree; submerged*

2.2.2 Data analysis

We constructed single-trait linear regression models to elucidate the role of variables in driving the three wetland plant adaptive traits. We used trait values recorded at the individual plant level. In some papers, measurements were summarised as a species mean ± standard deviation, in which case we simulated the original number of data points (recorded sample size) based on a normal distribution around the recorded mean and standard deviation. The response variables were $\log_{10}$-transformed to approximate normality, and logit transformed in the case of root porosity (Warton & Hui, 2011).

For the root porosity trait, we included all four sets of explanatory variables: bioclimatic variables, hydrological regime, habitat type and plant life form. Due to the limited data available for some of the combinations of categorical variables, we could add only the two-way interaction terms between the (continuous) bioclimatic variables and each of the three categorical variables. The full model for root porosity was therefore structured as:

$\log_{10}$(Root porosity/(1-Root porosity)) ~ Temperature + Precipitation + Hydrology + Habitat + Life form + Temperature: Hydrology + Precipitation: Hydrology + Temperature: Habitat + Precipitation: Habitat + Temperature: Life form + Precipitation: Life form + Temperature: Precipitation

Some of the study sites were geographically clustered, which might significantly affect the results. Given that we aimed to provide estimates of impacts of each driving factor, we were not interested in solving this clustering by including study sites as a random factor. Instead, after checking the amount of data available for each location, we randomly selected up to 5 measurements at each pixel (one pixel=0.01 PCA score *0.01 PCA score square cell) on the bioclimatic PCA surface (if there were fewer than 5 measurements, we included all the measurements) to maintain a balanced data structure for linear model construction.

We constructed the full model with the data set as generated by the above-mentioned resampling process. For each resampled dataset, we ran a model selection on the full model based on the Akaike Information Criterion weight (AIC weight). For some resampled datasets, some coefficients could not be estimated because a combination of variables was-coincidently- not sampled. We excluded candidate models with such undefined coefficients, and rescaled the AIC weight for the remaining candidate models to sum to 1. This resampling and model selection was repeated 1000 times.

Then we calculated the averaged AIC weight for each candidate model across all 1000 iterations, and the best model was selected as being the candidate model with the highest averaged AIC weight (Burnham & Anderson, 1998). To gain a robust parameter estimation for the best model, we calculated the average adjusted R^2, average coefficient values of the intercept and each variable, and the average relative importance of each main effect based on the model parameters generated in all 1000 iterations.

The root/shoot ratio had similar and even stronger data limitations in the categorical variables. Hence, we included only the main effects of the four set of variables: bioclimatic variables, hydrological regime, habitat type and plant life form without interaction terms. The full model for root/shoot ratio was therefore:

$\log_{10}$(Root/shoot ratio) ~ Temperature + Precipitation + Hydrology + Habitat + Life form

For this response variable, there was only one record in the habitat type ‘mangrove swamp’, which we excluded from further analysis. Following the same resampling approach as described above, we selected the best model and obtained its parameter estimates.

For the underwater photosynthetic rate, data were limited to three studies (see Appendix 2A Fig. 2S1& Fig. 2S3). Since these data were reasonably balanced across geographical space, we ran this linear model on the original data (without resampling). All data records were from within one habitat type (rivers and lakes) and one hydrological regime (submerged). We therefore used only bioclimatic variables, plant life form and the interactions between them to construct the linear model. Thus, the full model for underwater photosynthetic rate was:

$\log_{10}$(Underwater photosynthetic rate) ~ Temperature * Precipitation * Life form

The analyses were performed in the R language (R Core Team, 2018). We used the dredge() function in the MuMIn package (Barton, 2018) to simplify the full model and obtain the AIC weight based on AICs values. We visually assessed whether the most assumptions were met. We then calculated the relative importance of the main effects in the best models by using the calc.relimp() function in the relimpo package (Grömping, 2006). To compare the trait variances between different functional group and habitat conditions, we ran Tukey's honest significant difference test (TukeyHSD) using glht() function in the multcomp package (Hothorn *et al.*, 2008).

2.3 Results

2.3.1 Quantifying the driving factors for root porosity

The best model for root porosity included hydrological regime, temperature and the interaction term between them (Table 2.2; averaged adjusted R^2=0.42). Root porosity was overall positively correlated with temperature. Higher temperature conditions corresponded with a higher root porosity under drained and waterlogged conditions. Under submerged conditions, however, the impacts of temperature were rather weak (Fig. 2.1). In our best model, the interaction term had the highest variance explained (17%) in comparison to hydrological regime (13%) and temperature (11%) (Fig. 2.4). Post-hoc comparisons suggested that the root porosity in submerged conditions was significantly higher than in waterlogged and drained conditions, while no significant difference was detected between waterlogged and drained conditions. Without the interaction term between temperature and hydrological regime, the best model would have included only habitat as the explanatory variable (see Table 2.2). This suggests that habitat type contains part of the underlying information as related to the hydrological conditions and temperature.

Table 2.2 Summary of the top five models fit to explain root porosity, root/shoot ratio and underwater photosynthetic rate, respectively. The models were ranked based on the averaged Akaike Information Criterion (AIC) weight, which was calculated for each candidate model as the average AIC weight across 1000 iterations. Proportion variance explained (average adjusted R^2) for the top models are also displayed

Wetland adaptive trait	Top models	Averaged AIC weight	Rank	Adjusted R^2
Root porosity	~Temperature * Hydrology	0.219	1	0.42
	~Temperature * Hydrology + Precipitation	0.097	2	
	~Temperature + Precipitation + Habitat	0.059	3	
	~Precipitation + Habitat + Life form	0.054	4	
	~Habitat	0.052	5	
Root/shoot ratio	~Temperature + Precipitation + Habitat	0.346	1	0.57
	~Temperature + Precipitation + Habitat + Life form	0.136	2	
	~Hydrology + Habitat	0.131	3	
	~Hydrology	0.064	4	
	~Life form	0.040	5	
Underwater photosynthetic rate	~Precipitation + Life form	0.245	1	0.41
	~Temperature * Precipitation + Life form	0.196	2	
	~Temperature + Precipitation + Life form	0.128	3	
	~Precipitation * Life form	0.112	4	
	~Temperature * Life form + Precipitation * Life form	0.080	5	

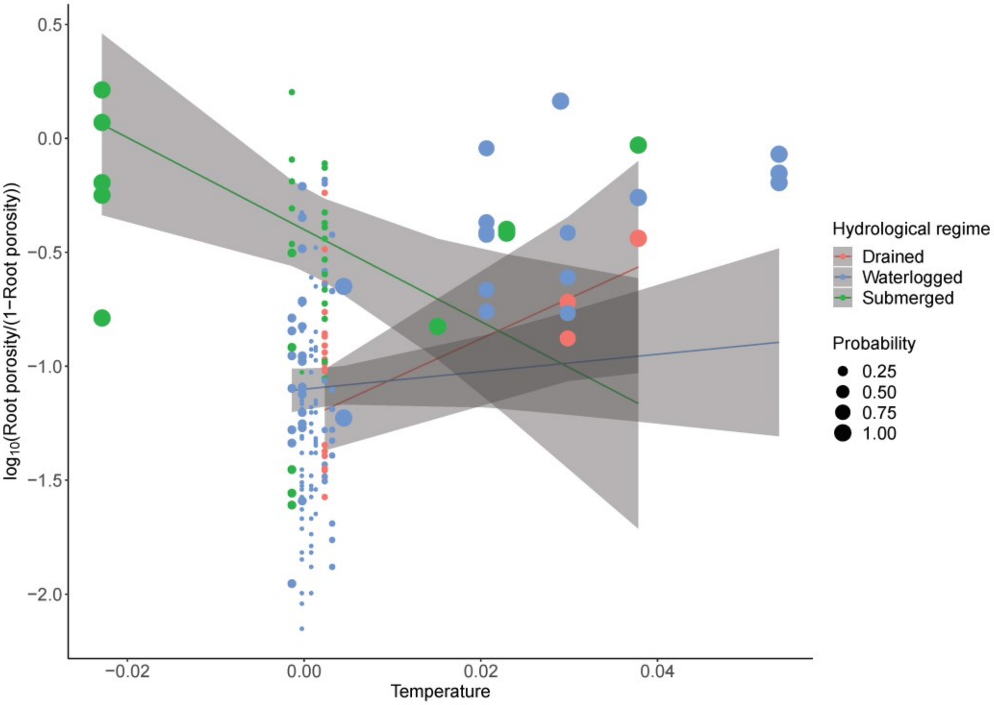

Figure 2.1 The relationship between logit transformed root porosity and temperature grouped by different hydrological regime. The regression line and the 95% confidence interval are obtained by taking the mean of the bootstrapped parameters of the best model for 1000 iterations, taking into account the biased spatial spread of the original data points. The bubble size indicates the sampling probability of each point in order to maintain a balanced spatial data structure (see details in method).

2.3.2 Quantifying the driving factors for root/shoot ratio trait

The best model for root/shoot ratio included temperature, precipitation and habitat type (Table 2.2; averaged adjusted R^2=0.57). Habitat type played the most important role in determining the root/shoot ratio (explaining 26% of the variance; Fig. 2.4). At higher temperatures, the root/shoot ratio was lower (Fig. 2.2), which indicates that in a warmer environment relatively more biomass is allocated to shoots (explaining 16% of the variance). The root/shoot ratio was also positively correlated with precipitation (explaining 15% of the variance). This suggests that at higher precipitation, more biomass is allocated to roots. Hydrological regime was potentially important driving factors, which could partially replace the explanatory power of bioclimatic variables. The second best model suggests that the root/shoot ratio varied across different plant life forms (Table 2.2).

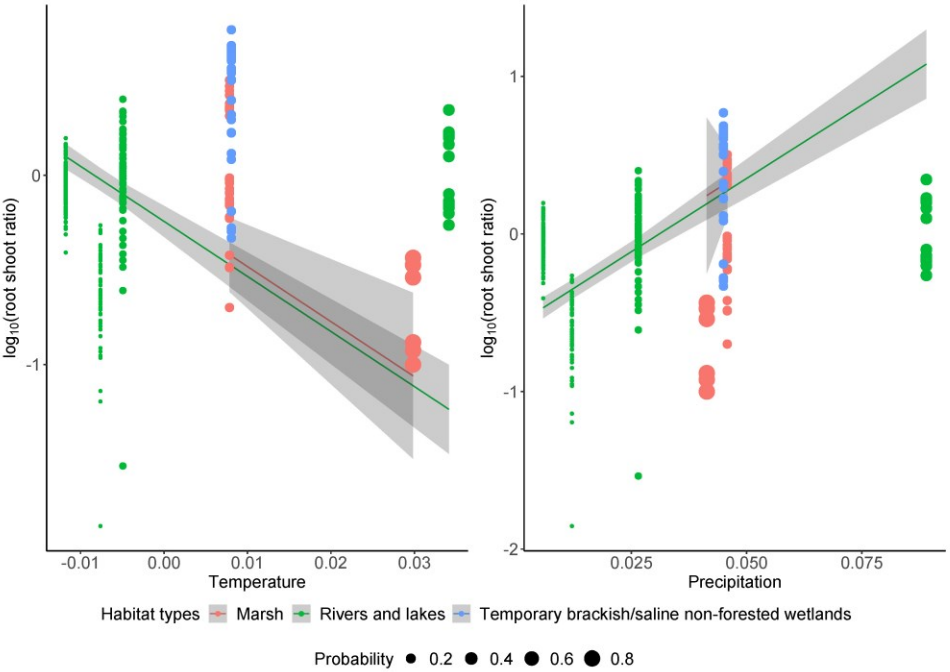

Figure 2.2 The relationship between $\log_{10}$-transformed root/shoot ratio and the bioclimatic variables (temperature left, precipitation right) grouped by different habitat types. The regression line and the 95% confidence interval were obtained by taking the mean parameters of the best model across 1000 resampled dataset, taking into account spatial bias in the original data points (see methods). Regression lines represent marginal estimates and include the mean value of the other variable(s) in the model. Points indicate observed values. We note the lack of an environmental gradient in the data from temporary brackish/saline non-forested wetlands, and the overall interaction effects may therefore have been underestimated. The bubble size indicates the sampling probability of each point in order to maintain a balanced spatial data structure (see details in method).

2.3.3 Quantifying the driving factors for underwater photosynthetic rate

The best model for underwater photosynthetic rate included precipitation and the plant life form (Table 2.2; adjusted R^2=0.41). The precipitation-related bioclimatic variables positively affected underwater photosynthetic rate (Fig. 2.3), explaining 22% of the variance (Fig. 2.4). Plant life form explained 19% of the variance. The TukeyHSD test suggested that the submerged leaves of floating-leaved plants had a significantly higher underwater photosynthetic rate compared to the submerged leaves of emergent and grass life forms. This indicates a major advantage of floating-leaved plants over emergent plants and grasses in deep water.

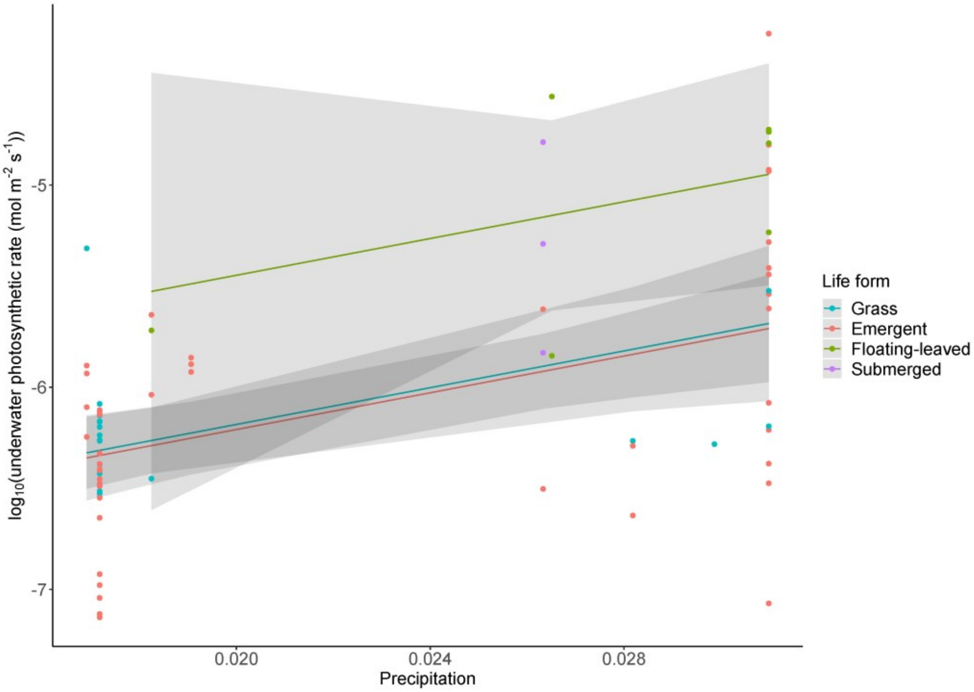

Figure 2.3 The relationship between $\log_{10}$-transformed underwater photosynthetic rate and precipitation grouped by different plant life forms, as estimated by the top-ranked model.

2.4 Discussion

The eco-physiology of wetland adaptive traits has been relatively well-studied, but the majority of this research has been limited to a small set of species under experimental conditions. A global analysis of the driving factors for wetland adaptive traits under natural environmental conditions is still missing. Using our newly compiled comprehensive wetland plant adaptive trait dataset, we explored the potential driving factors of three important wetland plant adaptive traits (root porosity, root/shoot ratio and underwater photosynthetic rate). Our models explained a substantial amount of the variation in the data, and revealed the importance of bioclimatic variables for all three traits – but for each trait in combination with different other driving factors, suggesting the existence of a myriad of wetland plant adaptive strategies. While based on a relatively small dataset, our study is a pilot exploration of available data of these wetland traits and attempts to bring wetland adaptive traits to the functional ecology context.

Among the four driving factors tested, bioclimatic variables were selected for all three wetland plant adaptive traits. Previous studies in terrestrial systems have shown that climatic variables not only drive the habitat conditions, but also various functional traits including the leaf economics spectrum (LES) (Wright *et al.*, 2005; van Ommen Kloeke *et al.*, 2012; Maire *et al.*, 2015), size-related traits (Wright *et al.*, 2017b), plant life form (Ordoñez *et al.*, 2009), and fine-root traits (Freschet *et al.*, 2017). Our results extend this consistent theme of climate impacts to a broader context; from plants in drier terrestrial ecosystems to wetlands. The importance of bioclimatic variables additionally implies that the functional structure of wetland plants can be further impacted in the context of global climate change. Besides the bioclimatic variables, we demonstrated that hydrological regime, habitat type and plant life form affected root porosity, root/shoot ratio and underwater photosynthetic rate, respectively (Fig. 2.4).

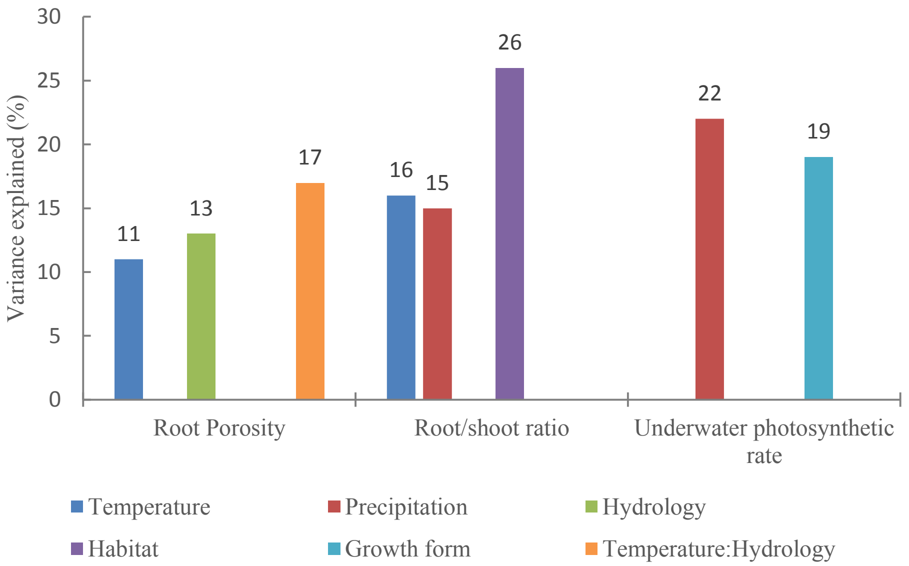

Figure 2.4 The contribution of each driving factor to the three wetland adaptive traits under study, as determined from the top-ranked models of each wetland adaptive trait.

When assessing the driving factors of the three wetland plant adaptive traits, we found that simple combinations of bioclimatic variables (expressed in PCA multivariate space), hydrological regime, habitat type and plant life form explained a substantial proportion of the trait expression (adjusted R^2 values range from 0.41 to 0.57). This proportion is similar to the filtering of non-wetland terrestrial traits by environmental conditions (Reich & Oleksyn, 2004; Wright *et al.*, 2005, 2017b; Maire *et al.*, 2015; Atkin *et al.*, 2015). The different drivers identified for different traits (Fig. 2.4) imply that the filtering mechanisms for wetland plant adaptive traits seem trait-specific, rather than related to a single driving factor selecting for all adaptive traits.

2.4.1 Ecological interpretation of the patterns in individual traits

Root porosity was driven by the temperature-related axis of bioclimatic variables. A positive response was detected under drained and waterlogged conditions. In warm areas, a higher temperature corresponds to a higher metabolic activity of plants resulting in a higher oxygen demand for transpiration and evapotranspiration. In those conditions, wetland plants need to develop a higher root porosity to ensure sufficient oxygen supply. Moreover, the oxygen solubility is reduced with increasing water temperature, amplifying the need for more porous tissues within roots for oxygen transport at higher temperature. In extremely cold habitats such as tundra areas where the soil water is frequently frozen, high root porosity might not be favourable since it results in reduced mechanical support (Striker *et al.*, 2007). In our model, the effect of air temperature on root porosity was much reduced under submerged conditions. This can be explained by the high specific heat capacity of water. When growing in submerged conditions, the atmospheric temperature has a limited impact on roots, whose temperature will be determined by relatively stable water temperatures. This suggests that future ecological modelling studies should include water temperature as a predictor variable for especially those submerged wetland plant species, for example, using global database of lake surface temperatures (Sharma *et al.*, 2015). The different impact of temperature in different hydrological regimes (as represented by the interaction term between temperature and hydrological regime) was the most important selected driving factor in the model, indicating the importance of these stabilising effects of water on the impact of air temperature. Without the inclusion of the interaction term in the model, the next-best model was represented by the single explanatory variable of habitat type. Habitat type (e.g. fens, forested/shrub wetlands, marshes) convey combined information regarding hydrological regime and climatic variables at each site. Previous greenhouse studies indicated a significant difference in root porosity between drained and waterlogged conditions (Justin & Armstrong, 1987). In our study, we did not detect such differences mainly because most variation in root porosity in our database occurred between species. Hence, impacts of hydrological regime on intraspecific variation were not picked up in our analysis.

Root/shoot ratio was driven by both temperature-related and precipitation-related axes of bioclimatic variables. At high temperature, plants need more oxygen to support the higher metabolic rates (Pedersen *et al.*, 2016). In this situation, it is advantageous for plants to maintain a lower root/shoot ratio, since this reduces the relative oxygen consumption in the root tissues, and at the same time, increases the gas transport from the atmosphere to the root system (van Bodegom *et al.*, 2005). Moreover, higher metabolic rates will ensure a faster biomass production, i.e., the capability to produce more shoot tissues when required by dynamic wetland conditions, which in turn, further reduces the root/shoot ratio. When it comes to forests, it has been found that low temperature induces a higher proportion of root biomass in adaptation to low available nutrient supply and limited soil solution movement (Poorter *et al.*, 2012; Reich *et al.*, 2014). While a matching case study in wetland is still lacking, our results indicate a similar pattern may exist here, albeit associated with a different mechanism.

In terrestrial conditions, more precipitation usually leads to a decrease in root/shoot ratio with increasing precipitation (Schenk & Jackson, 2002; Poorter *et al.*, 2012). In contrast, our model suggested an increase in root/shoot ratio with increasing precipitation. These contrasting patterns for non-wetland terrestrial and wetland environments are presumably related to the extent of water limitation - much less severe in the latter, and suggest potentially varying mechanisms driving biomass allocation between belowground and aboveground tissues. In wetland systems, water excess through precipitation and associated changes to submergence leads to limitations in oxygen availability. In contrast, in non-wetland terrestrial ecosystems, precipitation alleviates the water limitation and allows plants to invest less in root tissues to acquire water.

The rate of underwater photosynthesis was also positively related to precipitation. This result agrees with a meta-analysis on the response of global terrestrial ecosystems to precipitation (Wu *et al.*, 2011), although here the mechanism involved may be different. In our study, the impact of precipitation was stronger for underwater leaves of some life forms (floating-leaved and grass) than those of others (emergent and submerged plants), as indicated by the confidence interval of each life form in Fig. 2.3. We speculate that wetland plants in areas with more precipitation generally are more adapted to frequent flooding events, and therefore have a higher underwater photosynthetic rate. Another potential explanation for this pattern is that temporal wetlands generally differentiate from non-temporal wetlands by maximum water depth and sediment materials. The strategy of plants in coping with seasonal floods is anaerobic dormancy (a reduction of metabolic rates), and therefore do not need to maintain an optimum photosynthetic rate when fully submerged (Voesenek *et al.*, 2004). This reasoning should be confirmed by further studies, as it is currently based on relatively few observations.

Interestingly, for underwater photosynthetic rate, temperature was not selected in the top model. This contrasts with studies of terrestrial plants, where temperature is an important driver for photosynthesis (Wu *et al.*, 2011; Yamori *et al.*, 2014). Again, the high specific heat capacity of water compared to air, and resulting dampened temperature fluctuations in inundated conditions may explain the limited impact of air temperature on underwater photosynthetic rate. Inclusion of observations in tropical regions (the underwater photosynthesis studies included in our analysis were all from temperate regions) may reveal other trends, since warm atmospheric temperatures (e.g. as high as 38°C) can diminish the underwater photosynthetic rates of plants in shallow pools when the small volume of water heats up owing to solar radiation (Pedersen *et al.*, 2016). We also found that underwater leaves of floating-leaved and submerged plants had on average a higher underwater photosynthetic rate than the underwater leaves of emergent and grass life forms. Floating-leaved and submerged plants have evolved many traits (e.g. leaves with thinner cuticle, enhanced utility of HCO_3^-) in adapting to submerged conditions, which may help maintain underwater photosynthesis (Rascio *et al.*, 1999; Colmer *et al.*, 2011; Iversen *et al.*, 2019). Many floating-leaved and submerged plants are also able to use the CO_2 from sediment to facilitate underwater photosynthesis (Singer *et al.*, 1994; Colmer, 2003b; Winkel & Borum, 2009).

2.4.2 Ecological implications

While bioclimatic drivers were important for all three adaptive traits, different combinations of drivers were identified for each wetland adaptive trait. We hypothesize that a variety of driving mechanisms affect the expression of different wetland adaptive traits on a global scale. We therefore expect to see a decoupled pattern between some of the wetland adaptive traits. Along with the evidence that some wetland adaptive traits tend to be orthogonal to leaf economics spectrum traits (Pan *et al.*, 2019), our current results support the idea that these three (and potentially others as well) wetland adaptive traits are relatively cheap to develop, and therefore are not to a large extent constrained by other adaptive traits or by leaf economics spectrum traits.

Wetland adaptive traits are the premise of survival under the adverse conditions present in wetlands (Voesenek & Bailey-Serres, 2015; Moor *et al.*, 2017; Pan *et al.*, 2019). The identified environmental filters in wetlands select plants with suitable adaptive traits, along with other factors including soil fertility, light radiation, competition/facilitation in communities (Luo *et al.*, 2016). Disentangling the driving factors for wetland adaptive traits not only provides a theoretical basis for understanding the overall wetland plant functioning and strategy, but also creates new perspectives on modelling global wetland plant distributions and community structure (Lenssen *et al.*, 2000; Visser *et al.*, 2000a; Willby *et al.*, 2001). These results can be included in dynamic global vegetation models (DGVMs) (van Bodegom *et al.*, 2012, 2014), which can in turn contribute to a better prediction of ecosystem processes such as those related to carbon, nitrogen and water cycles. For example, current global methane models, such as CLM4Me and LPJ-WHyMe, have considered the effect of plants only to constant plant functional types (PFTs) parameters (Wania *et al.*, 2010; Riley *et al.*, 2011). The results of this study may improve global methane model accuracy by quantifying the continuous trait expression on the varying environmental gradients.

Our study has shown that bioclimatic variables explain a great deal of variation in wetland plant functional traits on a global scale, however, our analysis was limited by the number of species, sites, variables and traits studied. Future studies should seek to expand the dataset that we have developed, which is freely available (see Data Accessibility Statement) and curated by the correspondence author. Many of the traits are relatively cheap to measure. Therefore, contributions of only a few days of work by a global network of wetland scientists would easily and greatly expand the database as a common resource for all.

2.5 Conclusions

Understanding the potential drivers of wetland adaptive traits is a fundamental step towards future studies on wetland adaptive strategies and provides a reference for ecological modelling of wetland plants' distributions. Among the drivers we tested, bioclimatic variables are important driving factors for all three wetland plant adaptive traits. This finding extends the climatic variables as universal drivers of trait expression from non-wetland terrestrial ecosystems to wetlands. Perhaps more importantly, we show different drivers for different adaptive traits, which implies that each adaptive trait is most appropriate for a specific set of wetland conditions, and that there is not one common set of traits that best succeed in wetland conditions. This also suggests that there are a multitude of wetland plant strategies with potentially varied ecological mechanisms involved. Therefore, future wetland plant studies should consider a more complete set of driving factors to effectively bring wetland adaptive traits into the broad context of functional ecology.

2.6 Acknowledgements

The establishment of the wetland trait database was first discussed and started in 2008 at the Vegfunction WG39 which was funded by ARC-NZ Research Network for Vegetation

Function. We would like to thank all additional contributors to this original workshop, including Paul Adam (U New South Wales, Sydney, AU), William Armstrong (U Hull, Kingston upon Hull, UK), Jean Armstrong (U Hull, Kingston upon Hull, UK), Margaret Brock (U New England, Armidale, USA), George Ganf (U Adelaide, Adelaide, AU), Irving A. Mendelssohn (Louisiana State U, Baton Rouge, USA), Eliska Rejmánkova (U California, Davis, USA), Brian Sorrell (Aarhus U, Aarhus, DK), and Evan Weiher (U Wisconsin, Eau Claire, USA). We especially thank William Armstrong for his many insightful comments. Yingji Pan is grateful for support from the China Scholarship Council (Grant No. 201606140037).

2.7 Authors' Contributions

PvB initialized this research; YP, PvB and EC designed and planned the research. YP and PvB compiled the data with inputs from all co-authors. YP ran all analyses with inputs from all co-authors. YP, PvB and EC wrote the first drafts of the manuscript that was further improved by inputs from all co-authors, and finalized by YP. All authors contributed critically to the drafts and gave final approval for publication.

2.8 Data Accessibility Statement

Data deposited in the Dryad Digital Repository: https://doi.org/10.5061/dryad.7h44j0zqx, (Pan *et al.*, 2020)

2.9 Supporting Information

Appendix 2A

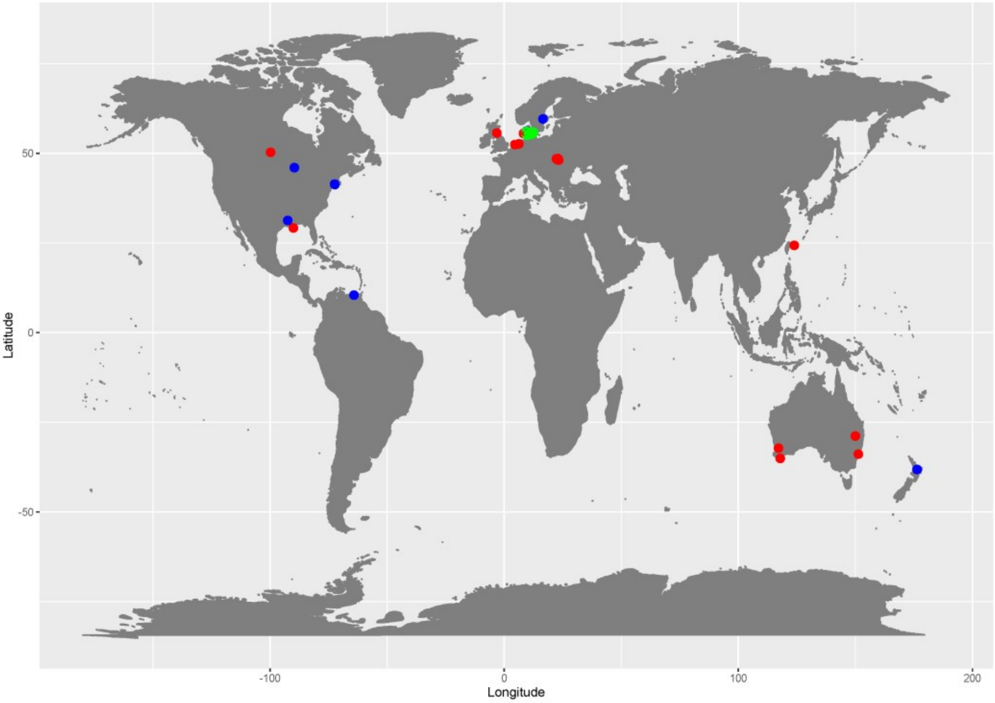

Figure 2S1 The location of the sampling sites. The root porosity, root/shoot ratio and underwater photosynthetic rate are presented in red, blue and green dots, respectively.

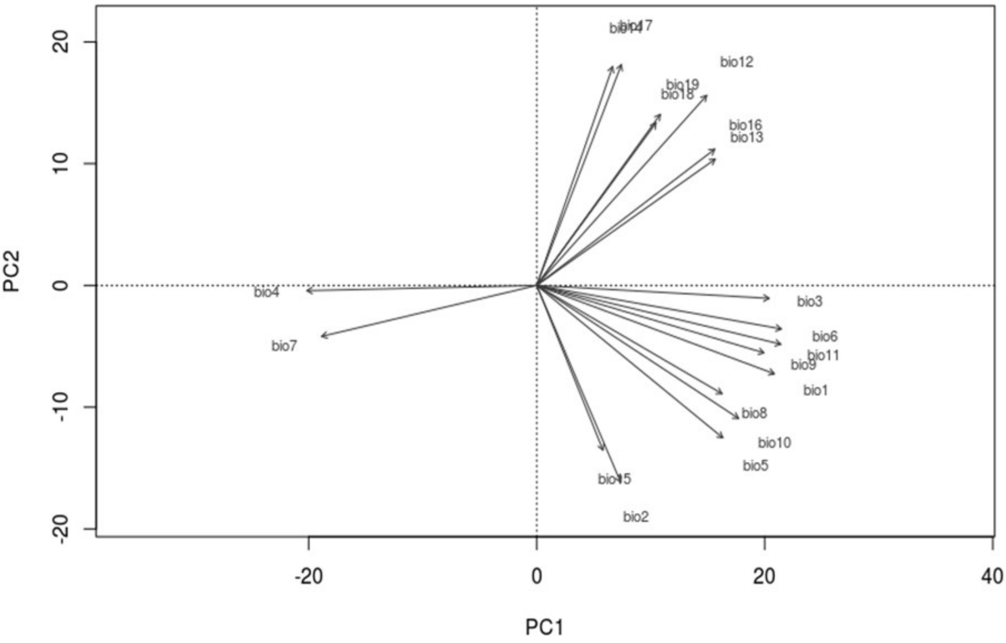

Figure 2S2 The PCA1 and PCA2 axes (explained 51.8% and 25.8% of total variance, respectively) of the 19 bio-climatic variables. (Bio1 = Annual Mean Temperature; Bio2 = Mean Diurnal Range (Mean of monthly (max temp - min temp)); Bio3 = Isothermality (Bio2/Bio7) (*100); Bio4 = Temperature Seasonality (standard deviation *100); Bio5 = Max Temperature of Warmest Month; Bio6 = Min Temperature of Coldest Month; Bio7 = Temperature Annual Range (Bio5-Bio6); Bio8 = Mean Temperature of Wettest Quarter; Bio9 = Mean Temperature of Driest Quarter; Bio10 = Mean Temperature of Warmest Quarter; Bio11 = Mean Temperature of Coldest Quarter; Bio12 = Annual Precipitation; Bio13 = Precipitation of Wettest Month; Bio14 = Precipitation of Driest Month; Bio15 = Precipitation Seasonality (Coefficient of Variation); Bio16 = Precipitation of Wettest Quarter; Bio17 = Precipitation of Driest Quarter; Bio18 = Precipitation of Warmest Quarter; Bio19 = Precipitation of Coldest Quarter).

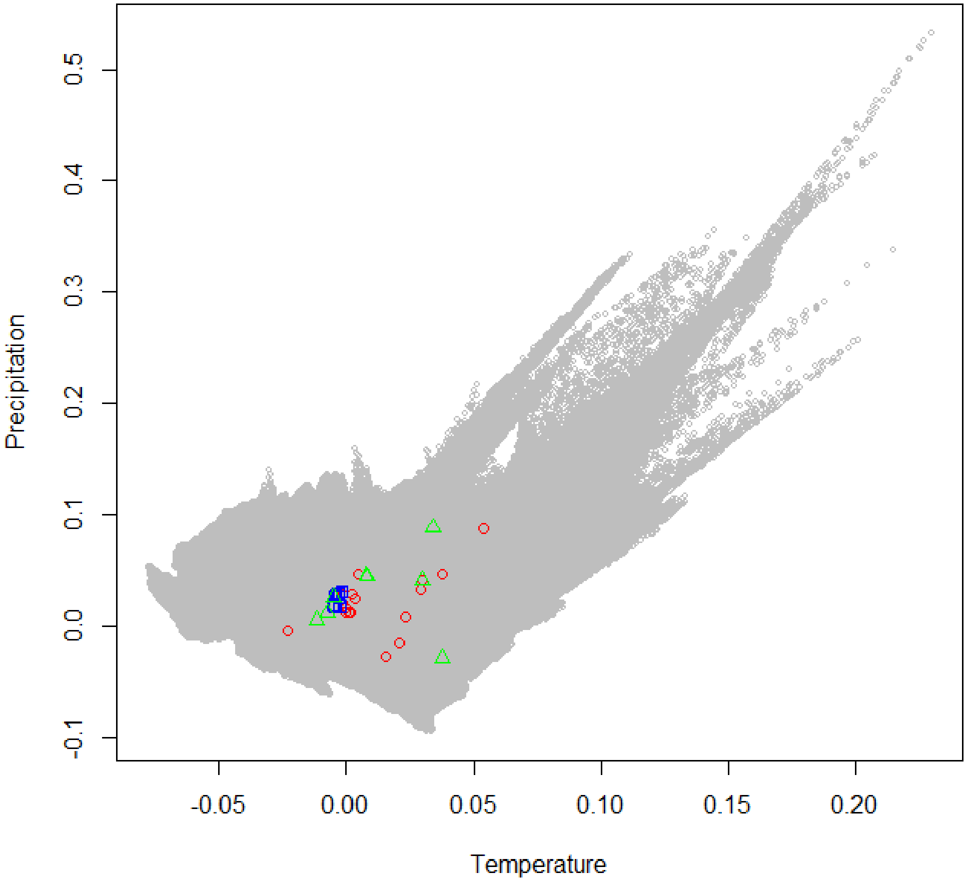

Figure 2S3 The layout of the sampling points on the global 19 bio-climatic variables PCA1 (temperature) & PCA2 (precipitation) surface. Grey circles indicate the bioclimatic environment of the global terrestrial surface at 2.5 minutes. The coloured circles indicate the locations in this same climate space of the measurements of root porosity (red circles), root/shoot ratio (green triangles) and underwater photosynthetic rate (blue squares) contained within the newly developed wetlands trait database.

Appendix 2B

Ramsar wetland type classification

Under the Ramsar Convention, wetland types have been defined to provide a very broad framework to aid rapid identification of the main wetland habitats represented at each Ramsar site. Wetland type is identified for each site on the relevant Ramsar Information Sheet.

The codes used to define wetland types for Ramsar sites are based upon the Ramsar Classification System for Wetland Type as approved by Recommendation 4.7 and amended by Resolutions VI.5 and VII.11 of the Conference of the Contracting Parties.

Marine/Coastal Wetlands
A — Permanent shallow marine waters in most cases less than six metres deep at low tide; includes sea bays and straits.
B — Marine subtidal aquatic beds; includes kelp beds, sea-grass beds, tropical marine meadows.
C — Coral reefs.
D — Rocky marine shores; includes rocky offshore islands, sea cliffs.
E — Sand, shingle or pebble shores; includes sand bars, spits and sandy islets; includes dune systems and humid dune slacks.
F — Estuarine waters; permanent water of estuaries and estuarine systems of deltas.
G — Intertidal mud, sand or salt flats.
H — Intertidal marshes; includes salt marshes, salt meadows, saltings, raised salt marshes; includes tidal brackish and freshwater marshes.
I — Intertidal forested wetlands; includes mangrove swamps, nipah swamps and tidal freshwater swamp forests.
J — Coastal brackish/saline lagoons; brackish to saline lagoons with at least one relatively narrow connection to the sea.
K — Coastal freshwater lagoons; includes freshwater delta lagoons.
Zk(a) - Karst and other subterranean hydrological systems, marine/coastal

Inland Wetlands
L — Permanent inland deltas.
M — Permanent rivers/streams/creeks; includes waterfalls.
N — Seasonal/intermittent/irregular rivers/streams/creeks.
O — Permanent freshwater lakes (over 8 ha); includes large oxbow lakes.
P — Seasonal/intermittent freshwater lakes (over 8 ha); includes floodplain lakes.
Q — Permanent saline/brackish/alkaline lakes.
R — Seasonal/intermittent saline/brackish/alkaline lakes and flats.
Sp - Permanent saline/brackish/alkaline marshes/pools.
Ss - Seasonal/intermittent saline/brackish/alkaline marshes/pools.
Tp - Permanent freshwater marshes/pools; ponds (below 8 ha), marshes and swamps on inorganic soils; with emergent vegetation water-logged for at least most of the growing season.
Ts - Seasonal/intermittent freshwater marshes/pools on inorganic soils; includes sloughs, potholes, seasonally flooded meadows, sedge marshes.
U — Non-forested peatlands; includes shrub or open bogs, swamps, fens.
Va - Alpine wetlands; includes alpine meadows, temporary waters from snowmelt.
Vt - Tundra wetlands; includes tundra pools, temporary waters from snowmelt.
W — Shrub-dominated wetlands; shrub swamps, shrub-dominated freshwater marshes, shrub carr, alder thicket on inorganic soils.
Xf - Freshwater, tree-dominated wetlands; includes freshwater swamp forests, seasonally flooded forests, wooded swamps on inorganic soils.
Xp - Forested peatlands; peatswamp forests.

Y — Freshwater springs; oases.
Zg - Geothermal wetlands
Zk(b)- Karst and other subterranean hydrological systems, inland

Human-made wetlands
1 — Aquaculture (e.g., fish/shrimp) **ponds**
2 — Ponds; includes farm ponds, stock ponds, small tanks; (generally below 8 ha).
3 — Irrigated land; includes irrigation channels and rice fields.
4 — Seasonally flooded agricultural land (including intensively managed or grazed wet meadow or pasture).
5 — Salt exploitation sites; salt pans, salines, etc.
6 — Water storage areas; reservoirs/barrages/dams/impoundments (generally over 8 ha).
7 — Excavations; gravel/brick/clay pits; borrow pits, mining pools.
8 — Wastewater treatment areas; sewage farms, settling ponds, oxidation basins, etc.
9 — Canals and drainage channels, ditches.
Zk(c) - Karst and other subterranean hydrological systems, human-made

Our wetland habitat types follow the Ramsar Convention (Ramsar Convention Secretariat, 2013, see details below) as well as the guidance given by the United States Environmental Protection Agency (EPA, https://www.epa.gov/wetlands/classification-and-types-wetlands#marshes). We summarized the Ramsar wetland type classification system as:

Marine/Coastal wetlands
1. Estuary: A, B, C, D, F, Zk(a)
2. Intertidal wetland: E, G, H, J, K
3. Mangrove swamps: I

Inland wetlands
4. Rivers and lakes: L, M, N, O, P, Q
5. Brackish and saline inland wetlands: R, Sp, Ss
6. Permanent non-forested wetlands: Tp, U, Y
7. Temporary non-forested wetlands: Ts, Va, Vt
8. Permanent forested wetlands: W, Xf, Xp

Human-made wetlands
9. Artificial waterbodies: 1-9, Zk(c)

We further divided the "Permanent non-forested wetlands" into "marsh", "bog" and "fen" according to the EPA guidance. The "swamps" defined in EPA guidance should be considered as "Permanent forested wetlands". The definition given by EPA for "marsh", "bog" and "fen" is as:

Marsh*: Marshes are defined as wetlands frequently or continually inundated with water, characterized by emergent soft-stemmed vegetation adapted to saturated soil conditions. There are many different kinds of marshes, ranging from the prairie potholes to the Everglades, coastal to inland, freshwater to saltwater. All types receive most of their water from surface water, and many marshes are also fed by groundwater. Nutrients are plentiful and the pH is usually neutral leading to an abundance of plant and animal life.

Bog**: Bogs characterized by spongy peat deposits, acidic waters and a floor covered by a thick carpet of sphagnum moss. Bogs receive all or most of their water from precipitation rather than from runoff, groundwater or streams. As a result, bogs are low in the nutrients needed for plant growth, a condition that is enhanced by acid forming peat mosses.

Fen***: Fens, are peat-forming wetlands that receive nutrients from sources other than precipitation: usually from upslope sources through drainage from surrounding mineral soils and from groundwater movement. Fens differ from bogs because they are less acidic and have higher nutrient levels. Therefore, they are able to support a much more diverse plant and animal community. These systems are often covered by grasses, sedges, rushes and wildflowers. Some fens are characterized by parallel ridges of vegetation separated by less productive hollows.

Table 2S1 The summary of the habitat types used in the analysis.

Habitat types in our analysis	Habitat types defined in Ramsar Convention and EPA guidance
Estuary	A, B, C, D, F, Zk(a)
Intertidal wetland	E, G, H, J, K
Mangrove swamps	I
Rivers and lakes	L, M, N, O, P, Q
Brackish and saline inland wetlands	R, Sp, Ss
Permanent non-forested wetlands	Tp, U, Y
Temporary non-forested wetlands	Ts, Va, Vt
Permanent forested wetlands	W, Xf, Xp
Artificial waterbodies	1-9, Zk(c)
Marsh	*
Bog	**
Fen	***

Chapter 3

The leaf economics spectrum revisited: global trait patterns in wetlands

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Abstract

The leaf economics spectrum (LES) describes consistent correlations among a variety of leaf traits that reflect a gradient from conservative to acquisitive plant strategies. So far, whether the LES holds in wetland plants at a global scale has been unclear. Using data on 365 wetland species from 151 studies, we found that wetland plants in general show a shift within trait space along the same common slope as observed in non-wetland plants, with lower leaf mass per area, higher leaf nitrogen and phosphorus, faster photosynthetic rates, and shorter leaf life span compared to non-wetland plants. We conclude that wetland plants tend to cluster at the acquisitive end of the LES. The presented global quantifications of the LES in wetland plants enhance our understanding of wetland plant strategies in terms of resources acquisition and allocation, and provide a stepping stone to developing trait-based approaches for wetland ecology.

3.1 Introduction

During the past two decades, trait-based ecology has advanced considerably. The leaf economics spectrum (LES) is an important component thereof. The LES provides convincing evidence of a consistent and continuous relationship among the leaf economics traits, reflecting a gradient of slow (conservative) to fast (acquisitive) strategies in terms of investment and use of nutrients and other resources (Reich *et al.*, 1997; Shipley *et al.*, 2016). The LES has been shown to be present across different plant life forms and varied habitat types at a global scale and to a large extent independent of climate (Reich *et al.*, 1997; Wright *et al.*, 2004). Along the LES, species with higher leaf mass per area (LMA) generally have a longer leaf life span (LL), but a lower leaf nitrogen content (leaf N, wt/wt), and lower photosynthetic rates (A_{mass} or A_{area}). This conservative strategy usually prevails in less fertile habitats. On the other hand, species with lower LMA, shorter LL, higher leaf N and photosynthetic rate have a faster return on investment of resources, commonly coinciding with nutrient-rich areas. Such trait-trait coordination in LES traits may be caused by underlying physiological and structural trade-offs (Onoda *et al.*, 2017).

Studies on trait-trait relationships, including those on LES, have focused mainly on non-wetland terrestrial plants from a variety of ecosystems, such as forests or grasslands (Dray *et al.*, 2014; Onoda *et al.*, 2017) or on global analyses (Wright *et al.*, 2004; Diaz *et al.*, 2016). However, whether the general LES also exists in global wetland ecosystems still remains unclear. This gap prevails despite the fact that leaf economics traits have been widely measured in wetland plants to study local plant functioning, community structure, growth and competition (Güsewell, 2002).

A better understanding of trait-based relationships in wetlands is profoundly needed in light of the important ecosystem services provided by wetlands, including their role as the major carbon sink at a global scale (Page & Baird, 2016). Important ecological processes in wetlands such as methane emission and denitrification are linked to wetland plant functional traits (Sutton-Grier & Megonigal, 2011; Alldred & Baines, 2016). LES traits in wetlands are likely to play a role in these ecosystem processes and services (Sutton-Grier *et al.*, 2013; Moor *et al.*, 2017). While the wide fertility gradient across different wetland types theoretically provides a natural gradient for the expression of LES from the acquisitive to conservative strategies (Pan *et al.*, 2019), additional constraints induced by adverse environmental conditions in wetlands compared to non-wetland systems mean that it cannot be taken for granted that LES traits will show similar patterns.

The varied environmental stressors unique to wetland ecosystems constrain plants that inhabit these systems. For example, intermittent/permanent flooding causes altered biogeochemical processes and the production of phytotoxic compounds such as ferrous iron (Fe^{2+}) and sulphide (H_2S, HS^-,S^{2-}) in the substrates, as well as a less efficient way of producing ATP in cells experiencing an O_2 deficit (Lambers *et al.*, 2008). In addition, reactive oxygen species (ROS), which can cause cellular macromolecule and membrane damage, accumulate in plant tissues especially upon return to aerobic conditions after flooding (Colmer & Voesenek, 2009). To survive in such adverse environment, wetland plants have developed a suite of adaptive strategies (Colmer & Voesenek, 2009). Whether the LES also exists in wetlands depends, to a large extent, on whether the prevalent adaptive strategies of plants to environmental stressors are generally costly or cheap (Pan *et al.*, 2019). If adaptations are cheap, the LES should be unaffected and similar to non-wetland ecosystems. But if adaptive traits are costly, the LES should be shifted along the same axes (or even shifted in trait space entirely) to compensate this cost (Pan *et al.*, 2019). Moreover, leaf mass per area (LMA, one of the LES traits) seems to also be directly involved in flooding tolerance of wetland plants (Douma *et al.*, 2012), which may also lead to deviations within the LES.

Therefore, our research question is: ***What is the global leaf economics spectrum in wetlands? And how does it differ from that of non-wetland ecosystems?*** We hypothesize that wetland plants in general follow the LES strategies with fast-return species usually having lower LMA with increased leaf nutrient (N and P) content (wt/wt). This would naturally lead to faster photosynthesis in the day and higher dark respiration rate in the night. Assuming the trade-off between LMA and leaf longevity that exists in non-wetland plants (Wright *et al.*,

2004) also applies to wetlands, a lower LMA would result in a shorter leaf life span. Despite this general pattern, we also expect that the cost of developing the adaptive traits might affect the trait-trait relationships of leaf economics traits, and consequently shift the overall LES trait pattern in wetlands.

To test these hypotheses, we collected the LES traits measured in 365 wetland species of 184 families from 151 studies of both published and unpublished sources from a global scale. These wetland species are mainly from 10 wetland habitat types (including, as adapted from the Ramsar Convention (Ramsar Convention Secretariat, 2013), artificial waterbodies, bogs, estuaries, fens, forested/shrub wetlands, mangrove swamps, marsh, rivers and lakes, temporary brackish/saline non-forested wetlands and temporary non-forested wetlands; see details in Appendix 2B). These habitat types occupy different positions along the gradients of two dominant drivers: hydrological regime (flooding depth and duration) and fertility (from oligotrophic to eutrophic) (Keddy, 2010). The wetland plant species analysed in this study represent a full spectrum of plant characteristics and belong to eight life form categories (emergent, floating-leaved, grass, isoetid, seagrass, sedge, shrub/tree and submerged). To take the effect of submergence on wetland plants into account, we carefully separated traits measured on plants of which only the root-zone or part of the stem was flooded of which tissues emergent above the water table were measured (hereafter called *waterlogged wetland plants*) vs. traits measured on plant tissues that were submerged (hereafter called *submerged wetland plants*).

By comparing these trait expressions with an extensive published dataset on non-wetland plants, we examined the trait-trait relationships of LES traits in wetland vs. non-wetland plants. Our global analyses on the LES in wetlands provide a new perspective on the acquisition and turnover of resources of plants under stressful wetland conditions at a global scale. The results provide the first step towards a leaf trait-based ecology in wetlands. In this way, we can better understand the strategies and functioning of wetland plants from a resource investment/gain perspective (Pan *et al.*, 2019). Therefore, studying LES traits in wetlands will not only extend our understanding of global plant strategies on resource acquisition and investment, but also give insight into wetland plant strategies and how these strategies are linked to ecosystem functioning (Moor *et al.*, 2017; Pan *et al.*, 2019).

3.2 Materials and Methods

3.2.1 Data compilation

We defined wetland plants as plants that mainly occur in (or are exposed to) wetland habitats as described by the Ramsar Convention (Ramsar Convention Secretariat, 2013). We collected leaf economics traits for wetland plants on a global scale including those plants exposed to intermittent/permanent wetland conditions (waterlogged or flooded) from both field and experiment measurements. The wetland plant leaf economics trait dataset was compiled based on a systematic search in Web of Science and Google Scholar (last updated on the 5th June 2018). The literature search included permutations of the following keywords: wetland plants, marsh plant, bog plant, isoetid, aquatic plants, macrophytes, submerged plants, floating-leaved plants, emergent plants, mangroves, leaf economics traits, leaf economics spectrum, leaf nitrogen, leaf phosphorus, SLA, LMA, leaf life span, photosynthetic rate, underwater photosynthetic rate, dark respiration rate. Additionally, our network of wetland experts from around the world contributed recommendations for possible literature that we had overlooked. Finally, we added unpublished data of our own and of our network. We did not include data from other trait databases that are dominated by terrestrial records, including TRY, because the few records available for wetland plants in these databases do not have a sufficiently detailed habitat description that would allow the differentiation between waterlogged and submerged required for our analysis.

We followed the nomination system in The Plant List (http://www.theplantlist.org) to unify all plant synonyms names from the original references to a unique and consistent accepted name.

We supplemented the trait observations in our database with Ellenberg moisture indicator values. The Ellenberg moisture indicator is a classic index which generally reflects the plants' adaptation/acclimation to habitat wetness. Plant species can be categorized into 12 levels from those occupying very dry habitats (level 1) to strictly aquatic plants (level 12) (Ellenberg, 1988). For the current meta-analysis, we selected plant species with Ellenberg moisture value > 7 to represent wetland plants, as described in detail in Appendix 3B. For these species, we selected records of the six LES traits (leaf nitrogen, leaf phosphorus, leaf dry mass per unit area, leaf life span, photosynthetic rate, and dark respiration rate). We took trait values for the same six traits for non-wetland plant traits (of 1569 species) from the GLOPNET database for comparison (Wright *et al.*, 2004). For a consistent analysis of trait-trait trade-offs, we expressed all leaf economics traits on a mass basis. Mass-based and area-based traits can be interconverted via a division by LMA. The mean value for each trait of each species was used (using the median did not alter the interpretation of the results, data not shown). We used species-mean values to attain a sufficient number of trait-trait combinations for a given species. We assume that the trait observations used for calculating the species-mean values were representative for the environmental/growth conditions in which the species occurs. Possible uncertainty in species trait mean values (for example due to intra-specific variation) will then result in noise in trait-trait relationships. In total, 365 wetland species of 184 families from 151 studies were compiled and analysed, comprising the largest dataset on wetland plant traits to our knowledge. A map of the sampling sites with accurate spatial location information can be found in Appendix 3A. The species are from varied life forms, including grasses, sedges, seagrasses, shrubs/trees, emergent, floating-leaved, isoetid, and submerged plants. Traits of most (308) species had been measured at waterlogged conditions, with submerged measurements being available for 75 species.

3.2.2 Statistical analysis

First, the slope and its associated coefficient of determination (R^2) of each trait pair within the six LES traits of waterlogged and submerged wetland plants at the species level was calculated by a standardized major axis (SMA) analysis (Warton *et al.*, 2012). The slopes and R^2-values were compared to those of trait-trait relationships of non-wetland plants as derived from the GLOPNET (Wright *et al.*, 2004). The evaluation was based on the comparison between waterlogged wetland plants and submerged wetland plants, with non-wetland plants, respectively.

We tested each trait-trait relationship within the above-mentioned six LES traits for deviations between wetland and non-wetland plants. No test was run for the associations between leaf life span and LMA, photosynthetic rate and dark respiration rate of submerged wetland plants due to too few data points. In our SMA analysis we conducted three tests, one to evaluate differences in slopes (i.e. steeper or shallower trait-trait relationships between wetland vs. non-wetland plants), a second to assess shift along slopes (i.e. a more predominant position of wetland plants on either the conservative or acquisitive end of LES), and a third to assess whether trait associations of wetland and non-wetland plants can be characterized as having elevated intercepts, resulting in parallel slopes (suggesting a specific trait would be more -or less- costly in wetland conditions) (Warton *et al.*, 2012):

Test A: sma(y~x*groups) tests for differences in slopes fitted for different groups

Test B: sma(y~x+groups, shift=T) tests for a shift along the common slope

Test C: sma(y~x+groups) tests for parallel slopes between groups

A significant difference in slope (Test A) implies a difference in the direction and location of the relationship in trait space. Since the location and direction of lines with different slopes are not comparable (Warton *et al.*, 2006), tests B and C were only run if there was no significantly different slope detected in Test A. If all three tests were non-significant, we conclude that wetland and non-wetland plants have similar trait-trait relationships.

The P-value is strongly depended on sample size, and it does not measure the size of an effect or the importance of a result (Wasserstein *et al.*, 2019). In this study, we set a rather conservative P-value threshold ($P<0.01$) for our tests. This was done to help reducing type I errors and to ensure that the most ecologically relevant relationships (with a reasonable effect size) were detected in these relatively large datasets (Nakagawa & Cuthill, 2007).

The statistical analysis used R software (R Core Team, 2018). The major axes analysis was conducted with the sma() and ma() function in the smatr package (Warton *et al.*, 2012).

3.3 Results

The overall trait-trait relationships of wetland plants showed similar trends as those among non-wetland plants in terms of the slope directions. Among the significant trait-trait relationships, five out of seven relationships of waterlogged plants had a lower R^2 than those of non-wetland plants (such as leaf P vs. leaf N and leaf N vs. LMA), while three out of four relationships for submerged plants had a lower R^2 than those of non-wetland plants (Table 3.1). In combination, these results indicate weaker trait-trait relationships between wetland plant traits than corresponding relationships among non-wetland plants (Table 3.1, lower left section), and suggests that wetland plants are less constrained within the LES with larger trait variation. A summary of the results of all standardized major axis (SMA) analyses is given in Table 3.2.

Table 3.1 Bivariate relationships between leaf traits of the Leaf Economics Spectrum. The bivariate relationships between including leaf life span (LL), leaf dry mass per unit area (LMA), photosynthetic rate (A_{mass}), leaf nitrogen (leaf N, wt/wt), leaf phosphorus (leaf P,wt/wt), dark respiration rate (R_{mass}), for wetland plants and with comparisons given for non-wetland plants. Standardized major axis (SMA) slopes with 95% confidence interval are given in the upper-right section of the table (y variable in column 1, x variable in row 1); coefficients of determination (R^2) of SMA and sample sizes are given in the lower-left section of the matrix. The statistical properties calculated respectively for waterlogged and submerged wetland plants are in bold, and for non-wetland species from the GLOPNET database (Wright *et al.*, 2004) in italic. The asterisk indicates significant correlation at $P<0.01$, see Methods for more information.

	log LMA	log N_{mass}	log P_{mass}	log A_{mass}	log R_{mass}	log LL	Plant type
log LMA		**-1.65 (-1.86, -1.46)**	**-0.99 (-1.15, -0.85)**	**-0.75 (-0.86, -0.66)**	**-0.45 (-0.89, -0.22)**	**0.79 (0.61, 1.04)**	**Waterlogged**
		-0.76 (-1.00, -0.58)	**-1.34 (-2.07, -0.87)**	**-0.50 (-0.65, -0.39)**	**1.19 (0.69, 2.06)**	--- --- ---	**Submerged**
		-1.26 (-1.31, -1.22)	*-0.83 (-0.88, -0.79)*	*-0.77 (-0.81, -0.73)*	*-0.96 (-1.05, -0.87)*	*0.62 (0.58, 0.67)*	*Non-wetland*
log N_{mass}	**0.33* (n=178)**		**0.63 (0.57, 0.69)**	**0.50 (0.42, 0.60)**	**0.42 (0.21, 0.85)**	**-0.53 (-0.82, -0.34)**	**Waterlogged**
	0.23* (n=42)		**0.65 (0.50, 0.85)**	**0.77 (0.53, 1.12)**	**1.68 (0.95, 2.97)**	**-0.59 (-14.95, -0.02)**	**Submerged**
	0.57 (n=1322)*		*0.66 (0.63, 0.69)*	*0.60 (0.57, 0.64)*	*0.70 (0.64, 0.76)*	*-0.48 (-0.51, -0.45)*	*Non-wetland*
log P_{mass}	**0.17* (n=135)**	**0.31* (n=264)**		**0.79 (0.64, 0.99)**	**-0.65 (-1.31, -0.32)**	**-0.77 (-1.25, -0.47)**	**Waterlogged**
	0.12 (n=21)	**0.31* (n=41)**		**0.63 (0.25, 1.62)**	**1.10 (0.44, 2.80)**	**-1.10 (-27.74, -0.04)**	**Submerged**
	0.52 (n=561)*	*0.70* (n=555)*		*0.96 (0.83, 1.09)*	*1.12 (0.94, 1.33)*	*-1.00 (-1.14, -0.88)*	*Non-wetland*
log A_{mass}	**0.59* (n=91)**	**0.27* (n=90)**	**0.12* (n=72)**		**0.96 (0.50, 1.84)**	**-1.41 (-2.31, -0.86)**	**Waterlogged**
	0.56* (n=31)	**0.49* (n=18)**	**0.11 (n=7)**		**-2.08 (-3.54, -1.22)**	--- --- ---	**Submerged**
	0.51 (n=579)*	*0.54* (n=537)*	*0.19* (n=171)*		*1.11 (1.02, 1.20)*	*-0.74 (-0.78, -0.70)*	*Non-wetland*
log R_{mass}	**0.03 (n=11)**	**0.02 (n=11)**	**0.13 (n=10)**	**0.14 (n=11)**		**1.89 (0.30, 11.80)**	**Waterlogged**
	0.00 (n=16)	**0.27 (n=12)**	**0.13 (n=7)**	**0.05 (n=16)**		--- --- ---	**Submerged**
	0.46 (n=228)*	*0.58* (n=221)*	*0.37* (n=84)*	*0.61* (n=220)*		*-0.66 (-0.72, -0.60)*	*Non-wetland*
log LL	**0.78* (n=16)**	**0.35 (n=16)**	**0.34 (n=14)**	**0.40 (n=13)**	**0.00 (n=4)**		**Waterlogged**
	---	**0.01 (n=3)**	**0.02 (n=3)**	---	---		**Submerged**
	0.43 (n=503)*	*0.45* (n=489)*	*0.27* (n=173)*	*0.69* (n=382)*	*0.62* (n=187)*		*Non-wetland*

Table 3.2 The comparison of the bivariate relationships in wetland vs. non-wetland plants. The significant differences in slopes (*Slop.*), shift along the common slope (*Shift*) and a change in elevation resulting in parallel slopes (*Par.*) between non-wetland plants vs. waterlogged wetland plants (*Wat.* first row) and vs. submerged wetland plants (*Sub.* second row), respectively, analysed by SMA. Significant differences are in black ($P<0.01$), non-significant differences in light grey ($P>0.01$). If slopes are significantly different, this implies differences both in the direction and location of the relationship in trait space (Warton *et al.*, 2006). In those conditions, shift along the common slope and the occurrence of parallel slopes cannot be tested (Warton *et al.*, 2006) (shown in dark grey).

		log LMA			log N_{mass}			log P_{mass}			log A_{mass}			log R_{mass}		
		Slop.	*Shift*	*Par.*	*Slop.*	*Shift*	*Par.*	*Slop.*	*Shift*	*Par.*	*Slop.*	*Shift*	*Par.*	*Slop.*	*Shift*	*Par.*
log N_{mass}	*Wat.*	■	▓	▓												
	Sub.	■	▓	▓												
log P_{mass}	*Wat.*	░	■	■	░	■	■									
	Sub.	░	■	■	░	■	■									
log A_{mass}	*Wat.*	░	■	░	░	■	■	░	■	░						
	Sub.	■	▓	▓	░	░	░	░	■	░						
log R_{mass}	*Wat.*	░	░	░	░	░	░	░	■	░	░	░	░			
	Sub.	░	■	■	■	▓	▓	░	░	■	░	░	■			
log LL	*Wat.*	░	░	░	░	░	■	░	░	░	░	░	░	░	░	░
	Sub.	╲	╲	╲	░	░	░	░	░	░	╲	╲	╲	╲	╲	╲

Leaf P and leaf N were positively correlated, across non-wetland plants (Wright *et al.*, 2004), waterlogged wetland plants (R^2=0.31) and submerged wetland plants (R^2=0.31). The SMA analysis revealed that there was no significant difference in slopes of leaf P-leaf N associations between non-wetland plants and wetland plants (P=0.30 and P=0.91 for waterlogged and submerged wetland plants, respectively). However, the parallel slopes of both waterlogged and submerged wetland plants were elevated compared to non-wetland plants (both P<0.001), which indicates that at a given leaf N, wetland plants tended to have a higher leaf P than non-wetland plants. Moreover, there was a significant shift along the common slope towards higher values in wetland plants (both P<0.001; Fig. 3.1a). This suggests that the proportional change of leaf P with leaf N of wetland plants was similar to non-wetland plants, while wetland plants generally had higher leaf N and leaf P than non-wetland plants.

Leaf N and LMA were negatively correlated in non-wetland and wetland plants (Table 3.1). The waterlogged wetland plants had a significantly flatter slope (P<0.001), while submerged wetland plants had a significantly steeper slope (P<0.001). Thus, as LMA decreases, the increase in leaf N was less pronounced in waterlogged wetland plants, while such increase of leaf N was steeper in submerged wetland plants, compared to non-wetland plants (Fig. 3.1b).

Leaf P and LMA were negatively correlated in both wetland and non-wetland plants with similar slopes (P=0.04 and P=0.03 for waterlogged and submerged wetland plants, respectively, Fig. 3.1c). Wetland plants had a parallel slope which is shifted towards the upper left corner (P<0.001) compared with non-wetland plants. This indicates that even though leaf P and LMA maintained similar relationships in non-wetland and wetland plants, wetland plants maintained a higher value of leaf P but a lower value of LMA (Fig. 3.1c).

The slopes of photosynthetic rate-leaf N in wetland plants were similar to those of non-wetland plants (P=0.06 and P=0.18 for waterlogged and submerged wetland plants, respectively, Fig. 3.2a). However, waterlogged wetland plants were significantly shifted along a common slope towards a higher photosynthetic rate and leaf N values (P<0.001) and had an elevated parallel slope (P<0.001) compared to non-wetland plants, indicating that at given leaf N, waterlogged wetland plants had a higher photosynthetic rate. This suggests that waterlogged wetland plants had a higher nitrogen use efficiency (photosynthesis per unit investment of leaf N). No significant shift along the common slope nor a parallel slope were detected for submerged wetland plants (P=0.61 and P=0.20, respectively).

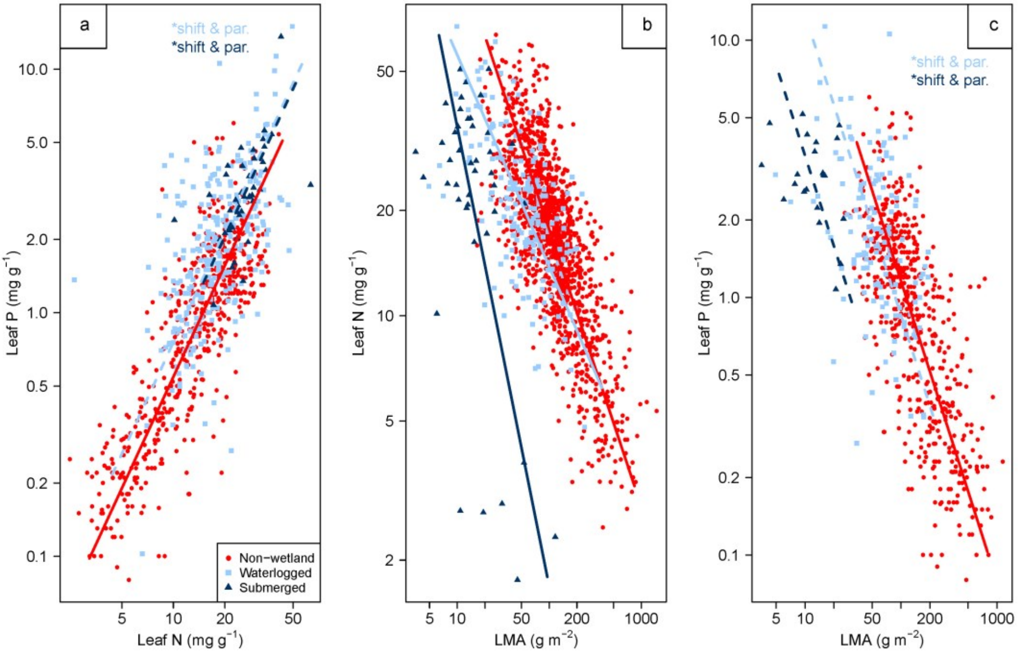

Figure 3.1 The bivariate relationships between leaf phosphorus (leaf P), leaf nitrogen (leaf N) and leaf dry mass per unit area (LMA), respectively. The waterlogged and submerged wetland plants are shown in light blue squares and dark blue triangles, respectively. The non-wetland plant data from GLOPNET (Wright *et al.*, 2004) are shown in red circles with a solid red line. If the slope for wetland plants differs significantly from that of non-wetland plants, this is indicated by a solid dark or light blue line, for waterlogged and submerged plants, respectively. Dashed lines with the notation of **shift* and/or **par.* identify a significant shift along the common slope, and/or a significantly different intercept resulting in a parallel slope, respectively. Note that graph axes are $\log_{10}$ scaled.

There were no significant differences in slopes of photosynthetic rate-leaf P between wetland plants and non-wetland plants (P=0.16 and P=0.36 for waterlogged and submerged wetland plants, respectively Fig. 3.2b). However, wetland plants of both conditions showed a significant shift along the common slope towards higher photosynthetic rate and leaf P values (both P<0.001). This suggests a similar proportional change between leaf P and photosynthetic rate of both wetland plants and non-wetland plants, while wetland plants had higher values of photosynthetic rate and leaf P than non-wetland plants. No parallel slopes were detected (P=0.10 and P=0.65 for waterlogged and submerged wetland plants, respectively), suggesting that wetland plants and non-wetland plants have a similar photosynthetic rate per unit leaf P.

The photosynthetic rate-LMA associations were similar between waterlogged wetland plants and non-wetland plants, except for a significant shift (*P*<0.001) along the common slope towards the corner of lower LMA values but higher photosynthetic rates. This suggests that waterlogged wetland plants generally had lower LMA, but a higher photosynthetic rate. For submerged wetland plants, the photosynthetic rate-LMA slope was significantly steeper than for non-wetland plants (*P*<0.01). This shows that the decrease of photosynthetic rate with an increase per unit of LMA was stronger in submerged wetland plants, indicating that the effect of changed leaf structure on the photosynthesis was bigger in submerged wetland plants. In other words, the photosynthetic rate of submerged wetland plants was even more reduced by an increase of LMA (Fig. 3.2c). The significantly different slopes of submerged plants also imply a shift in trait space.

For dark respiration rate vs. leaf N, we found no significant difference in the slopes (*P*=0.15), nor a shift along the common slope (*P*=0.06), nor parallel slopes (*P*=0.42) between the waterlogged wetland plants and non-wetland plants, suggesting that waterlogged wetland plants hold similar relationships between dark respiration rate and leaf N as non-wetland plants. However, submerged wetland plants showed a significantly flatter slope (*P*<0.01) than non-wetland plants. This suggests that submerged wetland plants maintained their respiration rate to a lower level as leaf N increases than non-wetland plants (Fig. 3.2d).

For dark respiration rate vs. leaf P, wetland plants had slopes similar to that of non-wetland plants (*P*=0.13 and *P*=0.97 for waterlogged and submerged wetland plants, respectively). Waterlogged wetland plants showed a significant shift along the common slope towards higher dark respiration rate and leaf P values (*P*<0.001). In addition, submerged wetland plants showed a significantly lower parallel slope (*P*<0.001), indicating that submerged wetland plants maintained a lower respiration rate at a given leaf P level (Fig. 3.2e).

For dark respiration rate vs. LMA, waterlogged wetland plants showed a similar slope (*P*=0.03), no shift along the common slope (*P*=0.04) nor parallel lines compared with non-wetland plants (*P*=0.49). Submerged wetland plants showed a similar slope (*P*=0.42), but with a significant shift along the common slope towards the lower-left corner (*P*<0.001) and a significantly lower parallel slope (*P*<0.001), indicating that submerged wetland plants in general had a lower LMA but a lower respiration rate at a given LMA (Fig. 3.2f).

In general, submerged wetland plants tended to have a lower dark respiration rate at a given leaf N, leaf P or LMA level. An increase in leaf N does not cause an increase in dark respiration to the same extent as in non-wetland plants (Fig. 3.2d, 3.2e & 3.2f).

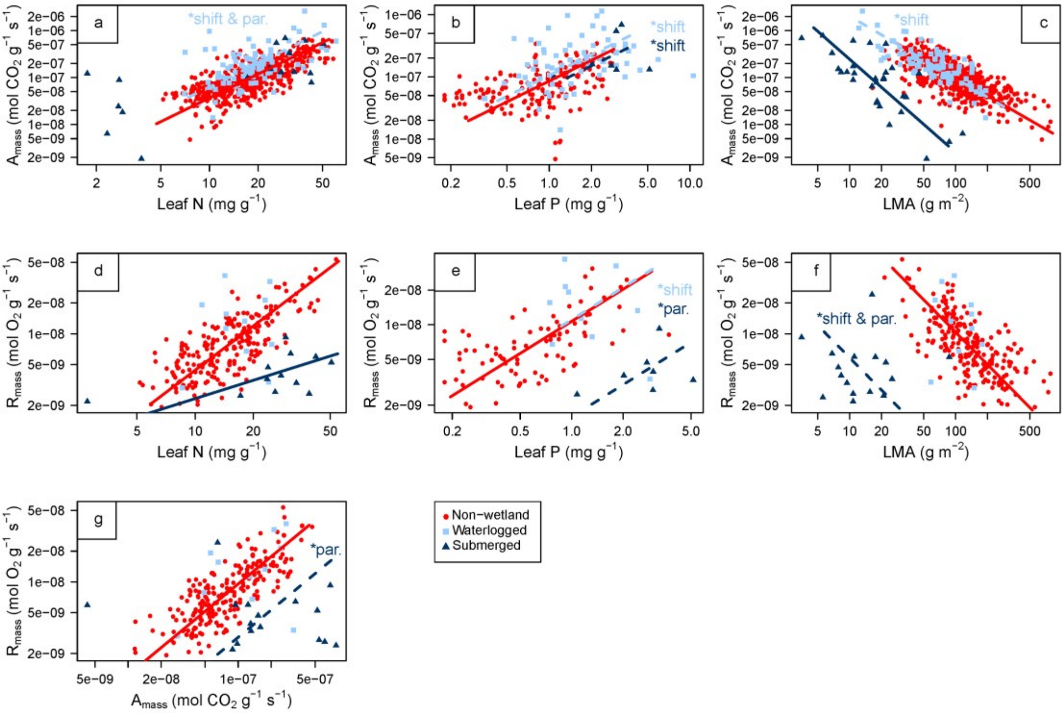

Figure 3.2 The bivariate associations between photosynthetic rate (A_{mass}), dark respiration rate (R_{mass}) and leaf nitrogen (leaf N), leaf phosphorus (leaf P), leaf dry mass per area (LMA), respectively. The waterlogged and submerged wetland plants are shown in light blue squares and dark blue triangles, respectively. The non-wetland plant data from GLOPNET (Wright *et al.*, 2004) are shown in red circles with a solid red line. If the slope for wetland plants differs significantly from that of non-wetland plants, this is indicated by a solid dark or light blue line, for waterlogged and submerged plants, respectively. Dashed lines with the notation of **shift* and/or **par.* identify a significant shift along the common slope, and/or a significantly different intercept resulting in a parallel slope, respectively. Note that graph axes are $\log_{10}$ scaled.

The analysis for dark respiration rate-photosynthetic rate revealed that submerged wetland plants had lower parallel slopes compared with non-wetland plants ($P<0.01$; Fig. 3.2g), suggesting that wetland plants had lower dark respiration rate at a given photosynthetic rate level than non-wetland plants.

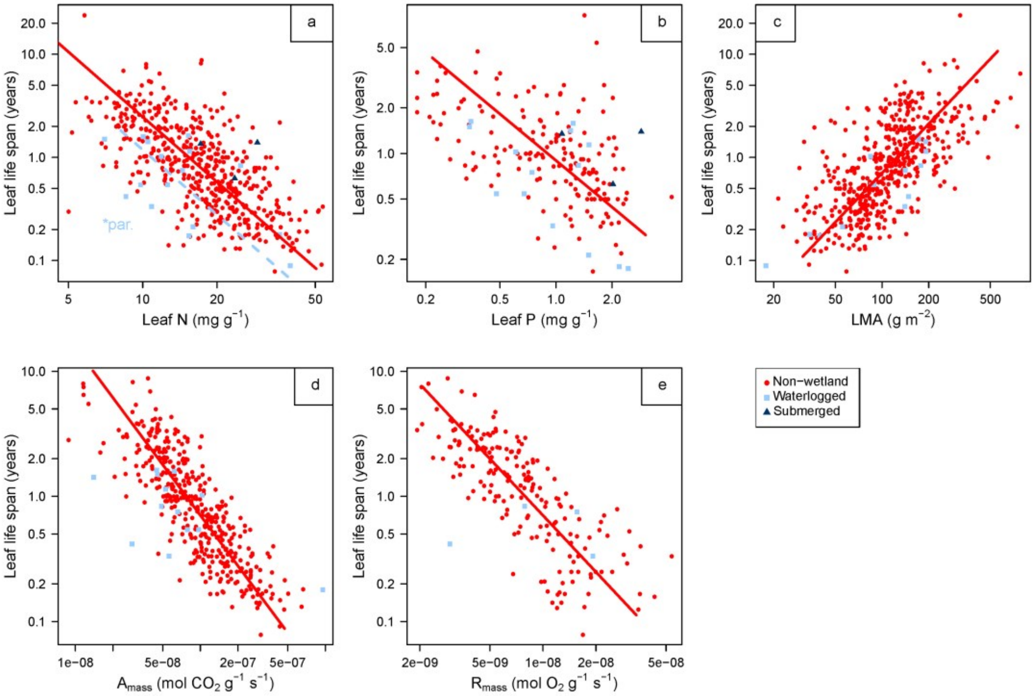

Figure 3.3 The bivariate relationships between leaf life span and leaf nitrogen (N), leaf phosphorus (P), leaf mass per area (LMA), photosynthetic rate (A_{mass}) and dark respiration rate (R_{mass}), respectively. The waterlogged and submerged wetland plants are shown in light blue squares and dark blue triangles, respectively. The non-wetland plant data from GLOPNET (Wright *et al.*, 2004) are shown in red circles with a solid red line. The dashed light blue line with the notation of **par.* identifies a significantly different intercept resulting in a parallel slope respectively. Note that graph axes are $\log_{10}$ scaled and the absence of leaf life span data coupled to LMA, A_{mass}, or R_{mass} for submerged plants.

How leaf traits co-vary with the leaf life span (LL) in submerged wetland plants remains uncertain, because of the limited number of data points (n=3 for LL-leaf N and LL-leaf P, and the absence of data linking LL-LMA, LL-photosynthetic rate and LL-dark respiration rate). For waterlogged wetland plants, we found parallel slopes between LL-leaf N, with wetland plants being significantly lower in trait space ($P<0.01$, Fig. 3.3a), suggesting that at a given leaf N, waterlogged wetland plants had a shorter leaf life span. We found no significant differences in the relationships between leaf life span and other traits for waterlogged wetland plants ($P>0.01$, Fig. 3.3b-3.3e).

In summary, compared with non-wetland plants, significantly different slopes were detected in the relationship between leaf N-LMA in both waterlogged and submerged wetland plants (Fig. 3.1b), and between photosynthetic rate-LMA (Fig. 3.2c) and dark respiration rate-leaf N (Fig. 3.2d) in submerged wetland plants only. This suggests that submerged wetland plants have even more trait deviations from non-wetland plants than waterlogged wetland plants. In general, wetland plants tended to have a lower LMA with higher leaf N and leaf P contents, and consequently higher photosynthetic rate and shorter leaf life span. For submerged wetland plants, the photosynthetic rate was constrained by an increase in LMA. However, this increase was compensated by a much more gradual increase in dark respiration rate with increasing leaf N, than was evident for non-wetland plants.

3.4 Discussion

We compared leaf economics spectrum (LES) trait associations of wetland and non-wetland plants and found that the LES does exist in wetland plants, but with weaker and often deviating/shifting trait-trait associations relative to the non-wetland LES. The weaker trait-trait associations (as indicated by the lower coefficients of determination (R^2) of trait-trait relationships) suggest that alternative strategies exist among wetland plants to deal with the complex and adverse wetland conditions with specific stressors. It may also suggest that besides nutrients and light, other limitations in wetlands also influence the LES and require alternative strategies and consequently the special leaf structure and function of wetland plants. This would cause a higher variation in LES traits. Besides habitat N and P fertility, leaf N can be driven by various factors, including potassium (K), temperature, phytotoxins, or the plants' intrinsic maximal growth rate (Güsewell, 2002). Habitat wetness may also drive leaf N through two indirect mechanisms. On the one hand, denitrification caused by prolonged soil flooding may decrease nitrate availability, thus reducing leaf N (Ordoñez *et al.*, 2010). On the other hand, species living in wet habitats usually have a lower LMA, and thus tend to have a higher leaf N (Mommer *et al.*, 2006; Pierce *et al.*, 2012). The more variable leaf N may further affect the expression of trait-trait associations in wetland plants, such as the leaf N-photosynthetic rate associations (Reich *et al.*, 1998a) and the leaf N-dark respiration rate associations (Reich *et al.*, 1998b).

Our results indicate that the directions of relationships among LES traits are maintained in wetland plants, which suggests that the principal ecological links behind the trait-trait associations have similarities with those in non-wetland systems (Wright *et al.*, 2004). However, our study also reveals differences and these support previous suggestions that wetland plants might possess a unique functional behaviour in photosynthesis-related activities due to their specific adaptation to wetland conditions (Mommer *et al.*, 2004; Herzog & Pedersen, 2014). There are five key aspects in which the LES of wetland plants seems to differ profoundly from the non-wetland LES:

1. In general, wetland plants have a lower LMA, higher leaf N and leaf P content, and a higher photosynthetic rate than non-wetland plants. The waterlogged wetland plants show a shorter leaf life span. Unfortunately, the pattern of submerged wetland plants is uncertain for leaf life span due to a limited number of data points. We conclude that wetland plants comply with a fast-return strategy in resource acquisition among the majority of the LES trait-trait associations (Reich, 2014). Thus, while nutrient and carbon cycling rates in wetland soils are generally slower compared with non-wetland systems (Moor *et al.*, 2017), the aboveground carbon and nutrient cycles in wetlands are expected to be faster.
2. A major deviation in LES trait-trait relationships of wetland plants compared to non-wetland plants occurs in the leaf N-LMA relationship (Fig. 3.1b). The different behaviour of LMA highlights the different functional role of LMA in wetland plants (Violle *et al.*, 2011; Douma *et al.*, 2012). This complies with experimental studies that have found some low-LMA leaves of hydrophytic wetland plants to be functionally highly acquisitive (Mommer *et al.*, 2006; Pierce *et al.*, 2012). However, in addition to further stimulating the acquisition of nutrients, we also expect that a lower LMA is essential to deal with the lower CO_2 and O_2 availabilities to the leaves in (partially) submerged conditions (Colmer *et al.*, 2011). Therefore, besides its leaf economics aspect, LMA should be considered also as a key wetland trait.
3. A lower LMA may have important implications for the functioning of the remainder of the LES in wetland conditions. In non-wetland low nutrient conditions, plants tend to conserve their nutrients by increasing their LMA to protect the leaves against herbivory and other damages (Westoby *et al.*, 2002). Our results suggest that such protection of leaves is not feasible in wetlands. In addition, the higher leaf N in wetland plants may also cause an increased risk of herbivory (Cyr & Face, 1993). Together, these processes partially explain the higher herbivory rates in wetland ecosystems compared to non-wetland terrestrial ecosystems (Cyr & Face, 1993). One way to compensate for the higher losses is to become more acquisitive. Such a strategy is supported by the shift in LES traits along the common slope, but may also relate to the elevated leaf P at a given LMA. The results on the leaf N to leaf P relationships suggest that leaf P is even more elevated in wetland plants than leaf N (Fig. 3.1a). Through these changes in leaf nutrient economics, wetland plant species

may raise their photosynthetic capacity in order to create faster growth dynamics (and concomitant higher turnover).

4. Wetland plant species seem to go even further in stimulating photosynthetic capacity. The photosynthetic rate of waterlogged plants was elevated at a given leaf N compared to the photosynthesis-leaf N relationships in non-wetland plants. Leaf N (and leaf P) expresses the combination of photosynthesis-related active nutrients and those nutrients used for storage and protection (Hikosaka & Shigeno, 2009). If wetland plants indeed invest less energy in the protection of their leaves, the fraction of nutrients involved in photosynthesis increases (Onoda *et al.*, 2017), which in turn would explain the elevated photosynthetic rate of waterlogged plants that we observed. The lower LMA itself may also influence the leaf N-photosynthetic rate relationships, thus increasing the leaf N efficiency of photosynthesis (Reich *et al.*, 1998a). Finally, some submerged aquatic plants are able to enhance their photosynthesis with special leaf structure, such as thin cuticles and oriented chloroplasts towards the epidermis (Mommer *et al.*, 2004; Pierce *et al.*, 2012).

5. Leaves of submerged wetland plants have a lower dark respiration rate (mass basis) than expected from a comparison with the non-wetland LES. Oxygen can decline to hypoxic levels during submergence, and especially in shallow water bodies during the night (Pedersen *et al.*, 2016). Low oxygen can restrict aerobic respiration, both in roots (Armstrong & Beckett, 2011) and in leaves (Colmer & Pedersen, 2008). The relatively low dark respiration rate in leaves of wetland plants may be due to a lower investment of resources in leaf construction and maintenance, and related reductions of energy requirements and respiration during the night (Reich *et al.*, 1998b). The lower respiratory demand allows to more readily face hypoxia when leaves become submerged. In addition, leaves with porous tissues will enhance the oxygen status of the innermost cells. Note that, although the adaptive formation of aerenchyma will significantly decrease the cell oxygen consumption on a tissue volume basis (Jackson & Armstrong, 1999), the data analysed here are measurements expressed on a tissue mass basis. Hence, aerenchyma formation *per se* does not explain the patterns found in this study.

Some of these mechanisms may be further amplified at submerged conditions, where we additionally observed that the altered leaf structure may also affect the photosynthetic rate through a deviating A_{mass}-LMA relationship (Fig. 3.2c), and through influencing the respiration rate by deviating R_{mass}-leaf N associations (Fig. 3.2d). We found a significant reduction of the photosynthetic rate at a given LMA in submerged wetland plants. The additional limitation to photosynthesis of submerged wetland plants can be due to the much lower light availability with water depth and turbid water (Colmer *et al.*, 2011). However, the unique adaptive traits evolved in wetland plants such as leaf gas films and aerenchyma tissues should enhance the gas exchange/flux in plant tissues (Colmer & Pedersen, 2008; Colmer & Voesenek, 2009), and therefore partially compensate the costs posed by the adverse wetland conditions. This may explain the observed pattern that the photosynthetic rate at a given leaf N and leaf P value was not affected (Fig. 3.2a & 3.2b).

All of the described significant changes in the slope of trait-trait relationship, in the position along the slope or due to shifted parallel slopes were detected based on a rather conservative P value threshold ($P<0.01$) in this study. This threshold was chosen to help ensure that the most ecologically relevant relationships were detected in these relatively large datasets (e.g. a relationship with an R^2 of only 0.05 is already significant at $P=0.05$ at a sample size of $n=77$). However, for those relationships with smaller sample sizes (e.g. in relation to dark respiration rate and leaf life span), this approach may have resulted in overly conservative interpretation. This indicates that deviations in the LES of wetland plants may include even more trait-trait relationships than identified here.

Altogether, our analysis suggests that the direct link between photosynthetic rate and dark respiration rate, as evidenced from non-wetland plants to complement N-rich enzymatic and other metabolic components that lead to a higher respiration cost when maintaining a high photosynthetic rate (Reich *et al.*, 1998b, 2008), also exists in wetland plants. However, such relationship is expressed differently in wetland plant species compared with non-wetland plants. The results from our analysis show that submerged wetland plants are capable of having lower dark respiration rate at a given photosynthetic rate than non-wetland plants.

When upscaling the findings to wetland ecosystem functioning, we ascribe the generally high productivity in wetland ecosystems globally to the adaptation of wetland plants by having generally fast-return strategies and a higher payback rate. In this way, the adverse wetland conditions may have very limited impact on the wetland plant functioning in terms of resource accumulation. The assumed trade-offs between the cost of adaptation to wetlands and plant function from the leaf economics spectrum perspective are therefore not profound in general (Pan *et al.*, 2019). In addition, there are some environmental stressors that rarely happen in wetlands. For example, drought stress, which is a common problem in terrestrial ecosystems, is less constraining in most wetlands, and might move LES traits of wetland plants to the optimum end with lower LMA with higher leaf nutrient content (Pagter *et al.*, 2005; Douma *et al.*, 2012). The combination of the high productivity in wetlands and the retarded biochemical cycling rate in the anoxic environments of the substrates together make wetlands the largest contributor to the terrestrial biological carbon pool (Page & Baird, 2016).

3.5 Acknowledgements

The establishment of the wetland trait database was first discussed and started in 2008 at the Vegfunction WG39 which was funded by ARC-NZ Research Network for Vegetation Function. We would like to thank all additional contributors to this original workshop, including Paul Adam (U New South Wales, Sydney, AU), Margaret Brock (U New England, Armidale, USA), George Ganf (U Adelaide, Adelaide, AU), Irving A. Mendelssohn (Louisiana State U, Baton Rouge, USA), Eliska Rejmánkova (U California, Davis, USA), Brian Sorrell (Aarhus U, Aarhus, DK), and Evan Weiher (U Wisconsin, Eau Claire, USA). Yingji Pan is grateful to support from the China Scholarship Council (Grant No. 201606140037).

3.6 Authors' contributions

PvB initialized this research, YP, PvB, EC designed and planned the research. YP and PvB compiled the data with inputs from all co-authors. YP ran all analyses with inputs from all co-authors. YP, PvB and EC wrote the first drafts of the manuscript that was further improved by inputs from all co-authors.

3.7 Data accessibility statement

Data used in this paper for analysis will be deposited in the Dryad Repository once accepted.

3.8 Supporting information

Appendix 3A

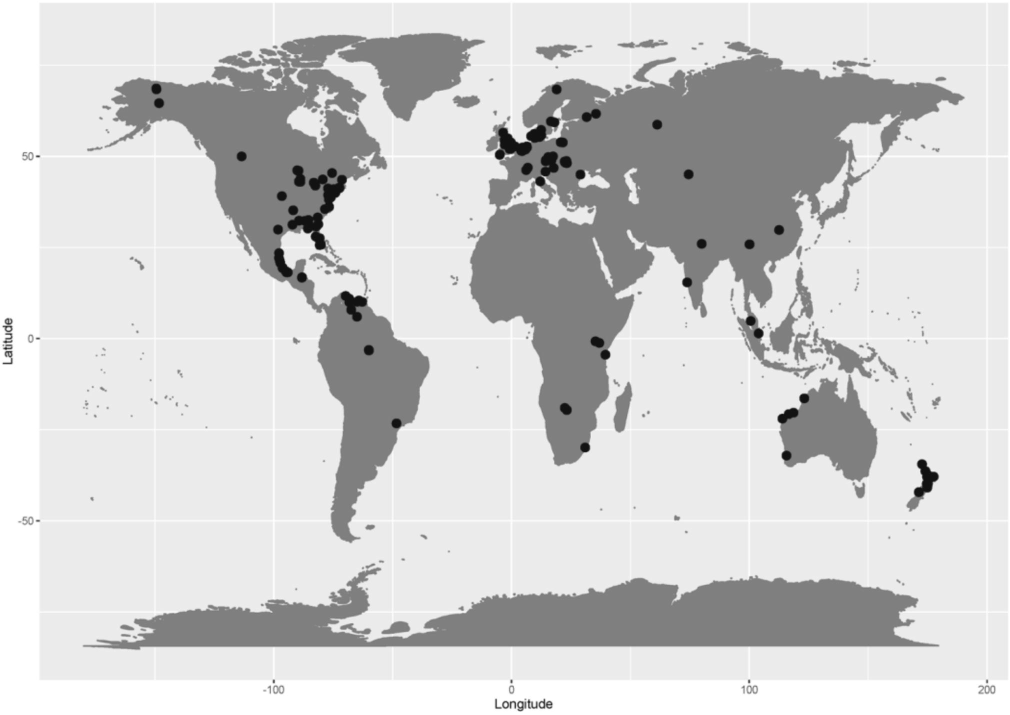

Figure 3S1. Map of the sampling sites of wetland plants for which accurate spatial location information is available (933 out of 2789 records).

Appendix 3B

When evaluating plants' performance along a gradient from dry to wet conditions, the Ellenberg moisture indicator is a useful summary of the plant general adaptation to habitat wetness (Ellenberg, 1988). It effectively represents the synergy of the adaptation to the complex adverse wetland conditions (the wet end of the gradient) and the suite of adaptation traits needed to cope with those conditions. The Ellenberg moisture indicator classification consists of 12 levels corresponding to prevalence along a wetness gradient from 1 (very dry) to 12 (aquatic) (Ellenberg, 1988). Wetland plants usually occupy the higher range from level 4 (Shipley *et al.*, 2017) up to level 12 containing obligate aquatic plants. Studies have shown that the Ellenberg moisture indicator is associated to plant functional traits and soil variables (Bartholomeus *et al.*, 2008; Bartelheimer & Poschlod, 2016; Shipley *et al.*, 2017).

In this study, the Ellenberg moisture indicator was obtained from both the European mainland (Ellenberg, 1988) and the British vegetation descriptions (Hill *et al.*, 2000). Moreover, to make the Ellenberg moisture indicator applicable for a global analysis, we related the Ellenberg moisture indicator values with the USDA wetland plant classification as proposed by Lichvar et al. 2016 (http://wetland-plants.usace.army.mil/). This system principally categorizes 8092 plant species occurring in the United States of America into five wetness indicator categories. The categories include sequentially Obligate (OBL) species with 99% occurrence in wetlands, Facultative Wetland (FACW) with 67%-99% occurrence in wetlands, Facultative (FAC) with 34%-66% occurrence in wetlands, Facultative Upland (FACU) with 1%-33% occurrence in wetlands, and Upland (UPL) with less than 1% occurrence in wetlands (Lichvar *et al.*, 2016). We coded the five USDA indicator categories from UPL to OBL into 1-5 ordinal classes and refer to this indicator system as the USDA indicator. All species selected in the analysis had an Ellenberg moisture or a USDA indicator value.

Using a simple linear regression of the Ellenberg moisture and USDA indicator for the 328 plants common to both datasets, we were able to convert USDA indicators to Ellenberg values for all remaining species using the following relationship:

*Ellenberg moisture indicator= 1.6531*USDA indicator+1.5084* ($R^2=0.744$, $n=328$)

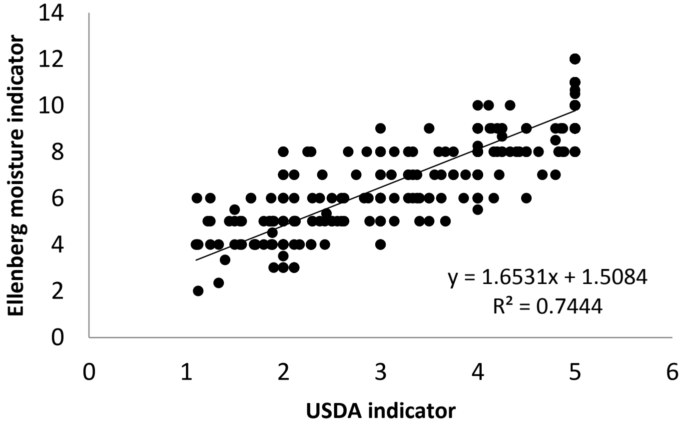

Figure 3S2 The joint Ellenberg moisture indicator value estimates were applied for the analyses presented in this paper.

Chapter 4

Are ecophysiological adaptive traits decoupled from leaf economics traits in wetlands?

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Abstract

- Wetland plants have developed a suite of traits, such as aerenchyma, radial oxygen loss, and leaf gas films, to adapt to the wetland environment characterised by e.g. a low redox potential and a lack of electron acceptors. These ecophysiological traits are critical for the survival and physiological functioning of wetland plants. Most studies on these traits typically focus on a single trait and a single or few species at the time.
- Next to these traits, traits of the leaf economics spectrum (LES) that reflect resources acquisition and allocation in plant species have also been frequently measured in wetlands. However, the performance of the LES has rarely been examined among wetland plants.
- Both suites of traits are critical for -but affect different aspects of- wetland plant functioning and survival. The interactions between them, potentially causing synergies or trade-offs, reflect wetland plant strategies to simultaneously deal with stress tolerance and resources utilization, and have ramifications for the functioning of wetland ecosystems.
- Based on a literature review and quantitative analysis of available data, we provide evidence suggesting that LES and ecophysiological traits may be decoupled (e.g., for root porosity & radial oxygen loss vs. leaf nitrogen) or coupled (e.g., for iron tolerance vs. SLA) in wetlands, depending on the trait combination concerned. This rather complex relationship between wetland adaptive traits and LES traits indicates that there can be multiple mechanisms behind the strategies of wetland plants.
- We further illustrate how adaptive and LES traits together contribute to wetland ecosystem functions, such as denitrification and methane emission. We highlight that both suites of traits should be considered simultaneously when applying trait-based approaches to wetland ecology.

4.1 Introduction

Wetland ecosystems include a wide variety of fresh and saltwater habitats (including for example marshes, peatlands, mangroves, rivers, lakes, intertidal mudflats and rice paddies) that are distinguished from terrestrial habitats by a different hydrological regime (Ramsar Convention Secretariat, 2013). This causes wetland ecosystems to have unique features in terms of oxygen availability, nutrient cycles, soil pH and redox potential. These deviating environmental conditions strongly affect the survival and functioning of wetland plants. In response, wetland plants have developed a suite of adaptive traits, including tolerance and escape traits, to waterlogging or inundation and other conditions characteristic of wetlands (Jackson & Armstrong, 1999; DeLaune & Pezeshki, 2001; Pezeshki & DeLaune, 2012). These traits are strongly related to wetland plant performance, sometimes even vital to their survival. Previous studies on these adaptive traits have commonly focused only on one or a few species at the individual level, which makes these adaptive traits hard to incorporate into trait-based wetland ecology. In contrast, leaf economics spectrum traits (LES) such as leaf nitrogen (leaf N), leaf phosphorus (leaf P), specific leaf area (SLA) and photosynthetic rate (A_{mass} or A_{area}) have received more attention, but do not include those traits that are considered vital to the survival of plants under wetland conditions in ecophysiological studies (Visser *et al.*, 2000b; van Bodegom *et al.*, 2005; Voesenek & Bailey-Serres, 2015).

Moreover, the functional importance of most traits is context-specific (Wright & Sutton-Grier, 2012; Baastrup-Spohr *et al.*, 2015; Shipley *et al.*, 2016). This context may well differ for wetland ecosystems compared to terrestrial ecosystems, because trait selection is strongly driven by environmental factors (DeLaune & Pezeshki, 2001; van Bodegom *et al.*, 2012). A recent review paper (Moor *et al.*, 2017) carefully reviewed both wetland adaptive traits and LES traits as well as their effect on ecosystem functioning, and the authors suggested not to simply employ the LES/PES (Plant Economics Spectrum) to understand wetland ecosystems, since they vary widely in site conditions (bogs, peatland, marsh etc.). The study called for the inclusion of LES/PES and adaptive traits to get a better understanding of wetland ecology. To move towards this goal we need to understand how these two groups of traits, if taken as the two major trait axes, position in relation to each other. In other words, it is important to disentangle the different roles that wetland adaptive traits and LES traits play in plant survival and resource utilization respectively, their relationships being orthogonal (reflecting a decoupling) or coordinated (reflecting coupling through synergies or trade-offs), and the consequent effects on ecosystem functioning.

The adaptive response and the physiological mechanisms of adaptive strategies to wetland conditions have been carefully examined in ecophysiological studies, which have shown adaptation in traits in relation to root morphology and plant physiology (Laan *et al.*, 1989; Colmer, 2003a; van Bodegom *et al.*, 2005). For instance, plants can adapt to cope with the oxygen deficiency associated to waterlogging/flooding by developing adventitious roots or aerenchyma in shoots or roots (Justin & Armstrong, 1987; Blom *et al.*, 1994; Wright *et al.*, 2017a), or enhancing root porosity (Justin & Armstrong, 1987; Garthwaite *et al.*, 2003). Likewise, radial oxygen loss (ROL) protects plant roots from anaerobic stress (Lemoine *et al.*, 2012), whereas barriers to ROL in basal zones enhance longitudinal oxygen diffusion towards the apex (Colmer, 2003a). Phytohormones such as ethylene, gibberellin and abscisic acid also play important roles in changing cellular and organ structure that alleviate the oxygen deficiency (Vartapetian & Jackson, 1997; Bailey-Serres & Voesenek, 2008). Most of these primarily ecophysiological studies on wetland plants, though, are limited to an experiment-based assessment of one individual trait for a few species at a time. Unfortunately, it is rather difficult to scale up results from such detailed studies to the impacts of different plants and communities on wetland ecosystem functioning. Therefore, we need to integrate these ecophysiological traits into a more general ecological framework (Fig. 4.1a).

There is some circumstantial evidence that wetland adaptive traits may be orthogonal to (i.e. independent of or decoupled from) LES/PES: wetland adaptive traits are the premise of plant existence in wetlands since they are vital to the survival of plants under hazardous anaerobic conditions. Based on that premise, one may expect trait selection processes in wetlands to be strong. At the same time, while LES traits are principally constrained by nutrient availability (e.g. Maire et al. 2015), wetland habitats span a wide fertility gradient from very infertile bogs to very fertile floodplains/marshes at a global scale. This provides the conditions to allow for a full range of leaf N if wetland adaptive traits are orthogonal to LES/PES (Fig. 4.1b). However, if trade-offs between the two axes predominate, one would expect only a subset of LES/PES would remain available for wetlands (Fig. 4.1c). The wide variety of growth strategies in wetlands, from conservative strategies associated with e.g. bogs to acquisitive strategies in highly productive systems such as reed lands, suggests that wetland plants can sufficiently develop adaptive traits to cope with multiple and varied wetland conditions. This pattern also suggests an orthogonal relationship between adaptive traits and LES/PES traits.

In this paper, we present an exploratory analysis to quantify the relationships between wetland adaptive traits and LES/PES traits. We hypothesize that adaptive traits are principally decoupled from LES/PES traits in wetlands, assuming that these adaptive traits are not costly to have. Consequently, we predict that we will see a wide range of LES/PES in wetland plants. Using published and unpublished data, we assess the relationship between wetland adaptive traits and LES/PES traits. Then we illustrate how wetland adaptive traits and LES/PES traits together impact wetland ecosystem functioning.

While the lack of integration of wetland adaptive traits into more generic trait-based approaches has formed a barrier to the direct employment of trait-based approaches to wetland ecosystems to date, we propose that a more comprehensive understanding of wetland ecology can be obtained through the quantification of the relationships between the two suites of traits. This will also allow us to make better-informed decisions with respect to one of the standard dilemmas in trait-based community ecology: the choice of measuring traits for ease of measurements and low cost vs. functional/mechanistic importance (Lavorel & Garnier, 2002; Wright *et al.*, 2010).

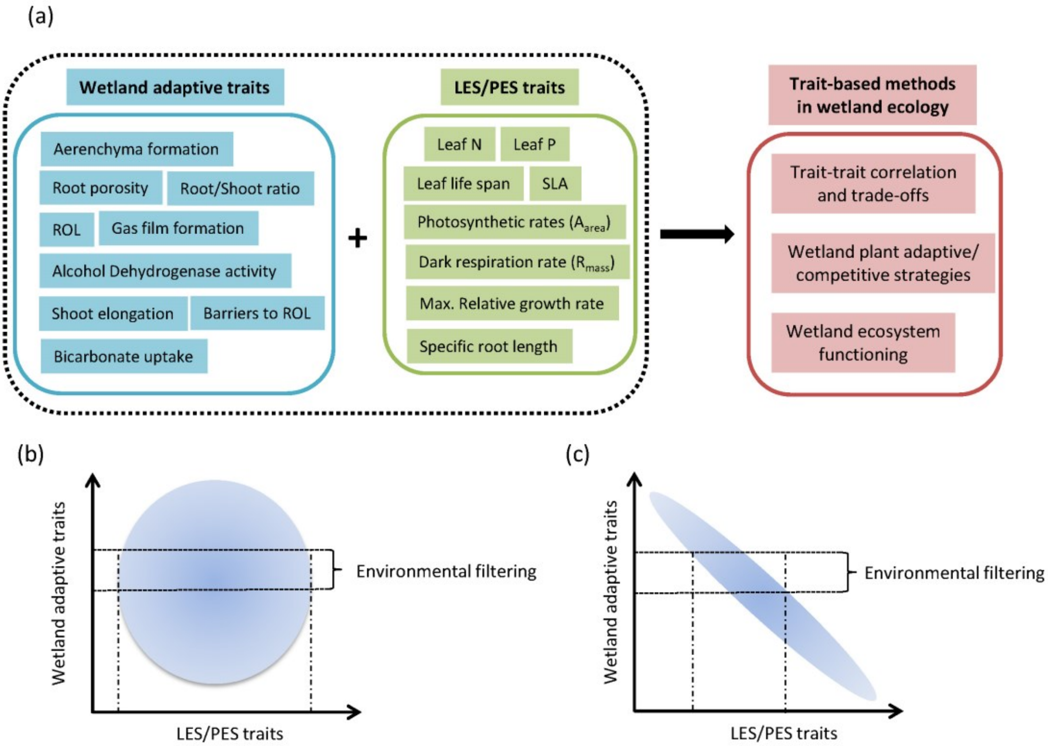

Figure 4.1 A summary of most commonly studied wetland adaptive traits and LES/PES traits (a); the relationships between these two suites of traits determine wetland plant adaptive and competitive strategies, and wetland ecological functioning. If wetland adaptive traits are orthogonal to LES/PES, even if environmental filtering to a specific setting of the water regime selects a subset of adaptive traits, almost a full range of LES/PES trait values would still be visible amongst wetland species (b). If trade-offs are predominant, environmental filtering of wetland conditions selects a subset of adaptive traits, consequently only a corresponding subset of LES/PES remains (c).

4.2 Literature review on the relationships between wetland adaptive traits and LES/PES

Some trade-offs among wetland adaptive traits and nutrient uptake have been described. In general, wetland plants may experience more nutrient stress than other plants under similar conditions of nutrient availability, because some adaptations to oxygen or redox stress result in a reduced adaptation to nutrient stress (Silvertown *et al.*, 2015). In turn, this is likely to negatively affect leaf nutrient contents, which are part of LES/PES. For instance, decreasing root respiration and increasing aerenchyma leave less energy and active root biomass, respectively, for the active uptake of nutrients (van der Werf *et al.*, 1988). A root barrier that retards oxygen leakage may also reduce the efficiency of nutrient uptake (Colmer, 2003b), although studies suggest that symplastic aquaporin activity can prevent this effect (Rubinigg *et al.*, 2002). In some cases, cortical aerenchyma also inhibits nutrient transport (Hu *et al.*, 2014). Another trade-off includes a decrease in phosphate availability in the presence of ROL by the oxidation of Fe^{2+} in the rhizosphere, inducing the precipitation of phosphate with iron. If these trade-offs are representative of the strategies of wetland plant species, then wetland plants species should occupy the lower ranges of the LES/PES.

In the case of specific leaf area (SLA), such a relationship is rather complex as SLA may be seen as part of LES/PES and other plant strategy axes, such as the size axis (Wright *et al.*, 2010), and it may also relate to wetland plant's adaptation to water stress. For example, community mean SLA increased with flooding, suggesting that SLA contributed to the plant's waterlogging tolerance (Violle *et al.*, 2011). Also, Mommer et al. (2007) found, across nine species, that the internal oxygen partial pressure, the trait that enhances waterlogging tolerance in plants, was positively correlated to SLA and negatively correlated to leaf thickness and cuticle thickness (while plasticity in these traits was not). Another extensive meta-analysis, comparing tens of species, suggested that the link between tolerance to oxygen stress and SLA response was significant but rather weak (Douma *et al.*, 2012).

While the examples above suggest some coordination for individual trait sets, when analysing tolerance towards waterlogging (presumably related to wetland adaptive traits) vs shade or drought (as related to LES/PES traits), a decoupling seems to prevail. A study of 806 shrubs/trees across continents suggested that correlations among shade, drought and waterlogging tolerance indices were significant but very weak (Niinemets & Valladares, 2006; Hallik *et al.*, 2009). This suggests that oxygen stress-related traits (waterlogging tolerance) might be decoupled from leaf economics traits (shade tolerance). Also, the fact that environmental drivers of the LES/PES traits are different from those driving wetland adaptive traits, suggests that some orthogonality may occur among these sets of traits.

Given the partially contradictory evidence listed in our qualitative literature review and since none of the above studies specifically tested the relationships of different trait axes, we provide an exploratory quantitative analysis in the next section.

4.3 Exploration of the relationships between wetland adaptive traits and LES/PES

To quantitatively explore the so far rather anecdotal and possibly contradictory relationships between wetland adaptive traits and LES/PES traits, we analysed a number of non-exhaustive published wetland ecophysiological studies and unpublished data sources, which presented trait measurements of both adaptive and LES/PES traits at the individual and species level under field or experimental conditions (see Appendix 4A for data description details). In our analysis, we assume that individual wetland plants exert their adaptive strategies in response to environmental stress, independent of whether the exposure happened in the field or at experimental conditions. For our exploratory analysis on the relationships between adaptive traits and LES/PES traits, we focused on three pairs of relationships (root porosity vs. leaf N, ROL vs. leaf N, iron tolerance vs. SLA), for which sufficient data were available for quantitative analysis. Root porosity and ROL are two very important ecophysiological adaptive traits at flooded conditions (Visser *et al.*, 2000b; Colmer, 2003b; Voesenek & Bailey-Serres, 2015), and reduced iron along with other reduced toxins is considered as the cause of the absence of non-wetland plants in wetland conditions (Snowden & Wheeler, 1993). Leaf N and SLA are leading traits driving the LES/PES axis (Wright *et al.*, 2004; Diaz *et al.*, 2016).

Previous studies have commonly observed a high degree of both interspecific and intraspecific variation in root porosity in wetland plants in response to oxygen stress (Lemoine *et al.*, 2012; Mei *et al.*, 2014), while leaf N varies according to soil fertility (following a gradient of acquisitive to conservative strategies) at the interspecific level (Ordoñez *et al.*, 2009; Maire *et al.*, 2015). To test the relationships between root porosity and leaf N, we collated data from three sources where both variables were measured on the same individuals (see Appendix 4A for further details): a) greenhouse experiment in which six wetland plant species were measured in a 2*2 factorial design with soil oxygen demand (SOD) and partial submergence as the main factor (van Bodegom *et al.*, 2008); b) a field study in Ukraine, where root porosity and leaf N of 53 species from forested/shrub wetlands and marsh habitats were measured at field conditions (unpublished data, Appendix 4A); c) a field study in the Netherlands, where root porosity and leaf N of 22 species from fens were measured at field conditions (unpublished data, Appendix 4A).

A linear regression between leaf N and (log-transformed) root porosity (Fig. 4.2) showed that, despite a significant correlation (*P*<0.01), the very low R^2 (adjusted R^2=0.030; n=267) indicates that only three per cent of the variation can be explained by the model. At a high sample size -such as here- a significant relationship does not necessarily imply ecological relevance (Yoccoz, 1991; Møller & Jennions, 2002). The low effect size effectively represents a decoupling (Fig. 4.2).

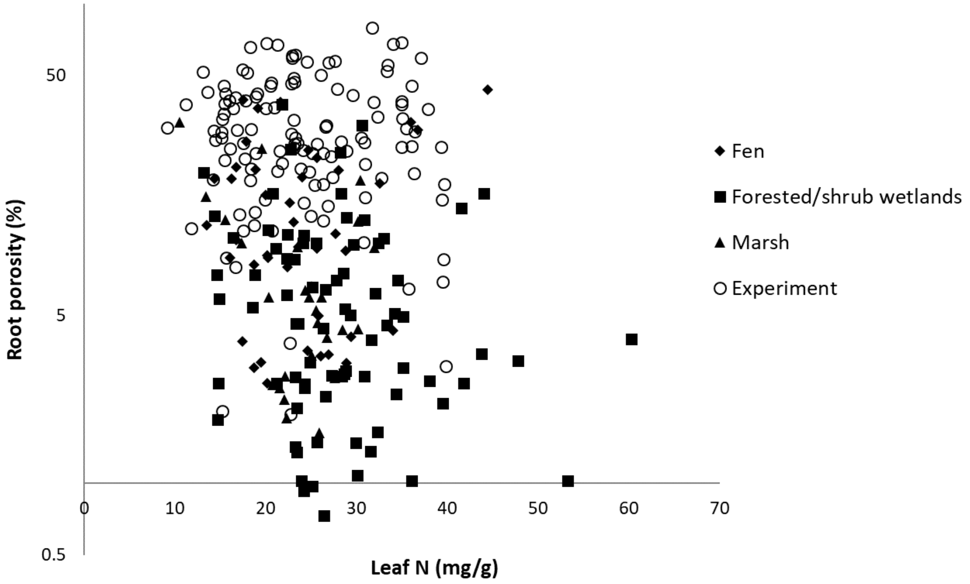

Figure 4.2 The relationships between root porosity and leaf N. The data are from measurements from a greenhouse experiment (van Bodegom *et al.*, 2008) and field measurements of three habitats: fen, marsh and forested/shrub wetlands (van Bodegom, unpublished data) (see details in Appendix 4A).

To test the relationships between ROL and leaf N, data were available from a greenhouse experiment, where five typical wet dune slack species were grown under all possible combinations of treatments with two (strongly differing) levels of light, fertility, reduced metal concentration, and water regime gradients (van Bodegom *et al.*, 2005). To be able to test this relationship, and because ROL data were heavily zero-inflated (92 out of 209 measurements showed no ROL), we grouped the ROL data into four classes in order to meet the normality assumption. The first class contained all 92 ROL observations, and the remaining 117 points were evenly divided into the other three classes in the ascending order (39 measurements for each bin). Subsequently, a linear model was run to test whether log-transformed leaf N varied as a function of ROL class. Despite a significant *P* value (which, again, we would consider induced by the large sample size), the overall lack of relationship (R^2=0.053) between log-transformed leaf N and ROL classes again suggested decoupling (Fig. 4.3).

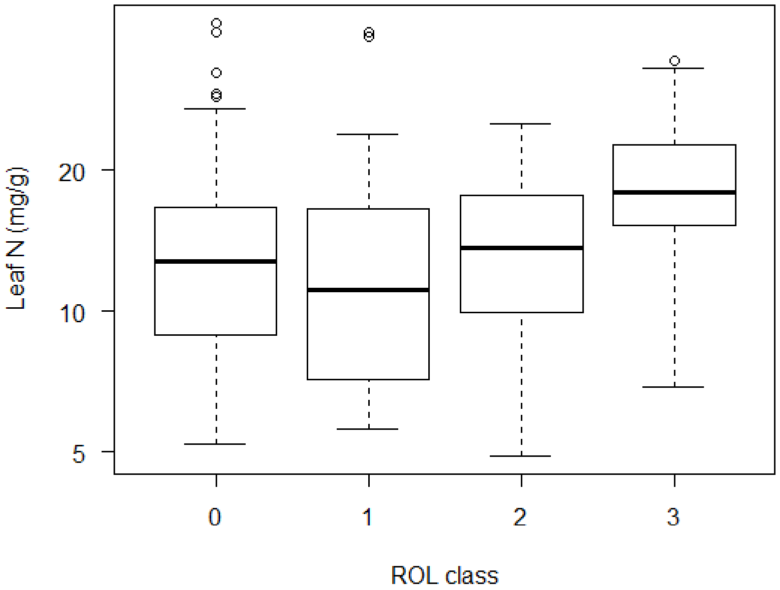

Figure 4.3 Box plot of leaf N across ROL class (adjusted R^2=0.053, P<0.01, n=209). Class 0: ROL=0 μmol O_2 h^{-1} per g root dry weight, n=92; class 1: ROL= 2.5 - 21.5 μmol O_2 h^{-1} per g root dry weight, n=39; class 2: ROL=21.6 - 85 μmol O_2 h^{-1} per g root dry weight, n=39; class 3: ROL=90 - 1212 μmol O_2 h^{-1} per g root dry weight, n=39. Data source: van Bodegom et al. (2005).

Results from these datasets suggest that: (i) potentially decoupled relationships between wetland adaptive traits and LES/PES traits may exist. Such decoupling indicates that the cost of, for example, root porosity formation might be relatively low for wetland plants and that a higher transportation capacity of oxygen to the rhizosphere (ROL) does not necessarily impede the nitrogen uptake capacity or the nitrogen utilization within plants, and (ii) almost a full range of leaf N was covered (3.4 to 60.3 mg/g) compared to the leaf N range of terrestrial plants worldwide (2.48 to 68.98 mg/g) (Diaz *et al.*, 2016). This full range of leaf N in wetland plants suggests that adaptation to wetland conditions are not necessarily costly (in agreement with Fig. 4.1b). This is also supported by evolutionary evidence: aquatic species have evolved at least 200 times from terrestrial species (Cook, 1999).

Another type of adaptive traits relates to the tolerance, rather than avoidance or escape, of stressful conditions in wetlands. As a key stress tolerance characteristic of wetland plants, iron tolerance has been long considered as the cause for differential survival, growth and distribution among wetland plants (Snowden & Wheeler, 1993). Iron reduction along with manganese reduction takes place in the redox sequence after the depletion of nitrate, and produces phytotoxic ferrous iron. The physiological mechanisms behind iron tolerance are probably a combination of oxidation of the rhizosphere (partly contributed by ROL) and a true tolerance for Fe^{2+}. Due to a lack of quantitative traits expressing these true iron tolerance mechanisms, we used the iron tolerance index proposed by Snowden & Wheeler 1993 as a proxy trait. In that study, an iron tolerance experiment was set up for 44 British fen species seedlings, cultivated under in 10% Rorison solution containing reduced iron (as ferrous sulphate). The iron tolerance index was estimated based on the impact of iron on the relative growth rate (RGR) in comparison with the RGR in a control group (Snowden & Wheeler, 1993). To test how iron tolerance relates to LES/PES traits, we derived SLA of the corresponding species (with the exception of *Oryza sativa* which was not available) from the LEDA database (Kleyer *et al.*, 2008). A linear regression between the iron tolerance index and SLA showed that the iron tolerance index decreased strongly and significantly with an increasing SLA (R^2=0.237, Fig. 4.4).

This pattern may indicate a true trade-off between iron tolerance trait and LES/PES traits. We hypothesize that tolerance -in contrast to avoidance or escape traits- may be costly and hence induce coupling with LES traits. It will require further experimental work to test this hypothesis more fully with other traits and in other systems. Such experimental evaluating should consider other LES traits than SLA in relation to tolerance, given that SLA may also directly play a role in wetland adaptation (as discussed in section 2).

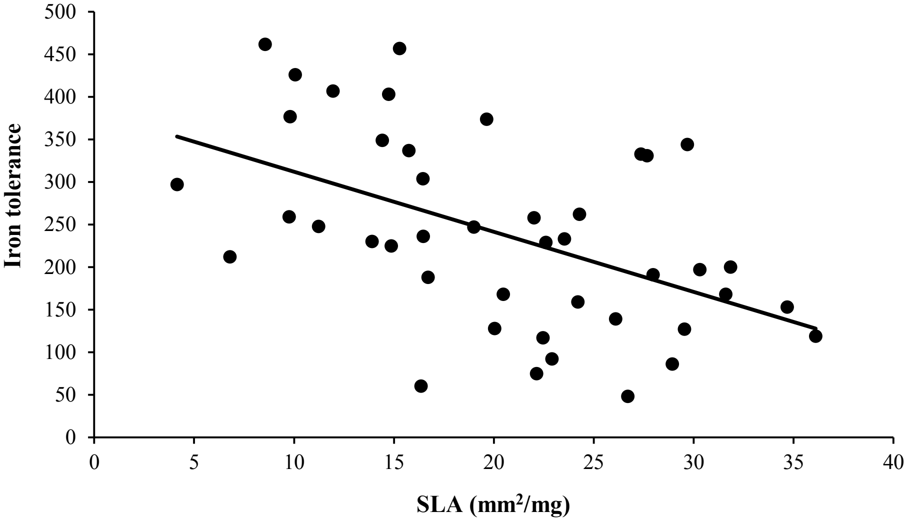

Figure 4.4 The relationship between SLA and iron tolerance (linear regression, adjusted R^2=0.237, P<0.001, n=43). SLA data were from the LEDA database (Kleyer *et al.*, 2008), iron tolerance data were estimated by Snowden and Wheeler (1993).

The three exploratory investigations presented here, suggest that both potentially coupled and decoupled relationships exist between wetland adaptive traits and LES/PES traits. The varied wetland adaptive traits may therefore not position along one trait axis, but some of them may be decoupled from one another. This implies that the selective forces in wetlands act in varied directions. The cost of developing a wetland adaption trait may vary, depending on the trait and the conditions. The varied relationships between the two suites of traits suggest a variety of possible adaptive strategies to deal with specific combinations of wetland conditions, including both flooding stress and nutrient acquisition aspects.

4.4 Scaling from wetland plant traits to ecosystem functioning

Considering the importance of wetland ecosystems to humans, with regards to ecosystem services including water quantity and quality regulation and habitat provisioning for water birds and fish (Zedler, 2003; Doherty *et al.*, 2014), more and more attention is being paid to understanding wetland ecosystem functioning. Trait-based approaches have been applied to characterize plant strategies and their effects on ecosystem functioning of wetlands (Moor *et al.*, 2017), but such studies have mainly focused on LES/PES traits (Douma *et al.*, 2012).

However, given the unique adaptive traits in wetland ecosystems, these need to be additionally considered to fully understand trait-based impacts on wetland ecosystem functioning. For instance, two important biogeochemical processes in wetlands, denitrification and methane production, depend on soil organic matter content - which are strongly influenced by community mean leaf nitrogen and carbon concentrations (LES/PES traits) (Koschorreck & Darwich, 2003) - and suitable aerobic/anaerobic conditions, which relate to ROL and root porosity (adaptive traits) (Engelhardt, 2006; Sutton-Grier *et al.*, 2013; Alldred & Baines, 2016).

Knowledge of the combined effects of adaptive traits and LES/PES traits can thus improve our understanding of denitrification and methane production, which is important for the sustainable management of wetlands, including the reduction of greenhouse gas emissions by wetlands and the relief of eutrophication in wetlands.

In addition to affecting the functioning of wetlands, wetland adaptive traits may also affect the community structure of wetlands in a complicated way. ROL relates to oxygen leaking from roots into the soil which results in microaerophilic conditions in the rhizosphere (e.g. van Bodegom and Scholten 2001). This allows detoxification of several potentially toxic compounds like S^{2-} and Fe^{2+}. The micro-aerophilic conditions induced by ROL do not only favour growth of the plant species that have ROL, but also facilitate the growth of less-adapted species that would not survive under purely anoxic soil conditions (Schat, 1984). As a consequence, the facilitation of these less-adapted species leads to a competition with the adapted species and a higher turnover of species than would have occurred otherwise (Grootjans *et al.*, 1998).

ROL also contributes to community composition in a more direct way, through its coupling of the nitrification and denitrification processes. Compared to cases in which ROL is absent, the increased availability of soil oxygen in communities with ROL induces nitrification. The produced nitrate diffuses into the anoxic bulk soil and is denitrified, and hence leads to increased nitrogen losses and decreased nutrient availability in wetland ecosystems (Reddy *et al.*, 1989; Adema *et al.*, 2005). Low nutrient availability makes it harder for competitors to invade, as many grow less effectively in such an environment. As a consequence, the community of stress-tolerating plant species, that grow less quickly at high nutrient levels, may remain more stable (Adema & Grootjans, 2003).

This feedback loop between ROL and denitrification is further complicated because both ROL (through oxygen supply for nitrification) and LES/PES traits by a combination of direct and indirect relations determine nitrate availability. If ROL is orthogonal to leaf N (as suggested by the exploratory analyses described above), these two influences on nitrate availability and hence denitrification may occur independently from each other. However, if there is a trade-off between ROL and leaf N, then nitrate sources can be limited by low ROL leading to a natural reduction of denitrification. In that case, a strong nitrification/denitrification coupling is not expected to occur. This example again demonstrates the importance of understanding the relationships between wetland adaptive traits and LES/PES.

Methane emission is another example that shows how wetland adaptive traits and LES/PES traits together affect ecosystem functioning. Methane production only takes place after most other alternative electron acceptors have been depleted. Both production and emission of methane are affected by wetland plants in many aspects. First of all, organic compounds released by root exudation can be used as electron donors for methane production (e.g. Aulakh et al. 2001). Secondly, oxygen released from the roots may be used by bacteria to oxidize methane to CO_2, decreasing methane emissions (e.g. van Bodegom et al. 2001). Thirdly, the aerenchyma channels of wetland plant species act as chimneys that effectively transport methane from the soil to the atmosphere. This plant-mediated transport pathway is much more effective than diffusion through the soil alone (e.g. van Bodegom et al. 2001b, Fig. 4.5) and decreases the probability of methane oxidation. The combination of adaptive traits and local conditions (such as temperature, water level, soil texture) determines whether the net effect of wetland plants is an amplification or decrease of methane emissions.

To further advance our quantitative understanding of strategies and functioning (including denitrification and methane emission) in wetlands, we identified a number of critical research topics that would benefit from an inclusive approach. First, we need to target specific pairs of wetland adaptive traits and LES/PES traits and study them quantitatively to better understand the nature and patterns of this relationship. Specifically, such analysis may test the hypothesis that tolerance traits may be coupled while avoidance and escape traits are not. Second, the drivers determining the selection of these different trait sets will have to be analysed. Third, based on an understanding of which traits do and which don't couple to LES traits and under which conditions, combined with knowledge on how the interplay of adaptive and LES traits affect important wetland ecosystem functions, the variation in these ecosystem functions at the global scale can be quantified and understood. Such insights will help recognise the importance of wetland ecology in times of global change.

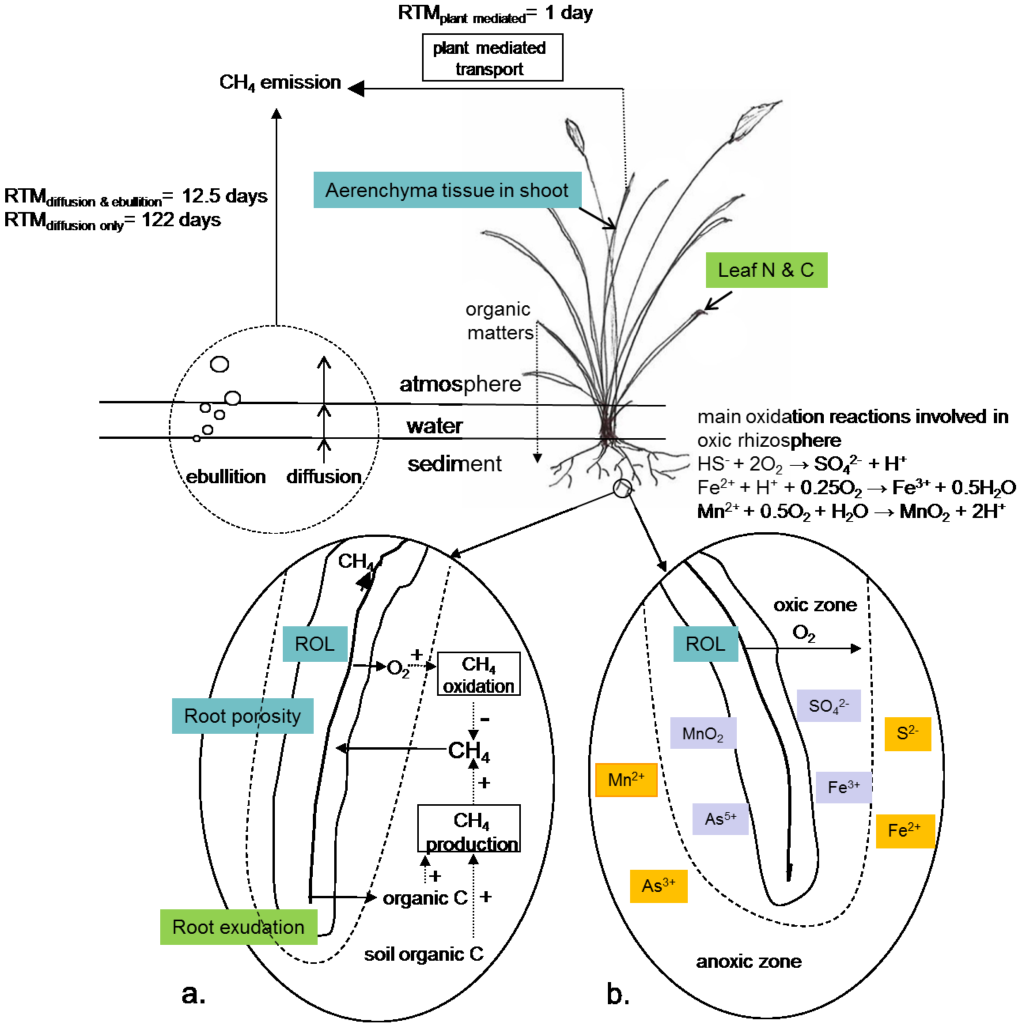

Figure 4.5 Schematic presentation of the wetland adaptive traits (in blue boxes) and LES/PES traits (in green boxes) impact on a.) the gas transportation through wetland plants and organic compounds release b.) oxidation reactions in oxic rhizosphere (with oxidized elements in purple boxes and reduced elements in orange boxes). The residence time of methane in soil (RTM) is based on data discussed in van Bodegom et al. (2001c).

4.5 Conclusions

By bridging the fields of study of wetland adaptive traits and LES/PES traits and their relationships, we can unravel wetland plant strategies and obtain a broader picture of wetland ecology. Our work provides a first exploration of such relationships through a qualitative literature review and a quantitative assessment between examples of the two suites of traits; this can be further explored in future wetland ecology research. Our analyses suggest both coupled and decoupled patterns do occur between wetland adaptive traits and LES/PES, and provides a first glimpse at the complex character of adaptation in wetland ecosystems. Further unravelling the relationships between the two suites of traits will be critical to understanding wetland ecosystem functioning, especially for those processes to which multiple traits contribute, such as denitrification and methane emissions, and that are globally important processes of greenhouse gas emissions. To fully reveal the patterns between adaptive traits and LES/PES traits, we are in need of global compilation and analysis of traits datasets.

4.6 Authors' contributions

P.M.v.B. conceived the study; Y.P., E.C. and P.M.v.B. developed the ideas; P.M.v.B. and Y.P. collected the data; Y.P. wrote the first draft and conducted the analyses. All authors contributed critically to the drafts and gave final approval for publication.

4.7 Acknowledgements

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4.8 Data accessibility statement

Data deposited in the Dryad repository: http://doi.org/10.5061/dryad.4v1s6b5 Pan, Cieraad & Van Bodegom 2019

4.9 Supporting information

Appendix 4A

To explore the relationships between wetland adaptation traits and LES/PES (leaf/plant economics spectrum) traits in our manuscript, we collated published and unpublished data from 5 sources, including three sources having an experimental setup, and two describing a field study. Here, we provide (1) more detailed descriptions of the data in these studies, and (2) show how different experimental/field settings have effects on the both wetland adaptation traits and LES/PES traits, using box plots and scatter plots.

We assume that individual wetland plants develop their adaptation strategies to the environment, independent of whether the exposure happened in the field or at experimental conditions. For our proof-of-principle exploration on the relationships between adaptation traits and LES/PES traits, we focused on three pairs of relationships for which we had concomitant and sufficient data (root porosity vs. leaf nitrogen (N), radial oxygen loss (ROL) vs. leaf N, iron tolerance vs. specific leaf area, SLA). Root porosity and ROL are two very important ecophysiological adaptation traits at flooded conditions (Visser *et al.*, 2000b; Colmer, 2003b; Voesenek & Bailey-Serres, 2015), and reduced iron and other reduced toxins is considered as the cause of the absence of non-wetland plants in wetland conditions (Snowden & Wheeler, 1993). Leaf N and SLA are leading traits driving the LES/PES axis (Wright *et al.*, 2004; Diaz *et al.*, 2016).

To evaluate the effects of experimental/field setting on traits, we can directly relate categorical fertility/water regimes/toxicity/light availability treatments with the wetland adaptation traits (root porosity and ROL) and leaf N for the experimental studies.

For the field studies, we do not have direct measurements of environmental conditions. Instead, we evaluate each species' Ellenberg indicator value for nitrogen (Ellenberg N) as well as leaf N (at both at individual and species level) against the habitat types to indirectly show the fertility differences between habitats and how different habitats drive the leaf N.

The full range of the Ellenberg N is from 1 (least) to 9 (excessive supply); the most intensive survey of the global vascular plants' leaf N database reported the range between 2.48 to 68.98 mg/g (Diaz *et al.*, 2016). Our data showed an almost full range of Ellenberg N and leaf N (Fig. 4S3A to Fig. 4S3C below) suggesting our data is representative of the wide range of habitat fertility. Similarly, the variability of Ellenberg N and leaf N within each habitat type also reflects a fertility gradient within habitat types in our research data.

Experimental studies:

1. Dataset from van Bodegom *et al.* 2008

In this study, six species from wet dune slacks were selected to represent different habitat fertility and wetness. All individuals were trimmed and then moved to greenhouse for one week's acclimatization.

Then four treatments with six replicates each were established in a 2*2 factorial design. The two waterlogging treatment were saturated (with standing water layer of 0-1 cm) and inundated (with standing water layer of 10 cm). The two soil oxygen demand (SOD) factors are increased SOD or no added SOD. After nine weeks, the plants were harvested and root porosity and leaf N were measured. Fig. 4S1A to Fig. 4S1C describe how the water regime (flooded and waterlogged) affects root porosity and leaf N and the relationships between the two traits.

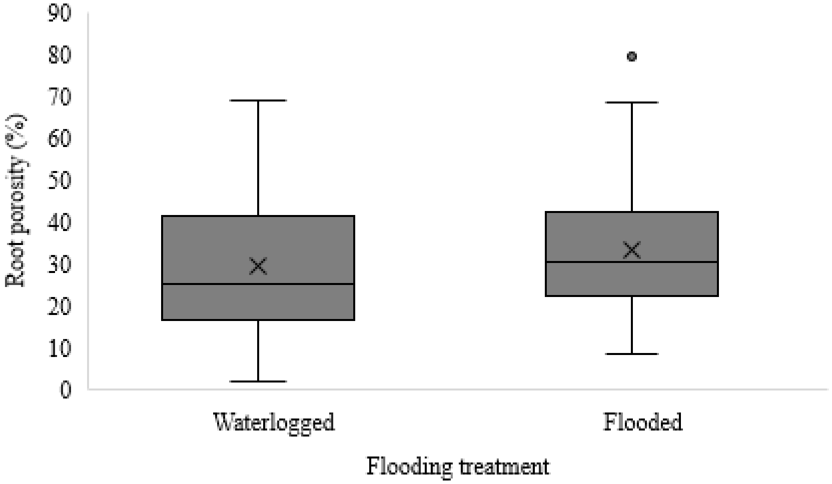

Figure 4S1A Boxplot of individual measurements of root porosity grouped by water regime (n=120).

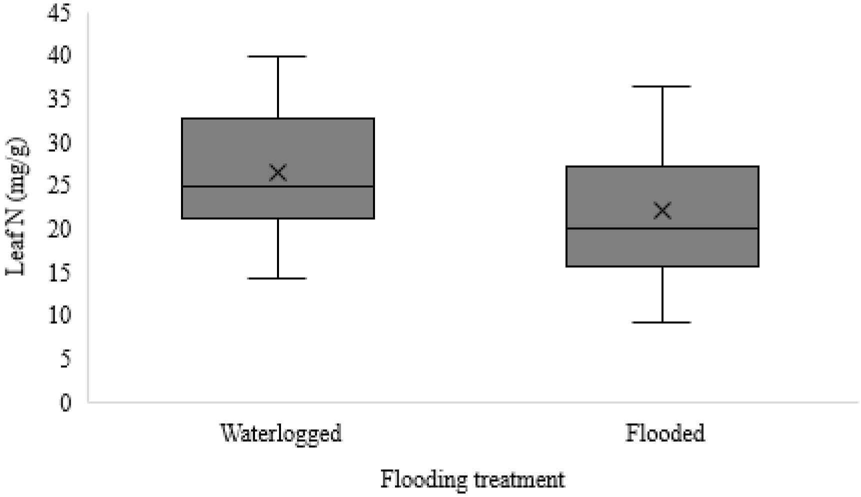

Figure 4S1B Boxplot of individual measurements of leaf N grouped by water regime (n=120).

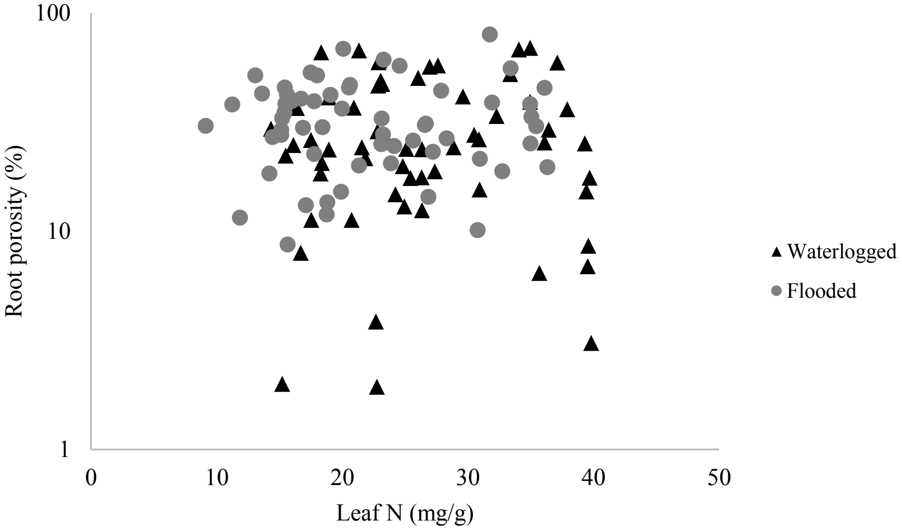

Figure 4S1C The relationships between root porosity and leaf N grouped by water regime (n=120).

2. Dataset from van Bodegom *et al.* 2005

In this study, five species representing pioneer or late-successional dune species living at dry to wet habitat were collected and cultivated in a greenhouse. Under all possible (16) combinations of treatments including light (shaded/full light), fertility (high/low), reduced metal concentrations (high/low) and water regime (waterlogged/field moisture) in six replicates for ten weeks, radial oxygen loss (ROL) and leaf N were determined. The ROL data were heavily zero-inflated (92 out of 209 measurements showed no ROL), so we grouped the ROL data into four classes. The first class contained all 92 measurements of no ROL, and remaining 117 points were evenly divided into the other three classes in the ascending order (39 measurements for each bin).

Class 0: ROL=0 µmol O_2 h^{-1} per g root dry weight, n=92; class 1: ROL=2.5 - 21.5 µmol O_2 h^{-1} per g root dry weight, n=39; class 2: ROL=21.6 - 85 µmol O_2 h^{-1} per g root dry weight, n=39; class 3: ROL=90 - 1212 µmol O_2 h^{-1} per g root dry weight, n=39.

Fig. 4S2A to Fig. 4S2D describe the how fertility (with/without nutrient addition), light availability (light/shade), water regime (flooded and waterlogged), toxicity affect leaf N and the relationships between the two traits. The relationships between leaf N and root porosity are shown in Fig. 4S2E. Fig. 4S2F shows the distribution of ROL classes under the above experimental treatments.

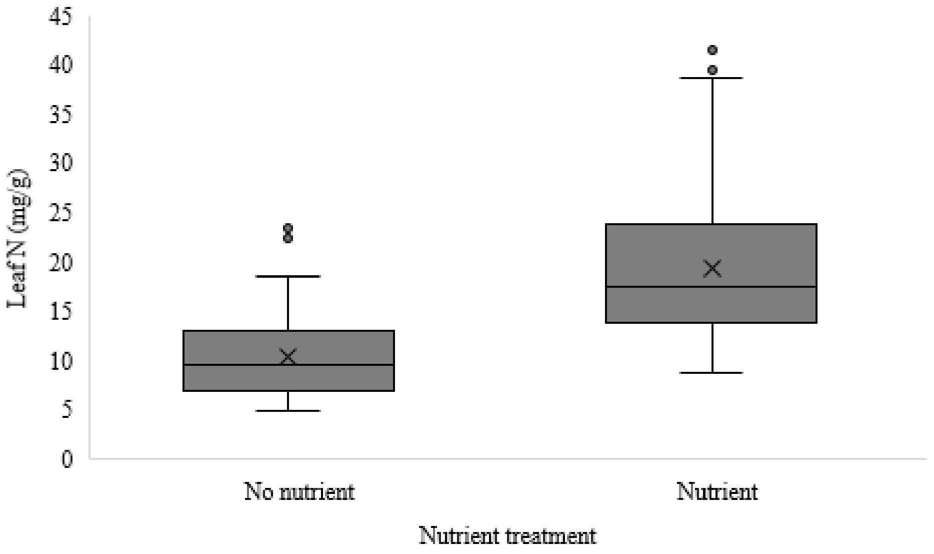

Figure 4S2A Boxplot of individual measurements of leaf N grouped by nutrient addition (n=209).

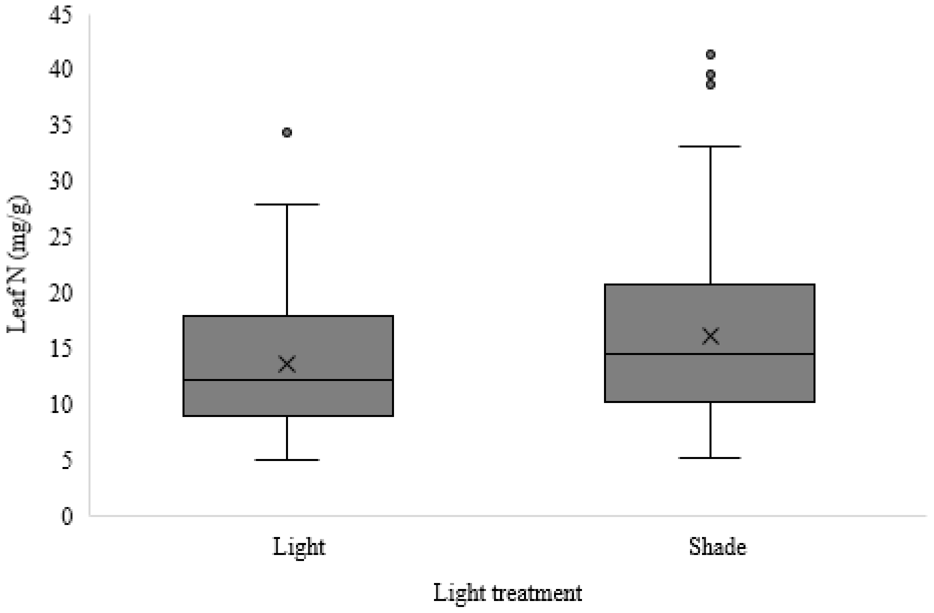

Figure 4S2B Boxplot of individual measurements of leaf N grouped by light availability (n=209).

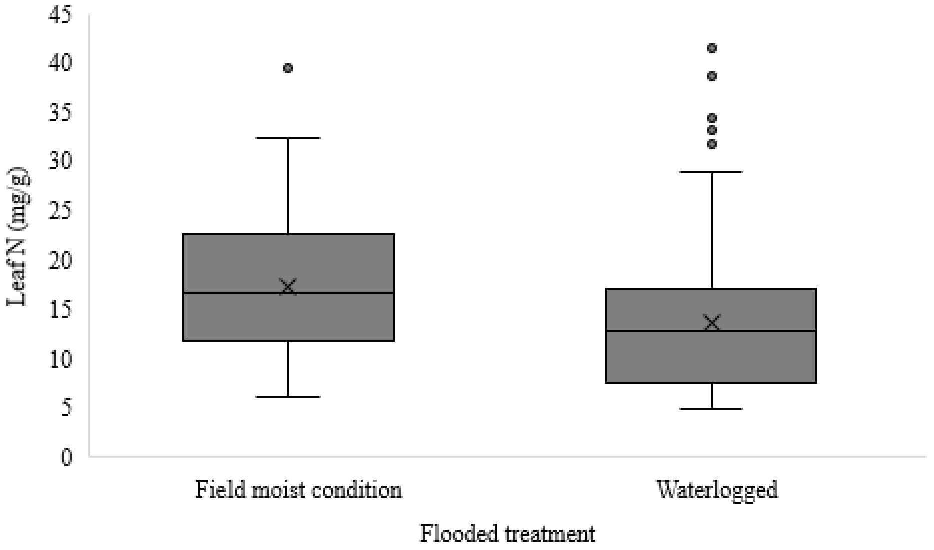

Figure 4S2C Boxplot of individual measurements of leaf N grouped by water regimes (n=209).

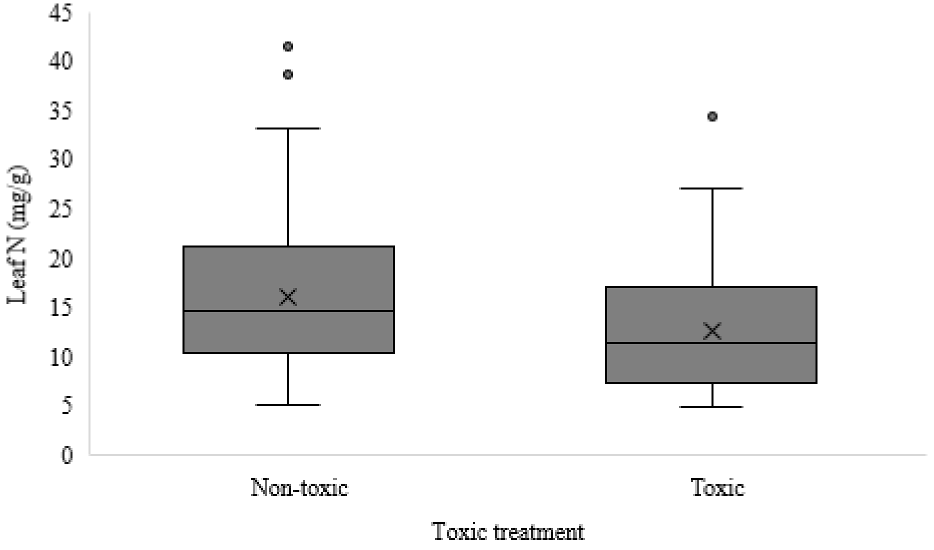

Figure 4S2D Boxplot of individual measurements of leaf N grouped by toxicity treatment (n=209).

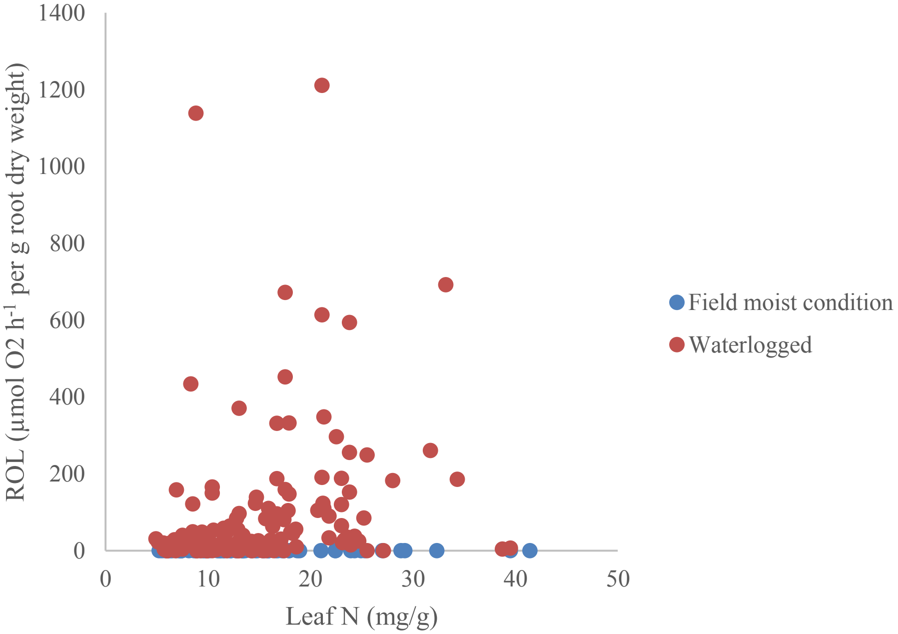

Figure 4S2E The relationships between ROL and leaf N grouped by water regime (n=209).

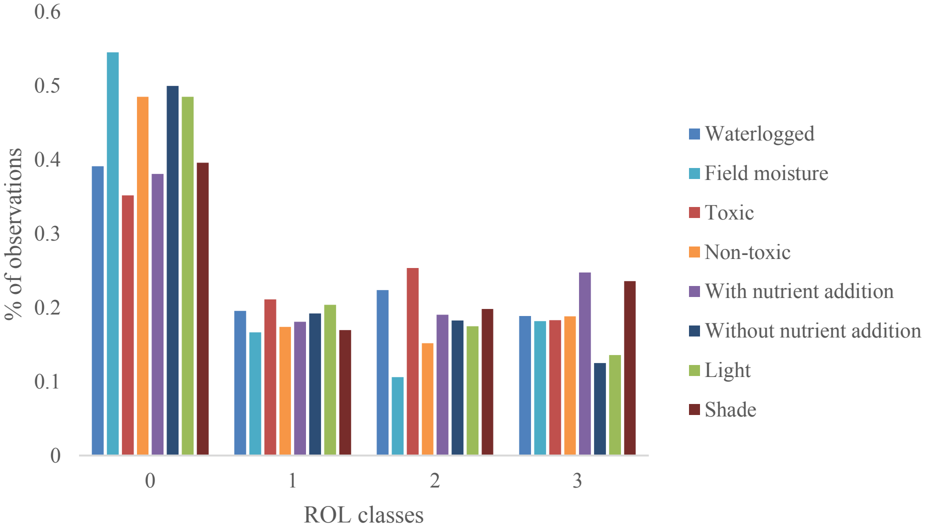

Figure 4S2F The distribution of ROL classes under each treatment.

3. Dataset from Snowden & Wheeler 1993

In this study, seedlings of 43 wetland species native to Britain were cultivated under experimental conditions for two weeks, in 10% Rorison solution containing iron (as ferrous sulphate) at concentration of 3.8 (control), 10, 25, 50,75 and 100 mg Fe/L. The relative growth rate (RGR) was calculated by:

*RGR (per day) = (final dry weight-mean initial dry weight)/ (mean initial dry weight*14)*

The standardized RGR (RGRc) was expressed as a percentage of the RGR to the control treatment. The iron tolerance index was then calculated as the sum of all treatments (except for the control). This index comprises the data available from this study (and can potentially range from 0 to 500%).

Field studies:

4. Dataset from Ukraine unpublished data (Van Bodegom, unpublished a).

In this study, root porosity and leaf N of 53 species from forested/shrub wetlands or marsh habitat were measured in the field. We used each species' Ellenberg indicator for nitrogen (Ellenberg N) and leaf N (both individual and species level) against the habitat types to indirectly show the fertility differences between habitats and how different habitats drive the leaf N (Fig. 4S3A to Fig. 4S3C).

5. Dataset from the Netherlands unpublished data (Van Bodegom, unpublished b).

In this study, 22 species from fen habitat were measured in the field for root porosity and leaf nitrogen. Data is displayed as together with those from field study 4 (Fig. 4S3A to Fig. 4S3C)

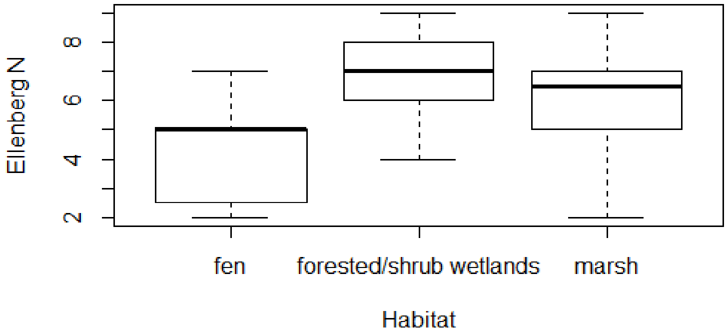

Figure 4S3A Boxplot of Ellenberg N value for species grouped by habitat type (n=40).

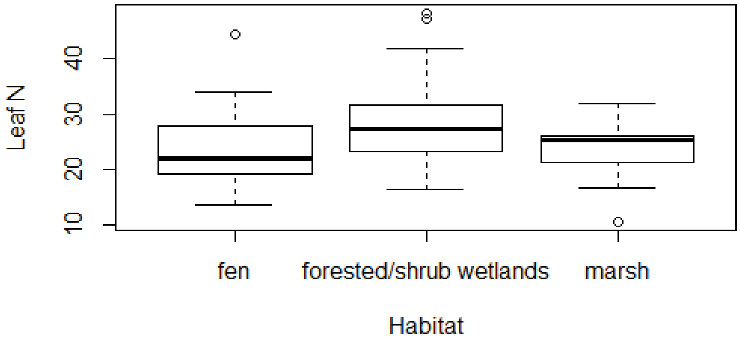

Figure 4S3B Boxplot of mean species' leaf N grouped by habitat type (n=83).

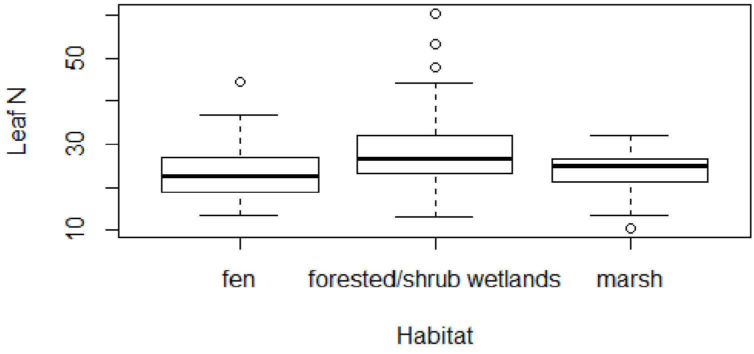

Figure 4S3C Boxplot of individual measurements of leaf N grouped by habitat type (n=147).

Chapter 5

Adaptive strategies are decoupled from leaf economics traits and size-related traits in wetlands

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Abstract

- Plants may have to cope with specific stresses, in addition to dealing with water, nutrient and light limitations. While trait-based approaches have provided critical insights in general plant functioning, we lack a comprehensive quantitative view on the role of adaptations to stressful habitats in plant strategies.
- We analysed trait-based plant strategies in wetlands, with its unique hydrological regime and oxygen limitations, and evaluated the relationships between three key traits indicative of adaptations to wetland conditions (root porosity, root/shoot ratio, shoot elongation) vs. leaf economics traits and size-related traits on a global scale. We evaluated how key trait dimensions are expressed along moisture gradients and between wetland habitats and life forms.
- Wetland adaptive traits are on different trait dimensions than leaf economics traits or size-related traits, indicating that there is no generic trade-off involved in adapting to wetland conditions. Moreover, we observed that adaptive traits themselves are to a large extent independent of each other. These results suggest that even plant strategies vital to surviving in stressful environments are species-specific without generic impacts on whole plant functioning.
- Hence, there are diverse strategies to promote plant adaptations and global plant distributions across multi-faceted stressful environments, such as wetlands. Our results provide a backbone for applying trait-based approaches in wetland ecology considering adaptive strategies as an additional key trait dimension. The decoupled trait dimensions in relation to environmental stressors and habitat resources may offer a promising path for a flexible wetland management approach for wetlands and stressful environments.

5.1 Introduction

To understand the functioning of organisms and the impacts of (a)biotic conditions thereupon, trait-based approaches are increasingly applied to surmount the boundaries across species groups of different life forms and habitat types. Trait-based ecology applies the concept of plant functional traits to study morphological, physiological, or phenological heritable features from the level of organisms to ecosystems (Lavorel & Garnier, 2002; Violle *et al.*, 2007, 2012), and to understand species strategies in terms of growth, production and survival (van Bodegom *et al.*, 2012; Reich, 2014). For plant species, the successful application of trait-based approaches has resulted in the concept of the leaf economics spectrum (Wright *et al.*, 2004). This conceptual framework allows plant strategies to be distinguished based on investment and turnover of resources to leaves, ranging from conservative to acquisitive strategies (Reich *et al.*, 1997; Wright *et al.*, 2004; Reich, 2014). Additionally, size-related traits are considered as another important but independent trait dimension in competition for light and water. The quantitative analysis of these two trait dimensions helps us to understand the fundamental strategies for plant growth, survival and reproduction (Diaz *et al.*, 2016). Applications of these two trait dimensions have led to increased insights into critical ecosystem processes, such as the feedbacks between litter decomposition and fire regimes (Cornelissen *et al.*, 2017).

In addition to dealing with various habitat resources, as expressed in these two trait dimensions, many plants have to adapt to specific stresses in their environment. Wetlands constitute one such environment and are distinguished from terrestrial ecosystems by frequent or permanent flooding, and consequent anaerobic soil conditions. The biochemical processes and their products constrained to anaerobic metabolic pathways can cause adverse impacts on plants that inhabit wetlands (Greenway *et al.*, 2006; Voesenek *et al.*, 2006; Pezeshki & DeLaune, 2012). Wetland plants have specific traits to deal with these stressful conditions (as have plants in other stressful environments, such as waxy leaves in deserts or dauciform roots at extreme phosphate deficiencies, e.g. Bakker *et al.* 2005). Previous studies on wetland plant traits have focussed largely on the eco-physiological aspects of such adaptations (Armstrong *et al.*, 1994; Visser *et al.*, 2000b; Colmer & Voesenek, 2009; Voesenek & Bailey-Serres, 2013). Consequently, adaptive traits, including root porosity, decreased root/shoot ratios, shoot elongation, gas film formation, and underwater photosynthesis, have been intensively examined (Voesenek & Bailey-Serres, 2015; Winkel *et al.*, 2016; Moor *et al.*, 2017). These studies have mainly concentrated on the trait expression of a single or few species within the local species pool, which forms a major barrier to apply trait-based approaches in wetland ecology (Moor *et al.*, 2017; Pan *et al.*, 2019). Thus, we still do not have a comprehensive trait-based view on wetland plant strategies at a broader scale (Pan *et al.*, 2019).

Moreover, it is yet unclear whether and how these traits adaptive to specific habitat stresses relate to the two dominant trait dimensions (i.e. leaf economics traits and size-related traits) (Pan *et al.*, 2019). Since wetland plant adaptive traits, leaf economics traits and size-related traits play important but ramified roles in wetland plant functioning, it is critical to understand whether and how these different groups of traits generally relate to each other (Pan *et al.*, 2019). Therefore, quantitative analyses on the trait interrelationships are fundamental towards a comprehensive view of wetland plant strategies and will significantly improve our knowledge of wetland plant strategies that balance survival, growth, and competition under wetland conditions on a global scale. Moreover, it will provide a basis towards a fundamental understanding on the position of adaptations to specific environmental stresses in comparison to other key trait dimensions.

The relation between wetland adaptive traits and both leaf economics and size-related trait dimensions can have multiple outcomes (Fig. 5.1). For example, if wetland adaptive traits are decoupled (i.e. independent or orthogonal) from leaf economics traits, it suggests that adaptive traits are quite cheap to develop. Therefore, adaptation to wetland conditions would not intrinsically hinder plant functions in relation to the acquisition or allocation of resources (Fig. 5.1, A). Wetland plants should therefore not be constrained by habitat resources when adapting to habitat wetness. If, on the other hand, wetland adaptive traits are tightly coordinated with leaf economics traits, it indicates that either adaptation to wetlands facilitates the other leaf functions in terms of resources acquisition (positively related; Fig. 5.1, B), or that wetland plants have to optimise their adaptation to wetness with a considerable cost for leaf economics traits (trade-offs; Fig. 5.1, C). If wetland adaptive traits are tightly correlated with size-related traits, it suggests that either larger plants may more easily outgrow the water column and profit more from aerenchyma tissues (Fig. 5.1, D) or need less shoot elongation (Fig. 5.1, E).

So far, evidence from previous studies seem to support the case of decoupled relationships (as shown in Fig. 5.1, A). One line of evidence is that the environmental drivers for the different trait groups are different with nutrient and water availability driving leaf economics traits, and light availability steering size-related traits (Reich, 2014; Diaz *et al.*, 2016), while the water regime and the consequent availability of oxygen to belowground (waterlogging) and aboveground (submergence) tissues are general driving factors for wetland adaptive traits (Colmer & Voesenek, 2009). Also the observation that global wetland habitats cover a wide fertility range (e.g. from oligotrophic bogs to eutrophic floodplains) suggest that a trait decoupling prevails. If there would be significant trade-offs between adaptive traits and leaf economics traits, we would find wetland plants to be constrained to some specific wetland types (Pan *et al.*, 2019).

In this paper, we test the hypothesis that wetland adaptive traits constitute an independent trait dimension from the other two dominant trait dimensions (i.e. leaf economics traits and size-related traits) in wetlands. We also hypothesize that the prevalence of traits adaptive to wetland conditions is closely aligned to the stress gradient in wetlands, as represented by habitat affinities of plant species to wetness. We analysed 7 key wetland plant traits: root porosity, root/shoot ratio and shoot elongation as representative of wetland adaptive traits based on their ecological importance and availability of quantitative records; leaf nitrogen (leaf N), leaf phosphorus (leaf P), and specific leaf area (SLA) to represent key leaf economics traits (Wright *et al.*, 2004; Diaz *et al.*, 2016); and plant height as representative of size-related traits. Through our analyses, we aim to understand the key trait dimensions related to wetland plant strategies across different species and biomes. We envision that this study may inspire research on the role of specific adaptations to habitat stress in trait-based strategies.

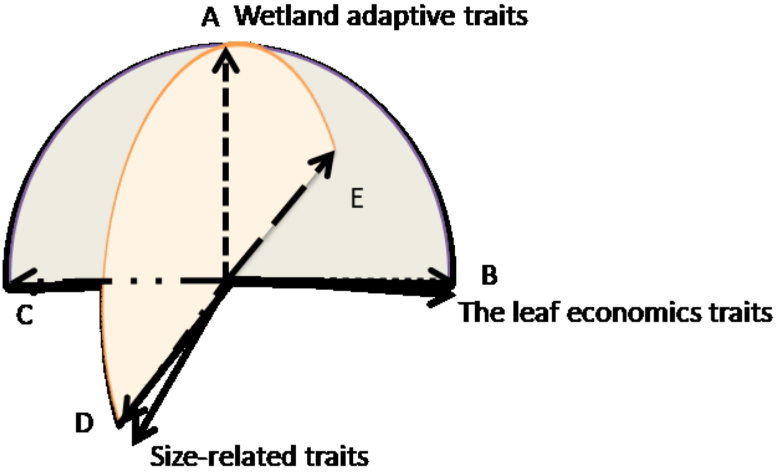

Figure 5.1 Possible positions of wetland adaptive traits (dashed lines) relative to the leaf economics trait and size-related trait axes (solid lines): A) wetland adaptive traits are decoupled from the leaf economics trait axis, indicating that adaptation to wetlands does not intrinsically hinder plant functions on resources acquisition or allocation; B) wetland adaptive traits are positively correlated to the leaf economics trait axis, suggesting that adaptation to wetlands facilitates plant functioning; C) wetland adaptive traits are negatively correlated to the leaf economics trait axis, implying costly trade-offs between adaptation and leaf functioning; D & E) wetland adaptive traits are correlated to the size-related trait axis, indicating the choices of varied wetland adaptive strategies depending on the plant size.

5.2 Materials and Methods

5.2.1 Data compilation

We compiled a global database of traits as prevailing in wetland plants. For this purpose, we defined wetland plants as those plants that occur in wetland habitats following the definition of the international Ramsar Convention (Ramsar Convention Secretariat, 2013). We compiled wetland plant traits under both field and laboratory measurements by a combination of expert knowledge of existing literature and systematic searches in Web of Science and Google Scholar (last search on the 5th of June 2018). The literature search included, but was not limited to, the following keywords: wetland, marsh, bog, floodplain, macrophytes, aquatic plants, hydrophyte, submerged, floating-leaved, emergent, isoetid, mangrove, root porosity, root/shoot ratio, shoot elongation, leaf N, leaf P, specific leaf area (SLA), leaf dry matter per unit area (LMA), plant height. We also checked the references of several important reviews of eco-physiological adaptive traits to wetlands and flooding events in the recent 15 years (e.g. Voesenek *et al.*, 2006; Bailey-Serres & Voesenek, 2008; Voesenek & Bailey-Serres, 2015). Moreover, we circulated enquiries around our network of wetland plant experts for recommendations for literature that we possibly had overlooked. We used The Plant List to eliminate synonyms in species names from our database (http://www.theplantlist.org). Our database is currently the largest database on wetland plant traits to our knowledge, containing more than 200 references for over 1200 species.

Root porosity was measured mainly as either the percentage of the hollow area in the root cross-section or the ratio of hollow volume to the whole root volume (these two methods generally show agreement in air-filled root porosity, while subtle differences between the two methods are discussed in Van Noordwijk & Brouwer, (1988)). Root/shoot ratio was measured by the root dry mass divided by the shoot dry mass. Shoot elongation was calculated as the percentage of the maximum shoot length increase upon submergence (%). We are aware that there are many other wetland adaptive traits (e.g. radial oxygen loss, leaf gas films) that have been emphasized in eco-physiological studies. However, they are either qualitative, or represented in our database by too few consistently measured observations to be included in our statistical analysis. We recorded the habitat type where each wetland plant species occurs. We added life form to each wetland plant species based on the descriptions in the original literature. For this study, we took species mean trait values to allow analysing trait-trait relationships (the distribution map of the sampling sites across the globe is shown in Fig. 5.2). Our analysis included a total of 131 wetland species of six life form categories (grass, sedge, emergent, submerged, floating-leaved and shrub/tree), with 113 species for root porosity, 60 species for root/shoot ratio, and 32 species for shoot elongation.

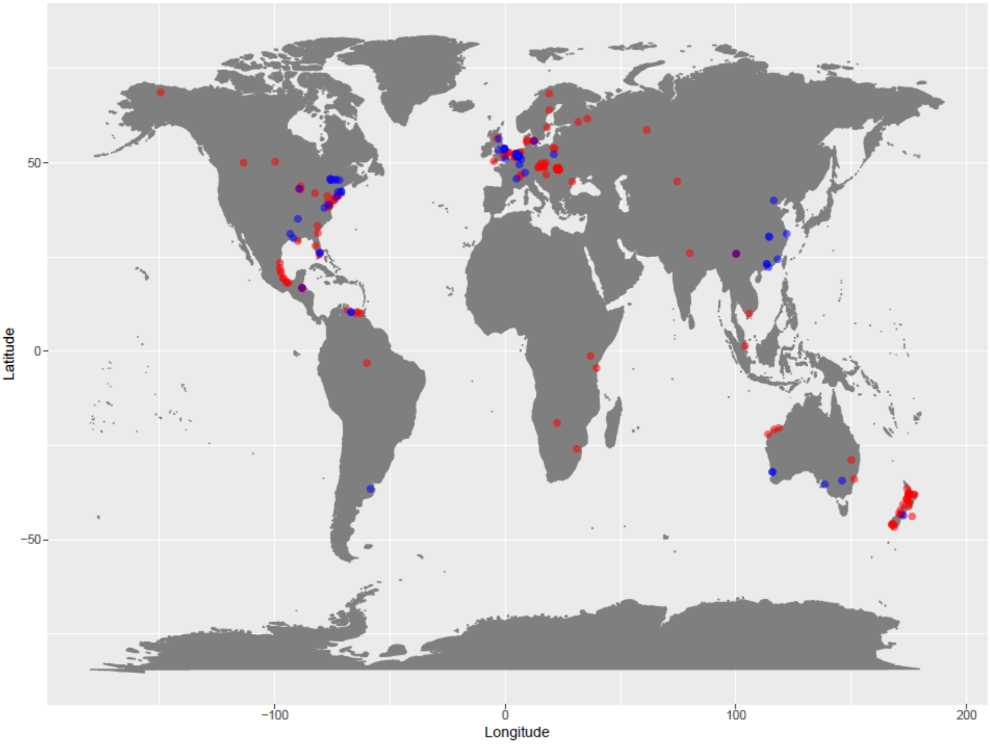

Figure 5.2 The location of the sampling sites. The field measurement data and laboratory measurement data are presented in red and blue dots, respectively. Note that the symbols are translucent and that brighter symbols indicate observations/studies at locations in close proximity of one another.

To investigate the effects of stress created by habitat wetness on trait expression, we applied the Ellenberg moisture indicator values (Ellenberg, 1988). These indicator values are based on expert knowledge of the distribution of plant species along a full gradient of habitat wetness, categorized into 12 levels from very dry habitats (level 1) to strictly aquatic (level 12). To make the Ellenberg moisture indicator applicable for a global analysis, we related the Ellenberg moisture indicator values to the USDA wetland plant classification to derive Ellenberg values for the flora of the USA (see details in Appendix 3B). In this study, the Ellenberg moisture indicator values were assigned to each wetland plant species for further analysis.

5.2.2 Data analysis

To reveal how wetland adaptive traits relate to the other two groups of traits at the inter-specific level, we conducted a principal component analysis (PCA) in R (R Core Team, 2018). Due to multiple gaps in the data set, we could not run a PCA on all of the traits selected in this study. Instead, we ran a PCA on each of the three adaptive traits separately with all leaf economics traits and size-related traits. The data points (one for each species) were labelled with their Ellenberg moisture indicator to represent each species' adaptation to habitat wetness, and their life form to present species' general characteristics of appearance. The data points labelled with habitat type are provided in Appendix 5A.

Then, we analysed trait-trait relationships between wetland adaptive traits by standardized major axis (SMA) analysis (Warton *et al.*, 2006) to estimate how one trait scales against another across samples (Warton *et al.*, 2012). The standardized axis slopes and coefficients of determination (R^2) were calculated using the sma() function in SMATR package (Warton *et al.*, 2012) in R (version 3.6.0) software (R Core Team, 2018). The traits data were $\log_{10}$ transformed before analysis.

Finally, we ran an ordinary linear regression to examine how each adaptive trait contributes to plants' adaptation to habitat wetness (as represented by Ellenberg moisture indicator values).

5.3 Results

The PCA on each of the adaptive traits along with the other two groups of traits showed that leaf economics traits were strongly related to PCA axis 1, with size and adaptive traits on the other axes. The detailed PCA scores on PCA axis 1 and PCA axis 2 are shown in Table 5.1.

Table 5.1 The loading scores of wetland adaptive traits, leaf economics traits and size-related traits on the first two PCA axes.

Root porosity			Root/shoot ratio			Shoot elongation		
	Axis 1	Axis 2		Axis 1	Axis 2		Axis 1	Axis 2
Root porosity	0.40	-0.42	Root/shoot ratio	0.03	-0.80	Shoot elongation	0.06	-0.87
Leaf N	-0.61	0.14	Leaf N	0.58	0.26	Leaf N	0.63	0.13
Leaf P	-0.51	-0.21	Leaf P	0.44	0.15	Leaf P	0.50	-0.14
SLA	-0.46	-0.31	SLA	0.57	0.00	SLA	0.40	0.38
Plant height	0.00	0.81	Plant height	-0.37	0.52	Plant height	-0.44	0.24
Var. explained	42.0%	22.8%	Var. explained	33.3%	20.6%	Var. explained	39.2%	21.8%

The PCA on root porosity as adaptive trait shows that root porosity was to a large extent decoupled from the leaf economics trait axis (as represented by leaf N, leaf P and SLA; Fig. 5.3A). Plant height (as representative of the size-related trait) was positioned on the third trait axis. The first two PCA axes accounted for 42.0% and 22.8% of the total variation, respectively.

Also the root/shoot ratio was to a large extent decoupled from the leaf economics trait axis (represented by leaf N, leaf P and SLA) and plant height as size-related trait (Fig. 5.3B). The first two PCA axes accounted for 33.3% and 20.6% of the total variation, respectively. The same applies to shoot elongation, which was decoupled from leaf economics traits and plant height as size-related traits. The first two PCA axes accounted for 39.2% and 21.8% of the total variation, respectively (Fig. 5.3C).

The trait-trait relationships between leaf economics traits and wetland adaptive traits were further examined by the standardized major axis (SMA) analysis. SMA analysis confirmed the largely decoupled nature of the trait-trait relationships. There were significant correlations between root porosity-SLA and root porosity-leaf N ($P<0.05$; Table 5.2). However, the root porosity-leaf N pair had only $R^2=0.22$, while the effect size of the root porosity-SLA pair was even smaller (only 9%). None of the other adaptive traits related significantly to any of leaf economics traits or size-related traits.

In addition, SMA analysis confirmed the significant strong correlations between the three leaf economics traits (SLA, leaf N and leaf P) (Table 5.2). However, there were no significant correlations among any of the pairs of wetland adaptive traits (i.e. of root porosity, root/shoot ratio and shoot elongation; $P>0.05$) tested, and the effect size R^2 was only between 0.00 to 0.02 (Table 5.2).

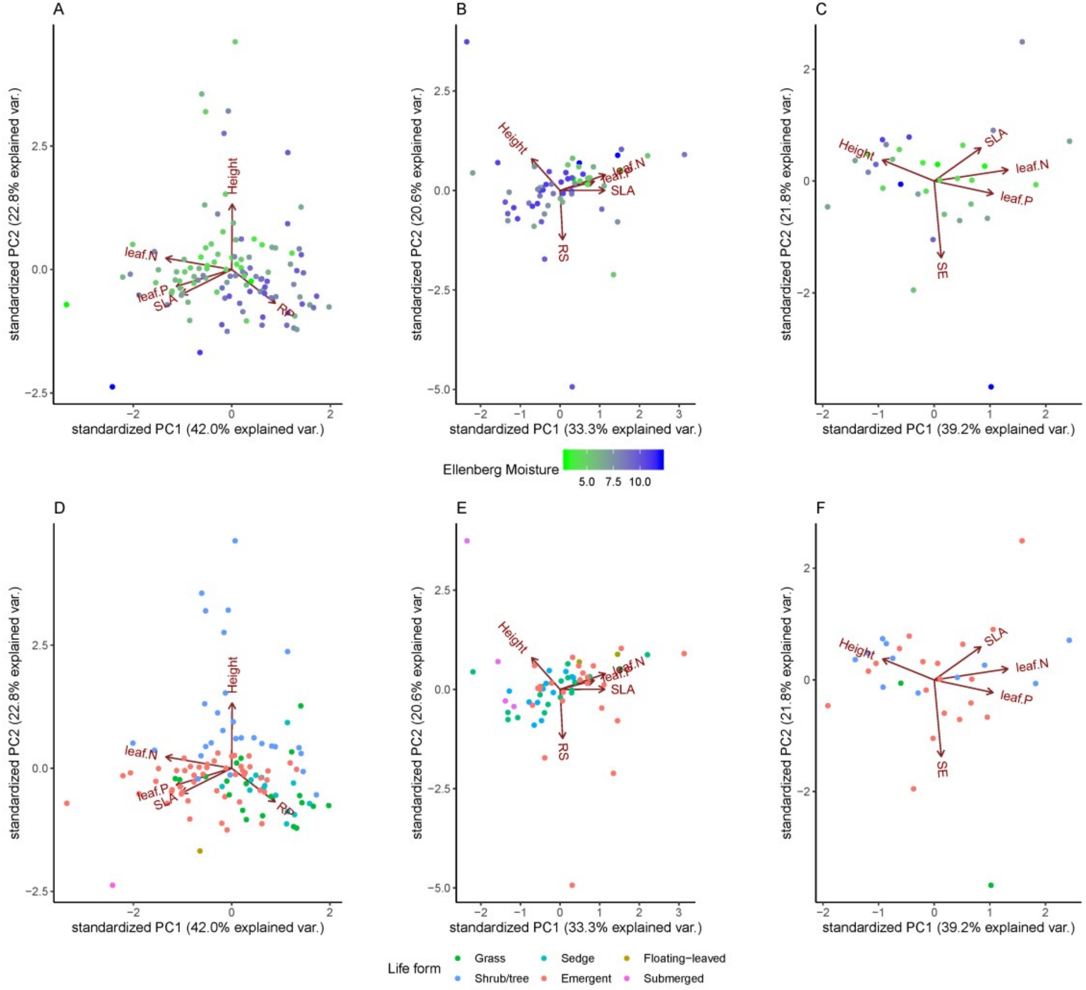

Figure 5.3 Principal Component Analysis (PCA) of leaf nitrogen (leaf N), leaf phosphorus (leaf P), specific leaf area (SLA), plant height (Height) and (A, D) root porosity (RP), (B, E) root/shoot ratio (RS) and (C, F) shoot elongation (SE) labelled by Ellenberg moisture indicator (A, B, C) and life form (D, E, F), respectively.

Table 5.2 Trait-trait relationships between leaf economics traits: specific leaf area (SLA), leaf nitrogen (leaf N), leaf phosphorus (leaf P); wetland adaptive traits: root porosity, root/shoot ratio, shoot elongation; and size-related trait: plant height. Traits were $\log_{10}$ transformed before analysis. The upper-right section shows standardized major axis slopes with 95% confidence intervals (referring to the y variable in the column and the x variable in the row). Coefficients of determination (R^2) and sample sizes are given in the lower-left section. Significant relationships ($P<0.05$) are highlighted in bold.

	Root porosity	Root/shoot ratio	Shoot elongation	SLA	Leaf N	Leaf P	Plant height
Root porosity		0.50 (0.37, 0.68)	1.15 (0.74, 1.80)	**-1.65 (-1.97, -1.38)**	**-2.74 (-3.23, -2.32)**	-1.86 (-2.23, -1.54)	-0.77 (-0.92, -0.63)
Root/shoot ratio	0.00 (n=44)		-1.56 (-2.41, -1.01)	-1.68 (-2.17, -1.30)	-2.93 (-3.79, -2.27)	-1.94 (-2.51, -1.50)	-1.05 (-1.36, -0.81)
Shoot elongation	0.02 (n=22)	0.02 (n=23)		-2.04 (-2.90, -1.43)	-3.21 (-4.62, -2.23)	1.81 (1.26, 2.60)	-0.99 (-1.42, -0.69)
SLA	**0.09 (n=113)**	0.03 (n=60)	0.07 (n=32)		**1.66 (1.43, 1.93)**	**1.07 (0.92, 1.26)**	**-0.47 (-0.56, -0.40)**
Leaf N	**0.22 (n=113)**	0.03 (n=60)	0.00 (n=32)	**0.28 (n=131)**		**0.65 (0.56, 0.75)**	-0.28 (-0.34, -0.24)
Leaf P	0.02 (n=113)	0.02 (n=60)	0.01 (n=32)	**0.17 (n=131)**	**0.25 (n=131)**		0.44 (0.37, 0.52)
Plant height	0.00 (n=113)	0.02 (n=60)	0.02 (n=32)	**0.07 (n=131)**	0.00 (n=131)	0.00 (n=131)	

None of the three adaptive traits seemed strongly related to differences in life form (Fig. 5.3D, E & F) or to the environmental conditions as summarized by wetland habitat type (Appendix 5A). To understand how an individual adaptive trait contributes to the prevalence of wetland plant species along a wetness gradient, we further tested the linear relationships between the Ellenberg moisture indicator and each adaptive trait (Fig. 5.4). Among the three adaptive traits, root porosity showed a significant relation with Ellenberg moisture indicator of a high effect size (R^2=0.31, P<0.001) and shoot elongation significantly explained 14% of the Ellenberg moisture indicator variance (R^2=0.14, P<0.05). There was no relationship detected between root/shoot ratio and Ellenberg moisture indicator (R^2=0.00, P=0.830). Hence, among the three adaptive traits, variation in root porosity and shoot elongation significantly contributed to the distribution of wetland plant species along a wetness gradient. Even though an increased root/shoot ratio is considered as an important wetland adaptive trait, it was not directly related to wetness adaptation.

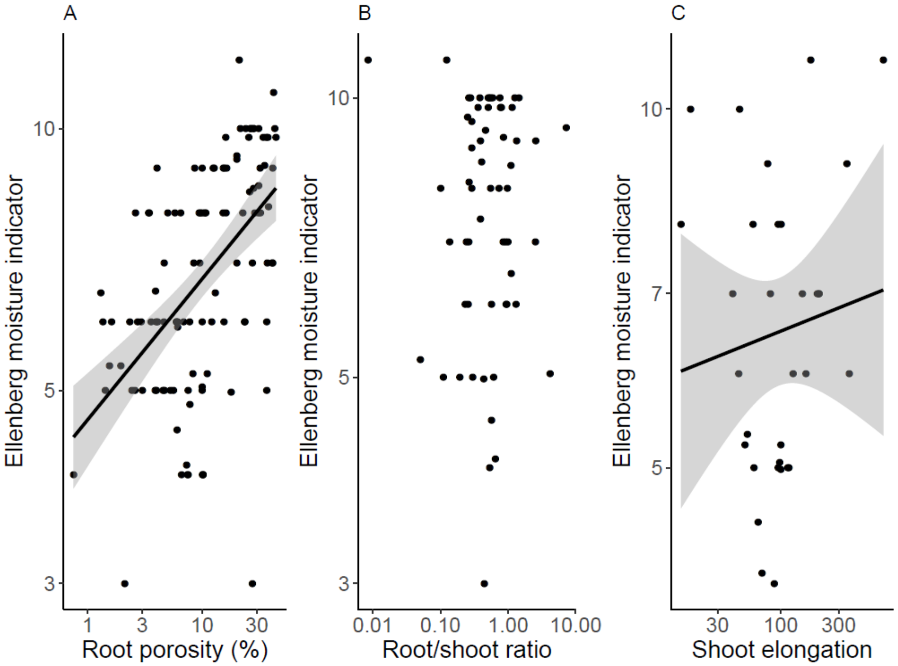

Figure 5.4 The linear relationships between Ellenberg moisture indicator and the three wetland plant adaptive traits. For root porosity (R^2=0.31, P<0.001, n=113), root/shoot ratio (R^2=0.00, P=0.830, n=60) and shoot elongation (R^2=0.14, P<0.05, n=32).

5.4 Discussion

5.4.1 Wetland adaptive traits as key component in wetland plant strategies

Based on the currently largest available dataset for wetland plant traits, our research explores the strategies of wetland plant species based on trait-trait relationships. Understanding the relationships between wetland adaptive traits, leaf economics traits and size-related traits will not only help us to understand wetland plant strategies in coping with the complex wetland conditions (including nutrient, light and flooding stress), but also provides a benchmark for upscaling the wetland plant traits to wetland ecosystems functioning (Moor *et al.*, 2017; Pan *et al.*, 2019).

Our research reveals that the three important wetland adaptive traits are, to a large extent, decoupled from the leaf economics and size-related trait dimensions (Fig. 5.3). Moreover, similar to the pattern in terrestrial systems, leaf economics traits and size-related traits also remain largely decoupled from each other in wetland ecosystems. This pattern suggests that besides leaf economics traits and size-related traits, wetland adaptive traits play an important but different ecological role in the adaptation to wetlands. As leaf economics traits relate to habitat fertility, and size-related traits confer a competitive power for light (and water), wetland adaptive traits mainly contribute to coping with the stressful aspects of wetland environments. Considering the tight associations between leaf economics traits and the root, stem and whole-plant economics spectra (Freschet *et al.*, 2010), we expect that wetland adaptive traits may also be decoupled from these traits of the whole plant. Together, these results indicate that the wetland adaptive strategies are a key dimension independent of other plant strategy components, such as growth and competitive strategies in wetlands.

The generally decoupled relationships between wetland adaptive traits and leaf economics traits provide an explanation for the broad distribution of aquatic plants (Santamaría, 2002; Chambers *et al.*, 2008) as they allow wetland plants to cope with both flooding stressors and habitat fertility limitations in a flexible fashion. This decoupling of adaptive traits from leaf economics traits may suggest that adaptation to wetland conditions is either cheap, or sufficiently beneficial to offset the costs of such adaptation on the wetland plant's overall resource budget. For example, with shoot elongation extra access to light, CO_2 and O_2 is gained (Colmer & Voesenek, 2009). However, the benefit of such extra access for the functioning of the underwater organs can still be limited (Rich *et al.*, 2013), and sometimes can be risky if leaves do not reach the air (Colmer & Voesenek, 2009). If flood is fast or deep, the cost for shoot elongation may offset the benefit from such adaptation from a nutrient acquisition and investment perspective (Voesenek *et al.*, 2004; Loreti *et al.*, 2016).

From a trait-based perspective, the decoupled wetland adaptive strategy from other plant strategy components may have wide implications for other stressful ecosystems. In nature, environment stressors, including drought, heat, freeze, shading, infertility and soil salinity, impose pronounced challenges to the adaptation and survival of plants (Bohnert *et al.*, 1995; Wolfe & Tonsor, 2014). While various adaptive mechanisms have been carefully examined from genetic, morphological to community points of view (Wolfe & Tonsor, 2014; Bechtold, 2018; Liu *et al.*, 2018), an integral perspective on plant's strategies as a whole is missing. We propose that other stressful environments may have similarly decoupled adaptive strategy components in response to those specific environmental stressors mentioned above. Such decoupled trait dimensions would allow plants to adapt to multifarious niche dimensions and facilitate species coexistence in stressful habitats (Westoby *et al.*, 2002; Li *et al.*, 2015).

5.4.2 Diverse plant strategies enable adaptations to a multi-faceted stressful environment

Despite their analogous functional roles in adaptations to wetland conditions, the interrelationships within the three wetland adaptive traits were all non-significant and weak (Table 5.2, P>0.05 with R^2 ranges from 0.00 to 0.02). Moreover, while root porosity and shoot elongation significantly contribute to the adaption of wetland plants along the gradient of stress induced by increasing wetness, root/shoot ratio is not directly linked to the patterns of the Ellenberg moisture indicator, life form or habitat type (Fig. 5.3, 5.4 & Appendix 5A). This suggests that the different adaptive traits are not similarly aligned to a wetness gradient, while these adaptive traits may contribute concordantly or accumulatively to the different aspects of the stressful wetland environment. We conclude that the driving mechanisms behind these different adaptive traits are complicated and likely highly case-specific for different wetland conditions, including the occurrence of anoxic substrate, phytotoxic compounds, and flooding events. For example, root porosity can be induced by waterlogging and provides more oxygen transport to the rooting system (Armstrong, 1980; Colmer, 2003a; Garssen *et al.*, 2015). Likewise, shoot elongation helps plants to reach above the water surface from fully submerged conditions to gain access to oxygen (Voesenek *et al.*, 2003; Nagai *et al.*, 2010), while root/shoot ratio is a proxy for oxygen balance within wetland plant tissues (Mommer *et al.*, 2004; Winkel & Borum, 2009).

Moreover, while mostly decoupled, some links were observed between wetland adaptive traits and leaf economics traits. For example, we detected an apparent trade-off between root porosity and leaf N at the inter-specific level (R^2=0.22, P<0.05; Table 5.2). The ecological causal links between root porosity and leaf N are complicated and experimental evidence has often been contradictory. On the one hand, the formation of root porosity impedes the nutrient acquisition efficiency and will lead to trade-offs (Kirk, 2003; Hu *et al.*, 2014). On the other hand, the production of large numbers of laterals in response to flooding conditions may increase the root surface area for nutrient acquisition (Lissner *et al.*, 2003). In addition, root porosity may positively coordinate with leaf N, because the oxygen released from the root, induced by increased root porosity, can oxidize nutrients such as NH_4^+ to NO_3^-, as the main source of stable and storable nitrogen for plants (Kirk, 2003). In our case, a reduced efficiency of nutrient transport by an incremented root porosity may exist at the inter-specific level, while evidence showed that such trade-offs seems extremely weak at the intra-specific level (Pan *et al.*, 2019).

We also observed weak but significant relations between root porosity-SLA (R^2=0.09, P<0.05; Table 5.2) and between plant height-SLA (R^2=0.07, P<0.05; Table 5.2). Even though the effect sizes are small (with 9% and 7%, respectively), it suggests SLA is a key trait interrelating with the three different trait dimensions simultaneously. Previous studies indicated that the relationships between SLA and to the position on flooding gradients could be either positive or negative depending on life form, season and community weighted SLA (Huber *et al.*, 2009; Violle *et al.*, 2011; Douma *et al.*, 2012; Wright *et al.*, 2017a). Even so, in general, amphibious/aquatic plants have a higher SLA than terrestrial plants (Mommer & Visser, 2005; Pierce *et al.*, 2012).

In combination, the specific connections between the traits of different trait dimensions indicate that the adaptation to wetland conditions involves rather complex and multifarious plant strategies as expressed in different plant trait dimensions. Apparently, multiple plant strategies across multiple trait dimensions have been developed to deal with these stressful environments.

5.4.3 Implications for ecosystem functioning & ecosystem management

Disentangling the relationships between wetland adaptive traits and leaf economics traits are also important for upscaling plant functional traits to wetland ecosystem processes, such as denitrification and methane emissions (Pan *et al.*, 2019). For instance, root porosity (an adaptive trait) helps to develop an aerobic rhizosphere (Engelaar *et al.*, 1993; Colmer, 2003b; Lai *et al.*, 2011) and affects both denitrification and methane emission processes, while leaf N and leaf P (leaf economics traits) are indicative of organic matter quality to support decomposition processes (Hobbie, 2015) and may hence enhance methane production (van Bodegom & Scholten, 2001; Bhullar *et al.*, 2013a). This may be further enhanced by the "chimney effect" of wetland plants, which is created by increased root and stem porosity, mediating methane transport to the atmosphere (Bhullar *et al.*, 2013a). The opposite driving forces complicate quantifying the facilitation vs. suppression role of wetland plants in methane emissions and denitrification. The decoupling between leaf economics traits (stimulating production) and adaptive traits (both stimulating and suppressing) further adds to the variation in impacts of wetland plants on these processes. Indeed, those influences are often considered to be species-dependent (Joabsson & Christensen, 2001; Laanbroek, 2010; Sutton-Grier & Megonigal, 2011). Our results thus highlight that precise and separate measurements are required of both adaptive traits and other key traits to adequately predict methane emission (Sutton-Grier & Megonigal, 2011; Bhullar *et al.*, 2013b).

Varied plant functional traits can enhance ecosystem management goals (Laughlin, 2014), and the decoupled patterns of adaptive, leaf economics and size-related traits can be useful for wetland environment management. Previous studies relate wetland adaptive traits to methane oxidation (Bhullar *et al.*, 2013b), water purification (Li *et al.*, 2013b) and heavy metal removal (Yang *et al.*, 2014). Leaf economics traits determine the biomass production and carbon sequestration potential of wetland ecosystems (Meerburg *et al.*, 2010; Lavorel, 2013; Doherty *et al.*, 2014). While size-related traits relate to the flooding abatement and storage potential (Bardgett *et al.*, 2014; Moor *et al.*, 2017). When adaptive traits, leaf economics traits and size-related traits are largely decoupled and correlated to different environmental drivers (such as water depth, fertility supply and plant community construction design, respectively), this implies that a flexible wetland management approach can serve different management goal by controlling different subsets of environmental conditions.

5.5 Conclusions

Our results reveal that wetland adaptive traits are largely decoupled from leaf economics trait and size-related trait dimensions, which suggests that traits adaptive to wetlands constitute an independent plant strategy dimension. This trait decoupling allows wetland plant species to cope with the multi-faceted stressful wetland environment (in terms of flooding, resources and competition). Our study indicates that no integral general strategy exists that explains the adaptation of wetland plants in coping with the complex wetland environments. Instead, the multiple facets of wetland plant strategies, as shown by the combination of functional traits including adaptive traits, leaf economics traits and size-related traits, allow wetland plants to survive in complex wetland environments and to prosper globally across a wide range of habitat fertilities. These insights provide a foundation to trait-based approaches towards understanding the general wetland plant strategies and the distributions of wetland plants worldwide and as well as to understanding adaptations to habitat stress in general.

5.6 Acknowledgements

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5.7 Authors' contributions

PvB initialized this research; YP, PvB and EC designed and planned the research. YP and PvB compiled the data with inputs from all co-authors. YP ran all analyses with inputs from all co-authors. YP, PvB and EC wrote the first drafts of the manuscript that was further improved by inputs from all co-authors, and finalized by YP. All authors contributed critically to the drafts and gave final approval for publication.

5.8 Data accessibility statement

Data used in this paper for analysis will be deposited in the Dryad Repository once accepted.

5.9 Supporting information

Appendix 5A

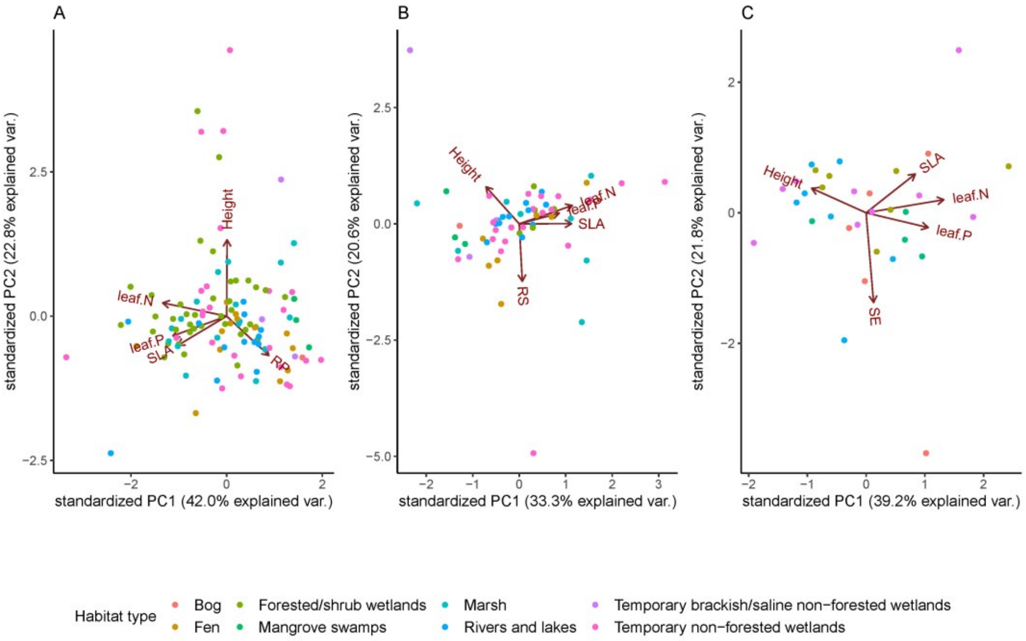

Figure 5S1 Principal Component Analysis (PCA) of leaf nitrogen, leaf phosphorus, specific leaf area, plant height and (A) root porosity, (B) root/shoot ratio and (C) shoot elongation labelled by habitat type.

Chapter 6

General discussion

The overall aim of this thesis was to apply trait-based approaches in wetland ecology to enhance our understanding of the wetland plant strategies and functioning in terms of adaptation to flooding (adaptive traits), resources acquisition and utilization (leaf economics traits) and competition (size-related traits). This chapter will synthesize the principal discoveries of the previous chapters and provide insights into the implications and directions for the future of trait-based wetland ecology studies.

This thesis reveals that wetland plant strategies are complex and flexible to specific wetland conditions, including different hydrological regimes, different fertility gradient and a range of light availability conditions (Chapter 2, 4 & 5). In addition, there seems to be a variety of driving mechanisms behind different wetland adaptive traits to cope with the flooding event in wetlands (Chapter 2). In terms of resources acquisition and allocation, wetland plants in general have a fast-return strategy but with relatively low respiration rates compared to other non-wetland plants (Chapter 3). When upscaling to wetland ecosystem functioning, wetland plants impact methane emission and denitrification processes through their functional traits (Chapter 4).

Trait-based approaches can be applied to wetland ecology by including three groups of traits, i.e. wetland adaptive traits, leaf economics traits and size-related traits, for their distinct ecological roles in wetlands (Chapter 4 & 5). The decoupled pattern of the three dominant trait axes in wetland plants not only reveals flexible wetland plant strategies in coping with the complex wetland conditions, but also provides the premise for studying the impact of wetland plants on ecosystem functioning (Chapter 4). The results of this thesis suggest the possibility of employing a flexible wetland management practice to enhance multiple ecosystem goals simultaneously through a separate control of individual environmental conditions in wetlands. This finding has wide implications for future wetland management and restoration.

6.1 Towards a trait-based wetland ecology

Plant functional traits are measurable properties of organisms, reflecting morphological, physiological or phenological characteristics, which impact the individual fitness through their effects on growth, reproduction and survival (McGill *et al.*, 2006; Violle *et al.*, 2007). Plant functional traits are therefore good proxies for quantifying the response of plants to their environment, and in turn, the impact of plants on the environment (Keddy, 1992). Moreover, plant functional traits can help us to explain and predict plant community assembly (Laughlin & Laughlin, 2013), and to understand plant strategies through projecting the different trait axes in the whole trait space (Kong *et al.*, 2014; Li *et al.*, 2015).

In contrast to the common driving factors (including rainfall, solar radiation, soil fertility and temperature) across a variety of terrestrial ecosystems, the main driver in wetlands is rather simply flooding and the consequent low redox potential (Colmer & Voesenek, 2009). The hydrological regimes in wetlands filter out plants lacking special capacities to adapt and prosper in wetlands. In this way, only those species with sufficient adaptive traits will survive (Visser *et al.*, 2000a; Pezeshki, 2001; Voesenek & Bailey-Serres, 2015). Thus, relatively tight associations between plant functional traits and their environment are expected in wetland ecosystems. Such species sorting processes according to their specific functional traits will consequently determine the vegetation community assembly in wetlands (Baastrup-Spohr *et al.*, 2015). As a result, wetlands provide a good system for the application of trait-based approaches, where ecological theories such as environmental filtering (Laughlin, 2014; Pan *et al.*, 2017), niche theories (Ellenberg, 1988; Van Veen *et al.*, 2013), and the mass ratio hypothesis (Engelhardt & Ritchie, 2001), can be tested and applied to understand community assembly and ecosystem functioning (Cornwell & Ackerly, 2009; Laughlin, 2014; Moor *et al.*, 2017).

When applying trait-based approaches in the context of wetland ecology, the well-studied plant functional traits, such as leaf economics traits and size-related traits, should be taken into consideration. Because these plant functional traits effectively represent the plant strategies towards resources acquisition and allocation, competition and reproduction across varied ecosystems at the globe (Chapter 3 & 5). At the same time, the unique adaptive traits that are fundamental and a prerequisite for plants to survive and thrive in wetlands should receive exceptional consideration (Voesenek *et al.*, 2006; Voesenek & Bailey-Serres, 2015; Pan *et al.*, 2019). This group of wetland plant functional traits provides good prospects in revealing the ecophysiological adaptive strategies, and quantifying the impact of plants on wetland ecosystems functioning (Chapter 5). Considering these different groups of traits together, along with the relationships among them, will give a comprehensive insight into plant strategies in terms of the resources allocation budget between survival, growth and competition.

Despite the scientific progress that trait-based approaches have provided on many other terrestrial ecosystems, the unique hydrological regime and the consequent distinct ecological processes in the substrate under the anoxic conditions make it hard to directly apply the trait-based concept to wetland ecosystems (Moor *et al.*, 2017). To begin with, the cost of adaptation to wetlands can be relatively expensive, and potential trade-offs between wetland adaptive traits and other trait axes may inevitably arise. The trait-trait relationships in wetlands can therefore be shifted and even deformed. As a result, the ecological principals found in other terrestrial ecosystems may demand careful correction before directly applied to wetlands (as discussed in Chapter 3 & 4). This is a fundamental step that needs to be clarified before exploring the wetland plant adaptive strategies based on trait-based approaches, and an important step towards trait-based wetland ecology (Moor *et al.*, 2017; Pan *et al.*, 2019).

To overcome these barriers and to, for the first time, apply trait-based approaches to wetland ecology at a global scale, this thesis is based on a purpose-built large wetland plants trait database. This global wetland plant trait database makes the quantitative analysis of wetland plant strategies possible from a trait-based perspective. The database included data both from published literature searching from Google Scholar and Web of Science and unpublished data contributed by collaborators. In total, the database included around 8000 observations of more than 1200 species from over 200 references. This thesis found that the correlations between wetland adaptive traits, leaf economics traits and size-related traits are very limited (Chapter 4 & 5).

The pattern of three largely decoupled trait axes makes it possible to distinguish the driving factors for each group of functional traits respectively. Moreover, the different driving factors for varied adaptive traits render wetland plants more flexibility in adaptation to the complex wetland conditions (Chapter 2). In addition, the leaf economics spectrum in wetland plants are presenting generally a fast-return strategy (Chapter 3). These preliminary findings are indicative for future trait-based wetland studies.

6.2 General strategies of wetland plants

For wetland plants, each group of functional traits reflects specific ecological roles. For example, wetland adaptive traits reflect the plant adaptive strategies for wetland conditions; leaf economics traits represent the strategies for resources acquisition and allocation; size-related traits indicate the capability to compete and reproduce. The positions of these different groups of traits in relation to each other reflect the plant strategies. If two suites of traits are coordinated, it suggests either facilitations or trade-offs between the two trait axes. If two suites of traits are decoupled to each other, it suggests two independent functioning sectors of the different plant strategies. Therefore, the positions of different groups of traits to each other reflect the plant strategies (Chapter 4 & 5).

Wetland plants need specific adaptive strategies to deal with the wetland conditions while in the meantime they have to manage their carbon budget to accommodate for other metabolic costs, such as growth and reproduction. This thesis reveals that the three dominant trait axes representing adaptive strategies, resources strategies and competitive strategies are largely decoupled (Chapter 5). This indicates that wetland plants can sufficiently cope with the multi-facetted wetland environment, including oxygen depletion, carbon/bicarbonate shortage and a range of nutrient conditions. Because otherwise, trade-offs between these trait axes should be observed. The generally decoupled relationships between wetland adaptive traits and leaf economics traits provide an explanation for the broad distribution of aquatic plants (Santamaría, 2002; Chambers *et al.*, 2008) as it allows wetland plants to cope with both flooding stressors and habitat fertility limitations flexibly without causing trade-offs between adaptations to wetlands and resources acquisition (Chapter 4). The decoupled relationships between wetland adaptive traits and leaf economics traits also suggest that the cost of adaptation to wetland conditions is generally cheap and flexible (Chapter 4 & 5). This warrants wetland plants to sufficiently cope with the complex wetland conditions, including flooding events, differences in habitat fertility and pressure from the competition (Chapter 5).

Moreover, many weak trait-trait relations were found among different adaptive traits despite their similar ecological roles. This suggests that wetland adaptive strategies are flexible depending on the specific situations and environmental stressors (Chapter 2 & 5), but there is no one ultimate solution to deal with the adverse wetland conditions (Chapter 5). The results also emphasize that instead of treating the occurrence of flooding events as the single main driving factor in wetlands, flooding events actually comprise a combination of complicated environmental stressors including inundation, lack of oxygen (low redox potential), low carbon sources (lack of CO_2 and HCO_3^-) and light limitation. Hence, when talking about adaptive plant strategies, it involves multiple wetland adaptive traits that collaboratively allow coping with specific wetland conditions.

With respect to the strategies that deal with resources acquisition and allocation, wetland plants generally show a fast-return strategy with a relatively low respiration rate. This leads to a potentially higher payback on leaf investment with a faster turnover of energy and biomass (Chapter 3). Such advantages may be a compensating mechanism for the extra adaptive costs on the anoxic conditions in wetlands because no further trade-offs have been observed for the adaptation to wetlands. However, the fast turnover and the leaf structure with low dry matter content per unit area may explain the high herbivory rate in aquatic systems, which may offset part of these advantages of aquatic plant species over other plant species (Cyr & Face, 1993; Cebrian & Lartigue, 2004).

6.3 Upscaling wetland plant functional traits to ecosystem functioning and ecosystem services

Wetland ecosystems provide more than 40% of global renewable ecosystem services while covering less than 3% of the global surface (Costanza *et al.*, 1998; Zedler & Kercher, 2005). The ecosystem services provided by wetlands include flood abatement, water quality improvement, biodiversity support, carbon sequestration and food provision (Zedler, 2003; Joyce, 2012). The wetland plant diversity and the functional traits strongly contribute to and determine ecosystem properties and the services they provide (Brauman *et al.*, 2007; Lavorel & Grigulis, 2012).

From a trait-based perspective, the effect of wetland plants on ecosystem functioning and services can be observed and quantified through the functional traits. Based on the well-known response-and-effect framework (Keddy, 1992; Violle *et al.*, 2007), plant functional traits can be grouped into effect traits and response traits (Laughlin, 2014). Response traits are those traits representing how species respond to changes of their surrounding environment (Keddy, 1992; Engelhardt, 2006), while effect traits can efficiently reflect the impact of plant species on ecosystem functioning (Lavorel & Garnier, 2002; Laughlin, 2014; van Bodegom & Price, 2015). There are many examples of how wetland plant traits affect ecosystem functioning. For example, the shape and size of wetland plants can reduce both temperature and light availability owing to shading effect (Carpenter & Lodge, 1986). Biomass and canopy structure of wetland plants can also retard flow speed (Carpenter & Lodge, 1986). Plants with higher root biomass apportioning tend to decrease substrate nutrient concentrations, while plants with a low root/shoot ratio commonly have a stronger effect on water column nutrients (Engelhardt, 2006). These ecosystem functioning components generate important ecosystem services. For example, the reduction of temperature and light availability of the water body can affect climate regulation services. Flood abatement capacity increases as the consequences of the flow speed detention. The removal of nutrients in the water column contribute to water purification.

Even though trait-based approaches provide opportunities to quantify and evaluate ecosystem services (Lavorel, 2013; van Bodegom & Price, 2015; Funk *et al.*, 2017), it is worth noting that the response-and-effect framework has its limitations. For example, the boundaries between response traits and effect traits are often vague, for response traits can have follow-on effects on ecosystem properties (Lavorel *et al.*, 2011). In addition, the links between plant traits and ecosystem services can largely depend on the trophic level investigated (de Bello *et al.*, 2010) and the relations between different ecosystem services (Bennett *et al.*, 2009;

Lavorel, 2013). Therefore, clarifying the ecological roles of certain wetland plant traits and quantifying trait-trait and trait-environment relationships are prerequisites for understanding wetland ecosystem functioning through trait-based approaches (Chapter 4).

Some other constraints come from data limitations at a broader spatial scale. For example, the trait-based approach has been successfully applied to understand the effects of plants on wetland methane emission at a local scale (Sutton-Grier & Megonigal, 2011; Pan *et al.*, 2019). Linking specific wetland plant traits (both adaptive traits and leaf economics traits) to methane emission processes indeed provides a promising framework for the future of global wetland ecological modelling. However, despite the critical role of wetland plant traits in methane production and emission (Sutton-Grier & Megonigal, 2011; Bhullar *et al.*, 2013a,b), the current state-of-the-art models for global wetland methane emissions mainly only focus on the abiotic drivers, such as wetland area, temperature, the soil carbon pool, and water tables (Melton *et al.*, 2013; Wania *et al.*, 2013). Few models, such as CLM4Me and LPJ-WHyMe, have considered the effect of plants, but only to a very limited extent by setting constant plant functional types (PFTs) parameters (Wania *et al.*, 2010; Riley *et al.*, 2011). Such limitations may partly explain the large discrepancy between the top-down methods (based on the satellite monitoring and inverse estimation of methane sources) and bottom-up methods (the process-based models for methane sources and upscaling to the global methane budget) (Bridgham *et al.*, 2013).

The current use of insufficient plant trait data in these models provides a prospect of applying trait-based approaches to improve the accuracy of global methane models. One solution to this problem would be replacing the PFTs by continuous plant functional traits, because plant functional traits can better capture the variance along the environmental gradient (van Bodegom *et al.*, 2012; Verheijen *et al.*, 2013). Such an idea of incorporating continuous functional traits to improve model accuracy has been implemented in the dynamic global vegetation models (DGVMs) in non-wetland terrestrial ecosystems (van Bodegom *et al.*, 2012, 2014). For wetlands, an equivalent approach would be to incorporate known plant traits, including methane oxidation and transportation correlations into a methane model as a new component under the ecophysiological study framework (Chapter 4). Instead of assigning fixed values to each PFT, trait-based approaches will be able to present the effect of trait variations on the ecological processes. For example, radial oxygen loss (ROL) has been related to methane emission in many studies (Ribaudo *et al.*, 2017; Zheng *et al.*, 2018). However, this trait has been only set to a fixed value depending on the plant life form in global methane models (Riley *et al.*, 2011; Xu *et al.*, 2016). Therefore, using the continuous ROL values to quantify the methane emission processes provides great potential for the improvement of global methane model accuracy. This emphasizes the power of establishing a global wetland plant trait database to improve our knowledge of wetland plants and ecosystem functioning (as proposed in section 6.1).

6.4 Implications for wetland ecosystem management and restoration

Ecosystem management goals can be enhanced by optimised plant functional traits through response-and-effect trait framework (Laughlin, 2014). Theories such as environmental filtering, niche complementarity, limiting similarities, can be applied to set certain trait targets (Laughlin, 2014). For example, we can manipulate the key environmental factors as environmental filters to select the ideal functional traits of certain species from the regional species pool (Keddy, 1992), and consequently enhance the underlying ecosystem services.

To achieve ecosystem management and restoration goals, we firstly need to recognize the quantitative relationships between environmental driving factors and the plant functional traits. Based on these relationships, we can then manipulate wetland plant traits through the control of environmental drivers, and consequently optimise certain ecosystem services. Moreover, an understanding of the trade-offs among traits and their selection by environmental drivers can help to better understand the multiple (and non-linear) relationships among ecosystem services (Bennett *et al.*, 2009). Understanding the driving mechanisms and interactions behind the multiple ecosystem management practices will maximize the coherency and aggregation of the different ecosystem services (Bennett *et al.*, 2009; Lavorel, 2013).

This thesis reveals that the strategies of wetland plants in terms of adaptation, growth and competition are largely independent. The main trait axes, including wetland adaptive traits, leaf economics traits and size-related traits that present these strategies are largely decoupled (Chapter 5). This finding has profound implications for future wetland ecosystem management from a trait-based point of view. It indicates that we can achieve multiple goals at the same time with a flexible wetland management practice through the control of individual environmental factors to optimise each specific plant trait axis (Chapter 5). By aiming at the three independent trait axes of wetland plants, we can approach and carry out wetland management practices individually for different management objectives (as shown in Figure 6.1):

a) The wetland adaptive traits dimension can be generally adjusted through controlled water depth (e.g. through water supply/drainage to the site and micro-relief construction designs) (Kutzbach *et al.*, 2004; Garssen *et al.*, 2015). The optimised adaptive traits can contribute to ecosystem functioning, such as methane oxidation (Van Der Nat & Middelburg, 1998; Bhullar *et al.*, 2013b), water purification (removal of ammonia through nitrification processes) (Li *et al.*, 2013a) and heavy metal removal (Li *et al.*, 2011; Yang *et al.*, 2014). This demands careful control of specific hydrological conditions, given their strong relationships to biogeochemical processes in wetlands (Zedler, 2000).

b) The leaf economics spectrum trait dimension can be managed through regulating the habitat fertilizer supply (Villagra *et al.*, 2013; Cantarel *et al.*, 2015). The plants with fast-return strategies usually favour habitats with a higher nutrient supply, and consequently stimulate the nutrient cycling and a high community biomass production (Reich, 2014). This can achieve ecosystem service goals for biofuel production (Meerburg *et al.*, 2010; Doherty *et al.*, 2014) and carbon sequestration (Lavorel, 2013). However, special attention needs to be paid to the side effect of nitrogen addition, which is the stimulation of the greenhouse gas emissions (Liu & Greaver, 2009) and concomitant reduction of the ecosystem service of carbon sequestration.

c) The size-related traits dimension can be optimised through community assembly design and restoration (Navas & Violle, 2009). An increased canopy height can correlate with plant density and leaf area index. These traits synergistically enhance the capacity for flow resistance (Nepf, 2012; Moor *et al.*, 2017). Other size-related traits, such as root length and rooting depth, can enhance soil pore volume and water holding capacity (Bardgett *et al.*, 2014; Moor *et al.*, 2017). These traits together contribute and improve the ecosystem services for flood abatement and storage.

Some specific ecosystem services are tightly correlated to only one of the trait dimensions above. Such as heavy metal absorption correlates to wetland adaptive traits; while the nutrient removal correlates to leaf economics traits (Figure 6.1). Therefore, the correlations between the two ecosystem services (heavy metal absorption vs. nutrient removal) can be weak. In this case, we can manipulate the independent trait dimensions separately for varied goals.

However, there are ecosystem services in which multiple functional trait dimensions are involved. For example, biodiversity generally provides a variety of ecosystem services (Kremen, 2005; Harrison *et al.*, 2014). In our three-trait dimension paradigm of wetland plants, biodiversity is affected by different trait dimensions simultaneously, and is potentially determined by multiple management practices together (Figure 6.1). Consequently, trade-offs are inevitable for biodiversity enhancement and the optimization of individual ecosystem services generated on each of the three wetland plant trait axes. This emphasizes that we should carefully deal with the complexity in wetland ecosystem management. Therefore, the primary ecological principles that are crucial in the restoration of wetlands should be carefully considered (Zedler, 2000).

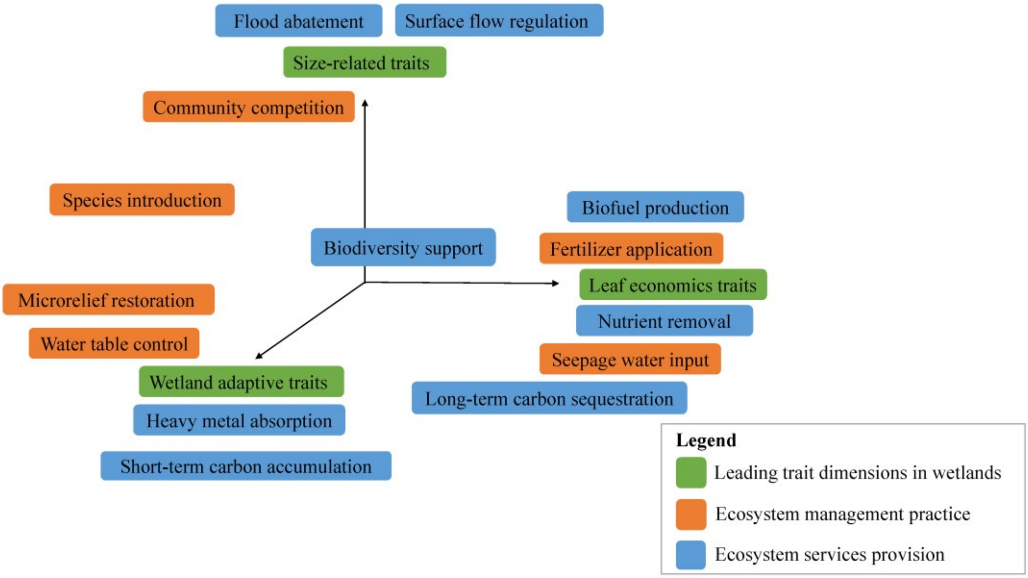

Figure 6.1 Conceptual scheme of the three decoupled trait dimensions in wetland plants with corresponding ecosystem services provision and related ecosystem management practices.

Even though we have theoretically proposed the possibility of realizing multiple wetland management goals through the controlling of the three decoupled trait dimensions, we still lack a systematic experimental verification on these practices. Future control experiments need to be carried out to test how the management of one trait axis may influence other trait axes, and the ecosystem services provided thereof. This will give a direction for future ecological application research.

6.5 Concluding Remarks

Wetland ecosystems are even more complex than many of other terrestrial ecosystems. Besides the competition for resources such as nutrient and light, wetland plants have to cope with the flooding stress and the consequent adverse products of the anoxic environment. This thesis discusses the general strategies of wetland plants in terms of adaptation and addresses how the strategies of wetland plants differ from those of terrestrial plants. The relative flexible adaptive strategies of wetland plants allow plants to cope with the complex stressors in wetland ecosystems. Based on the trait-based approach, we can quantify the wetland plant strategies and their impact on the ecosystem functioning on a broader scale. The pattern and relationships derived in this study have wide implications for future wetland management and restoration. This thesis demonstrates a promising perspective on the application of the trait-based approaches to wetland ecology.

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Summary

Wetland ecosystems provide important ecosystem services including water purification, flood abatement, biodiversity support and carbon sequestration. Wetland ecosystems are distinguished from non-wetland terrestrial ecosystems by their unique hydrological regime and consequent anoxic substrates. The quick depletion of oxygen in the rhizosphere and associated biogeochemical processes can cause the potential accumulation of phytotoxic compounds. Specifically, the utilization of electron acceptors alternative to oxygen results in the production of toxic chemical matter, including ferrous iron, sulphide and low-weight monocarboxylic acids (e.g. acetic, propionic, butyric and hexanoic acids).

To cope with the adverse environmental conditions and survive in wetlands, wetland plants have developed a suite of ecophysiological adaptive traits. Such traits include root porosity, shoot elongation, a decreased root/shoot ratio, a root radial oxygen loss (ROL) barrier, leaf gas films, and enhanced underwater photosynthesis. These adaptive traits do not only ameliorate the oxygen deficit in plant tissues and improve aerobic metabolism. Moreover, ecophysiological researches have shown that these traits also affect the biogeochemical processes in the sediment through enhancing the plants' inner aeration and releasing excess oxygen to the rhizosphere. However, previous studies on wetland ecophysiological adaptive traits mainly discussed these principles for single or few plant species across a local species pool or under experimental conditions only. Therefore, we lack the understanding of the general drivers of these adaptive traits at regional to global scales - a knowledge gap this thesis addresses. Chapter 2 explores the general potential drivers of wetland adaptive traits (root porosity, root/shoot ratio and underwater photosynthetic rate) at a broader scale, and reveals that bioclimatic variables (temperature and precipitation) are strong drivers for all of the three adaptive traits. Additional locally important drivers, e.g. local habitat, hydrology and plant life form, are also involved, but in different ways for each of these traits. This suggests that a variety of mechanisms affect the local expression of different adaptive traits.

Next to wetland adaptive traits that are critical for plants to survive in wetlands, leaf economics traits that express how plants acquire and allocate resources and are crucial in terrestrial systems may also play an important role. However, whether and to which extent this leaf economics spectrum (LES) also exists in global wetland ecosystems has remained unknown. In addition, the cost and consequent trade-offs in resources budget may modify the LES pattern compared to non-wetland terrestrial ecosystems. Chapter 3 tests the LES in global wetlands ecosystems and reveals that wetland plants in general show shifted trait-trait relationships, compared to non-wetland plants, with lower leaf mass per area, higher leaf nitrogen and phosphorus, faster photosynthetic rates, and shorter leaf life span. The different leaf structure and functioning of wetland plants may be the cause for a faster turnover of energy and biomass, and a potentially higher payback on leaf investment.

Chapter 4 reviews the important but distinct ecological roles of wetland adaptive traits and leaf economics traits, and proposes to incorporate the two suites of traits into a trait-based wetland ecology by first understanding the interactions between these two suites of traits. Chapter 4 shows that the two groups of traits may be largely decoupled based on preliminary evidences, indicating that there can be multiple mechanisms behind the strategies of wetland plants in terms of resources acquisition and survival under wetland conditions. Chapter 4 also illustrates from a conceptual view how wetland adaptive traits and leaf economics traits together impact wetland ecosystem functioning. The potentially decoupled relationships between the two groups of traits provides possibilities to quantify the functioning such as methane emission and denitrification processes.

Chapter 5 demonstrates that wetland adaptive traits, leaf economics traits and size-related traits are indeed along three independent trait axes, based on a comprehensive analysis of global trait database. This suggests that wetland plants have rather flexible strategies in adaptation, resources acquisition and competition, respectively.

In conclusion, this thesis reveals that wetland plants have flexible strategies in coping with the complex stressors in wetlands. Wetland plant adaptive strategies can be cheap to develop without necessarily causing trade-offs with other strategies (such as with leaf economics traits). In the meantime, even though ecological roles of different wetland adaptive traits are similar, the correlations between different wetland adaptive traits can be weak, and the driving mechanisms can be different. This provides a flexibility to wetland plants in adapting to different wetland environmental conditions, such as oxygen shortage, submergence, and phytotoxic compounds in the substrate. The largely independent strategies of wetland plants in relation to growth, competition and adaptation imply that flexible wetlands management practices are possible on the different trait dimensions. Through the control of individual environmental driving factors for each trait dimension separately, we can potentially achieve multiple management goals concurrently to optimise the ecosystem services provided by wetlands.

Samenvatting

Waterrijke ecosystemen zoals vennen en moerassen leveren belangrijke ecosysteemdiensten voor onze samenleving, b.v. waterzuivering, het voorkomen van overstromingen, het ondersteunen van biodiversiteit en het vastleggen van koolstof. De waterrijke ecosystemen onderscheiden zich van andere terrestrische ecosystemen door hun unieke hydrologische regime en de daaruit voortvloeiende leefomstandigheden waarin zuurstofbeschikbaarheid beperkend is. Rond de plantenwortels wordt zuurstof snel opgebruikt door de micro-organismen en planten. De biogeochemische processen die optreden onder deze zuurstofloze condities leiden tot de ophoping van stoffen die potentieel toxisch zijn voor planten. Hierbij valt te denken aan chemische stoffen zoals gereduceerd ijzer, sulfide en carbonzuren (b.v. azijnzuur, propaanzuur en boterzuur).

Om in dergelijke waterrijke ecosystemen te overleven, hebben planten zich aangepast met een diverse set aan ecofysiologische eigenschappen. Dit soort eigenschappen zijn b.v. de porositeit van wortels, de mate waarin stengelstrekking plaatsvindt, een aangepaste verhouding tussen wortel en spruit, barrières om het lekken van zuurstof uit wortels te voorkomen, luchtlaagjes rond het blad en versterkte fotosynthese onder water. Deze eigenschappen verbeteren de zuurstofbeschikbaarheid in de plant en hun metabolisme, maar beïnvloeden ook de biogeochemische processen in het sediment. Dit komt doordat deze eigenschappen leiden tot een verbetering in de beluchting van de plant en tot het lekken van het zuurstofoverschot naar de wortelzone. Eerdere studies aan deze adaptieve eigenschappen hebben vooral deze principes bediscussieerd voor één of enkele plantensoorten binnen een lokale soortengemeenschap of puur onder experimentele omstandigheden. Daarom missen we inzicht in de generieke sturende factoren van deze eigenschappen op regionale en mondiale schaal.

In hoofdstuk 2 presenteren we de eerste verkenning van de mogelijke generieke sturende factoren van adaptieve eigenschappen in waterrijke gebieden op een groter schaalniveau. We vonden dat klimatologische variabelen (temperatuur en neerslag) belangrijke sturende factoren zijn voor drie onderzochte eigenschappen; wortelporositeit, wortel:spruit verhouding en onderwater fotosynthese. Aanvullende sturende factoren op lokaal niveau, zoals de lokale leefomgeving, hydrologie en de levensvormen van de planten, werkten op verschillende manieren door voor elk van deze eigenschappen. Dit suggereert dat er een verscheidenheid aan mechanismen actief is die de lokale expressie van de verschillende adaptieve eigenschappen bepaalt.

Naast de adaptieve eigenschappen die cruciaal zijn voor de overleving van planten in waterrijke gebieden zijn ook de zogenaamde ''blad-economische'' eigenschappen van belang. De blad economie drukt uit hoe planten hun hulpbronnen verkrijgen en herverdelen.

Het was –tot dit proefschrift- onbekend of er ook een blad-economie bestaat in de mondiale waterrijke ecosystemen. Aangezien aanpassingen aan deze ecosystemen kosten en trade-offs met zich meebrengen, zou de blad-economie anders tot uitdrukking kunnen worden dan in terrestrische ecosystemen. In hoofdstuk 3 testten we daarom de aanwezigheid van een bladeconomie tussen waterrijke ecosystemen van over de hele wereld. We vonden dat eigenschappen van plantensoorten uit waterrijke gebieden verschoven zijn ten opzichte van die van drogere ecosystemen. In het algemeen hebben ze een lagere bladmassa per oppervlakte met hogere concentraties aan stikstof en fosfaat in het blad, een snellere fotosynthese en een kortere levensduur van het blad. De andere bladstructuur en verschillend functioneren van plantensoorten zou een verklaring kunnen zijn van de snellere omzettingen van energie en biomassa in waterrijke gebieden en van de noodzakelijke kortere terugverdientijd van investeringen in bladbiomassa.

Hoofdstuk vier gaf een literatuuranalyse van de verschillende rollen van adaptieve eigenschappen vs. eigenschappen gekoppeld aan de bladeconomie. Op basis van die analyse stellen we voor de verschillende rollen van deze groepen eigenschappen duidelijk te onderscheiden om de ecologie van waterrijke gebieden beter te begrijpen. Een beter begrip van de interacties tussen deze groepen eigenschappen is daarbij cruciaal. Hoofdstuk 4 toont aan dat deze groepen van eigenschappen grotendeels ontkoppeld zijn. Dit impliceert dat er verschillende mechanismen actief zijn rond het verkrijgen van hulpbronnen en overleving en dat die mechanismen gezamenlijk de strategie van plantensoorten in waterrijke ecosystemen bepalen. Deze visie illustreren we in hoofdstuk 4 met een conceptueel schema over hoe adaptieve en blad-economische eigenschappen gezamenlijk het functioneren van waterrijke ecosystemen beïnvloeden. Doordat deze groepen van eigenschappen mogelijk ontkoppeld zijn, geeft dit mogelijkheden om belangrijke functies van waterrijke gebieden zoals methaanemissies en denitrificatie te kwantificeren en te beheersen.

In hoofdstuk 5 tonen we op basis van een diepgaande analyse van een unieke mondiale database van planten-eigenschappen aan dat adaptieve, blad-economische en grootte-gerelateerde eigenschappen inderdaad drie verschillende assen vertegenwoordigen. Dit suggereert dat plantensoorten in waterrijke gebieden een scala aan strategieën voor aanpassingen, het verkrijgen van hulpbronnen en concurrentie hebben.

Concluderend: Dit proefschrift laat zien dat plantensoorten in waterrijke gebieden diverse strategieën kunnen hebben om met de complexe stressoren in deze ecosystemen om te gaan. De adaptieve eigenschappen lijken goedkoop om te ontwikkelen zonder dat dat leidt tot wisselwerkingen met andere onderdelen van de plantenstrategie (zoals met de blad-economische eigenschappen). Bovendien blijkt dat, hoewel de ecologische rol van verschillende adaptieve eigenschappen vergelijkbaar is, de correlaties tussen deze eigenschappen zwak zijn, en dat de sturende mechanismen verschillend zijn. Dit verschaft plantensoorten uit waterrijke gebieden de flexibiliteit om zich aan te passen aan een verscheidenheid aan milieuomstandigheden in dit type ecosystemen, zoals aan het gebrek aan zuurstof, onderdompeling en de aanwezigheid van toxische stoffen. De verschillende strategieën met betrekking tot groei, concurrentie en aanpassing maken het mogelijk om flexibele beheerpraktijken te ontwikkelen om zo het gewenste ecosysteem te creëren. Doordat langs elke eigenschapsas een andere milieufactor actief is kunnen we verschillende beheerdoelen tegelijkertijd verwezenlijken om op die manier de levering van ecosysteemdiensten geleverd door onze waterrijke gebieden te optimaliseren.

List of Publications

Publications in peer-reviewed Journals (English):

1. **Pan, Y.***, Cieraad, E., Clarkson, B.R., Colmer, T.D., Pedersen, O., Visser, E.J.W., Voesenek, L.A.C.J. & van Bodegom, P.M. (2020) Drivers of plant traits that allow survival in wetlands. *Functional Ecology*, **34**, 956-967. doi: 10.1111/1365-2435.13541
2. **Pan, Y.***, Cieraad, E., van Bodegom, P.M. (2019) Are ecophysiological adaptive traits decoupled from leaf economics traits in wetlands? *Functional Ecology*, **33**, 1202–1210. doi: 10.1111/1365-2435.13329
3. **Pan, Y.**, Zhang, X., Song, K. & Da, L. (2017) Applying trait-based method to investigate the relationship between macrophyte communities and environmental conditions in a eutrophic freshwater lake, China. *Aquatic Botany*, **142**, 16–24. doi: 10.1016/j.aquabot.2017.06.002
4. Cui, Y., Song, K., Guo, X., van Bodegom, P.M., **Pan, Y.**, Tian, Z., Chen, X., Wang, J. & Da, L. (2019) Phylogenetic and functional structures of plant communities along a spatiotemporal urbanization gradient: Effects of colonization and extinction. *Journal of Vegetation Science*, **30**, 341–351. doi: 10.1111/jvs.12724
5. Song, K., Cui, Y., Zhang, X., **Pan, Y.**, Xu, J., Xu, K. & Da, L. (2017) Enhanced effects of biotic interactions on predicting multispecies spatial distribution of submerged macrophytes after eutrophication. *Ecology and Evolution*, **7**, 7719–7728. doi: 10.1002/ece3.3294

Publications in peer-reviewed Journals (Chinese):

6. **Pan, Y.*** (2015). Applying the system dynamics model to the prediction of public and domestic water demand and the water savings for Shanghai city. *Water Resource Protection*. **31**(3), 103-107. doi: 10.3880/j.issn.1004-6933.2015.03.020
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In review/revision:

1. **Pan, Y.***, Cieraad, E., Armstrong, J., Armstrong, W., Clarkson, B.R., Colmer, T.D., Pedersen, O., Visser, E.J.W., Voesenek, L.A.C.J. & van Bodegom, P.M. The leaf economics spectrum revisited: global wetland trait patterns in wetlands.
2. **Pan, Y.***, Cieraad, E., Armstrong, J., Armstrong, W., Clarkson, B.R., Pedersen, O., Visser, E.J.W., Voesenek, L.A.C.J. & van Bodegom, P.M. Adaptive strategies are decoupled from leaf economics traits and size-related traits in wetlands.
3. Zhang, X., Song, K., **Pan, Y.**, Gao, Z., Pu F., Lu, J., Shang, K., Da, L., Cieraad, E. Seasonal and climatic adaptations in leaf traits of an evergreen oak at its upper limit.
4. Gao, Z., Song, K., **Pan, Y.**, Malkinson, D., Zhang, X., Jia, B., Xia, T., Guo, X., Liang, H., Huang, S., Da, L., van Bodegom, P.M. & Cieraad, E. Drivers of spontaneous plant richness of urban green infrastructures in Kunming, China.
5. Lin, F., Liu, S., Cornelissen, J.H.C., Ayi, Q., Su, X., Niu, H., Jing, S., **Pan, Y.**, Pan, X., Shi, S., Zeng, B. & van Bodegom, P.M. Differential responses in seed viability and germination of summer and winter annuals to extreme submergence.

Conference/Forum Abstracts:

1. **Pan, Y.**, Cieraad, E. & van Bodegom, P.M. Wetland plant functional traits, strategies and ecosystem functioning. Oral Presentation. *The International Young Scholars Shenzhen Forum of Sun Yat-sen University*. 2019, Shenzhen, China.
2. **Pan, Y.**, Cieraad, E. & van Bodegom, P.M. Global analyses on wetland plant strategies and ecosystem functioning. Invited Lecture. *School of Ecological and Environmental Sciences, East China Normal University*. 2019, Shanghai, China.
3. **Pan, Y.**, Cieraad, E. & van Bodegom, P.M. Drivers of a global spectrum of wetland traits: climate, habitats and plant adaptive strategies. Oral Presentation. *EGU General Assembly.* 2019, Vienna, Austria.
4. **Pan, Y.** General wetland plant strategies. Invited Speech. *The International Young Scholars Forum of Guangxi University*. 2019, Nanning, China.
5. **Pan, Y.** Wetland plant strategies and ecosystem functioning. Invited Speech. *The 4th Young Scholar Academic Forum, Yangzhou University*. 2019, Yangzhou, China.
6. **Pan, Y.**, Song, K. & Da, L. Macrophyte traits, environment and community composition in Dianshan Lake. Poster Presentation. *The 4th Young Scholar Academic Forum, Ecological Society of Shanghai.* 2016, Shanghai, China.
7. **Pan, Y.**, Song, K. & Da, L. Linking plant traits to the relationships between macrophyte community assembly and environmental variables in a eutrophic freshwater lake. Oral Presentation. *The 14th China Congress of Ecology, Ecological Society of China*. 2015, Chengdu, China.

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Curriculum Vitae

Yingji Pan was born on Feb. 7th, 1991, in Chengdu, China. From 2006 to 2009, he attended and graduated from Chengdu Shishi high school, the most famous high school in Sichuan province with its longest history in education in China.

Between 2009 and 2013, he studied his BSc degree in Major of Ecology at East China Normal University (ECNU), Shanghai, China. During that time, he was awarded the opportunity as an exchange student to study at Sun Yat-sen University (2011) and National Dong Hwa University (2012), respectively.

During 2013 to 2016, he obtained his MSc degree in Major of Ecology under the supervision of Prof. Liangjun Da and Dr. Kun Song at ECNU. Before accomplishing his Master's degree study, he was awarded a scholarship for excellent student funded by ECNU to study at Colorado State University, USA for half a year (2015), where he collaborated with Dr. Erick Carlson under the supervision of Prof. David J. Cooper to study wetland plant communities and their ecosystem functioning.

From 2016, he was, as a PhD student, awarded a scholarship funded by the CSC-Leiden University joint program to study at the Institute of Environmental Sciences (CML), Leiden University, the Netherlands. His PhD research project (2016-2020), under the supervision of Prof. Peter van Bodegom and Dr. Ellen Cieraad, focused on the wetland plant and wetland ecosystem functioning. His PhD research work aimed to understand wetland plant adaptive strategies and the relationship between wetland plants and wetland ecosystem functioning through trait-based approaches.