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

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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).

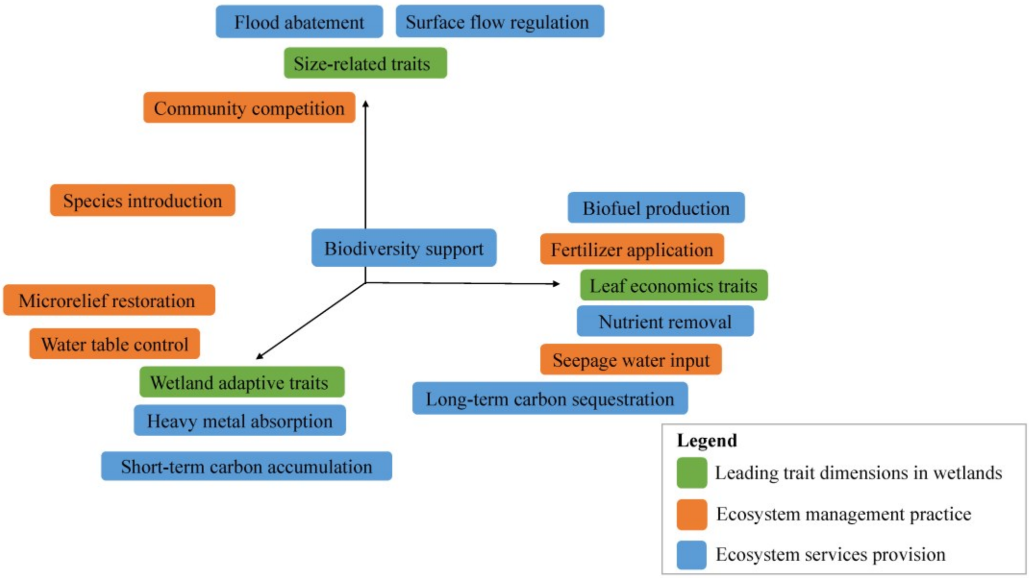

Figure 6.1 Conceptual scheme of the three decoupled trait dimensions in wetland plants with corresponding ecosystem services provision and related ecosystem management practices.

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.