PLANTS IN URBAN WETLANDS

From patterns to processes

Dissertation

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von

NIKOLA LENZEWSKI

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Crepis paludosa
Ballota nigra
V
Be
Limos
aqua
Caltha palustris
Vicia parviflora
Draba


Bellis perennis
Trifolium repens
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ica
Arctium tomentosum
Stellaria alsine
verna
Lathyrus pratensis

Plants in urban wetlands: from patterns to processes

Nikola Lenzewski

Erstgutachter:	Prof. Dr. Kai Jensen Universität Hamburg
Zweitgutachter:	Prof. Dr. Annette Eschenbach Universität Hamburg

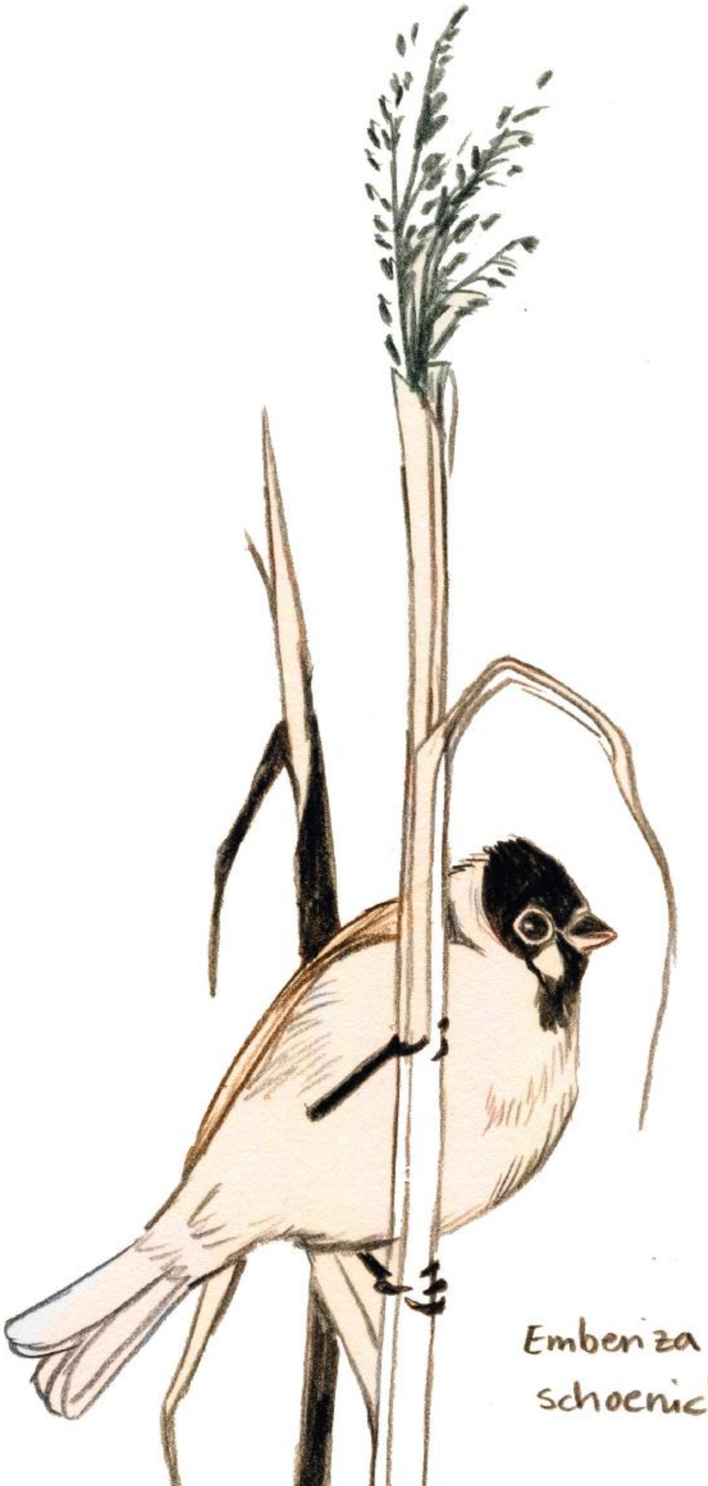
Datum der Disputation: 15.05.2020

Rückhaltebecken Farnhornstieg

Walk on, walk on

With hope in your heart

And you‘ll never walk alone



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Box 2

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Spadenländer Spitze, Hamburg

CHAPTER 1

General Indroduction

1.1 Current state and perspectives of global wetlands

Wetlands as defined by the Ramsar Convention on Wetlands (1971) 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 metres'. Following this definition, wetlands are a diverse group of ecosystems and in contrast to other definitions, aquatic ecosystems such as rivers and lakes are included (for further definitions see Mitsch & Gosselink (2000)). In addition to the permanently or temporarily presence of water, wetlands are further characterised by specialised vegetation or plant species adapted to wet conditions and by soils influenced by water saturation and/or flooding (Mitsch & Gosselink, 2000). The biological diversity, which is the diversity within species, between species and of ecosystems (United Nations, 1992), is an important feature of wetlands. Wetlands can contain high species diversity levels as they can harbour terrestrial as well as aquatic biota (Junk et al., 2006), and, furthermore, wetlands are known for their high proportion of rare and endemic species (Gopal, 2009). Worldwide, wetlands are identified as hotspots of biodiversity (Smol & Douglas, 2007; Xiang et al., 2009; Ackermann & Sachteleben, 2012; ten Brink et al., 2013; Tulbure & Broich, 2013).

Between 4% and 9% of the world's land surface is covered by wetlands (Maltby, 1986; Mitsch & Gosselink, 2000; Zedler & Kercher, 2005). Dependent on the region, between 30% and 90% of the world's wetlands have already been destroyed or heavily modified (Junk et al., 2013) with the largest wetland losses documented for Europe (56.3%) and North America (56.0%; Davidson, 2014). Human actions have led to wetland loss and degradation of inland and coastal/marine wetlands (Fig. 1.1; Leadley et al., 2014) by land-use change and utilisation of resources, river training and pollution (Mitsch & Gosselink, 2000). Urbanisation is known to be one major factor for wetland loss (Dahl, 2000), but concurrently man-made ('constructed') wetlands increased in their extent in the last decades (Fig. 1.1; Leadley et al., 2014). As wetlands have been destroyed or altered, wetland biodiversity is nowadays threatened globally (Alongi, 2002; Dudgeon et al., 2006). For protection and development of the remaining and often heavily modified wetlands, international and national laws, guidelines and programs were enacted, such as the Ramsar Convention on Wetlands (1971), the Water Framework Directive (European Commission, 2000) or the German program for development of federal waterways (Blaues Band Deutschland; BMVI & BMUB, 2018). As wetlands are known to be biodiversity hotspots, wetlands are further protected by biodiversity strategies, such as the Convention on Biological Diversity (United Nations, 1992) or the national strategy of biological diversity of Germany (BMUB, 2007).

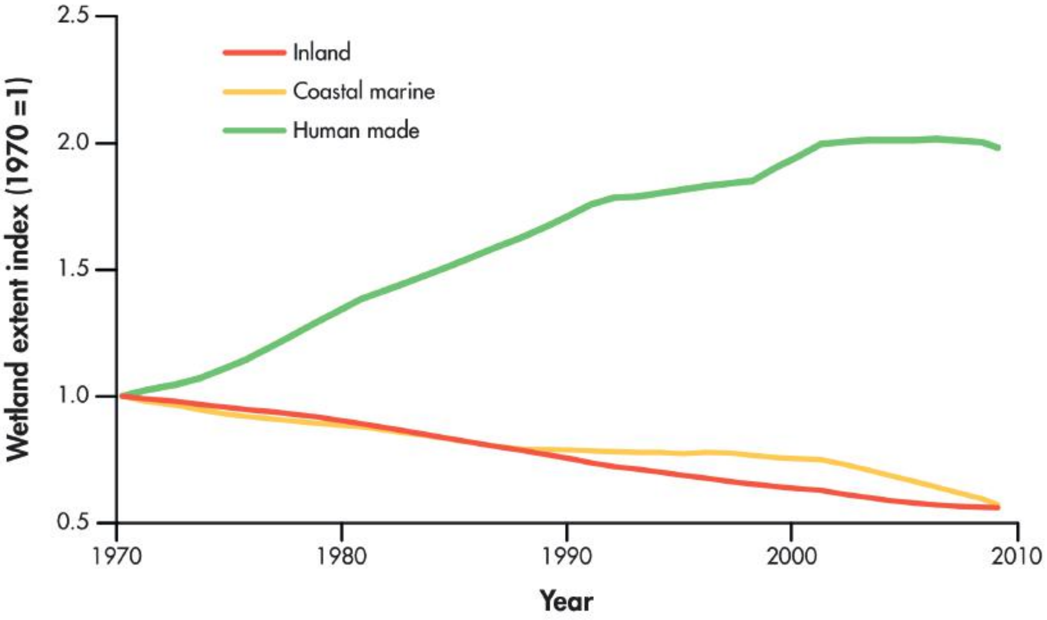

Fig. 1.1 The wetland extent index of global inland, coastal/marine and human made wetlands from 1970 to 2008. Development of the average extent of wetlands in comparison to the status in 1970 (index = 1). From Leadley et al. (2014).

1.2 Wetlands in the urban environment

Changes in land-use can have large impacts on ecosystems. With increasing land-use intensification, the extent of natural ecosystems is reduced and at the same time man-made ecosystems such as urban areas and agricultural ecosystems increase. In intensively used landscapes, protected and recreational lands increase in their extent (Fig. 1.2; Foley et al., 2005), which is of great importance as they may harbour the last natural or semi-natural ecosystems in an intensively used landscape. Aside from biodiversity, land-use change has large impacts on biogeochemical cycles, climate and hydrosystems on local, regional and global scales (Grimm et al., 2008). Land-use change is predicted to be one of the main drivers for biodiversity change in terrestrial and aquatic ecosystems worldwide by the year 2100 (Sala et al., 2000). Climate change and biotic exchange are further future threats for biodiversity of rivers and lakes. One specific process of land-use change is urbanisation, which will gain more and more importance in the future as the world urban population is estimated to increase to nearly 5 billion people and urban land cover to 1.2 million km^2 by the year 2030 (Seto et al., 2012).

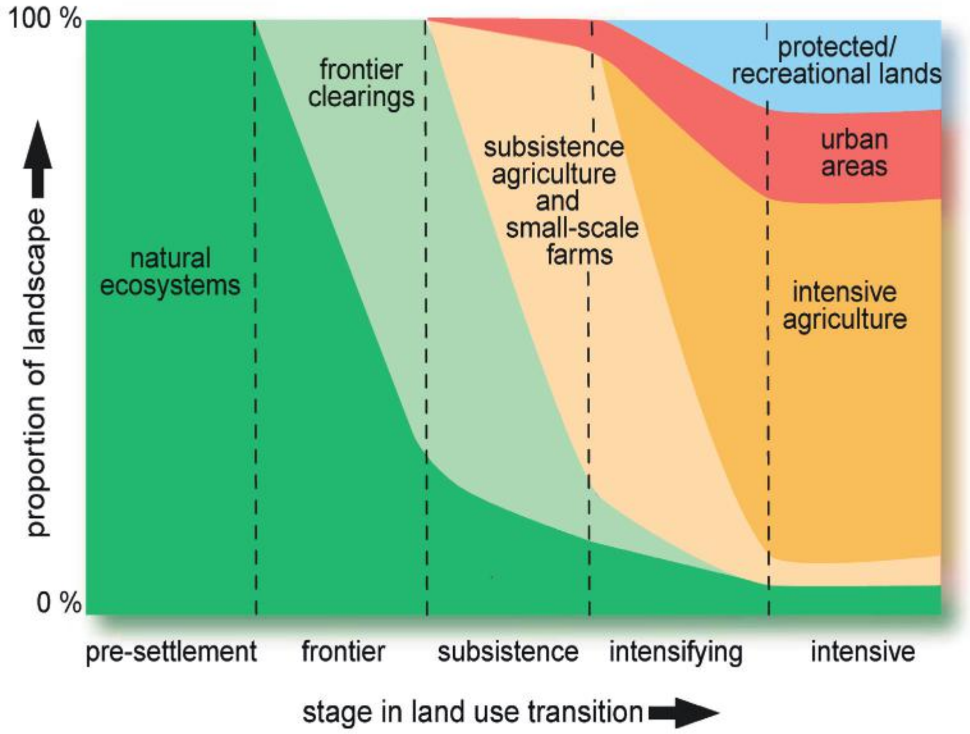

Fig. 1.2 Development of the relative abundance of different types of ecosystems under land-use intensification. Modified after Foley et al. (2005).

Urban areas are distinguished from rural and suburban areas as well as from natural landscapes by different climatic and environmental conditions (Sukopp & Werner, 1983). Due to energy release of buildings and streets, air temperatures can be higher in urban areas, especially during the night (Kalnay & Cai, 2003). This so-called 'urban heat island effect' can be up to 12 °C higher (Montreal; Oke & East, 1971) in cities in comparison to the rural surroundings, dependent on the city size (Oke, 1973; Watkins et al., 2002; Schlünzen et al., 2010). Sealed soils lead to altered hydrological conditions in time and space (Wiesner et al., 2016) by decreasing the infiltration capacity. Furthermore, altered geochemical cycles and lowered groundwater tables can be the consequence. High proportions of sealed soil surfaces in combination with a high building density and trained rivers can increase the risk of floods by increased surface runoff after heavy rainfall or snowmelt (Scalenghe & Marsan, 2009; Depietri et al., 2012). Urban soils can further be characterised by high amounts of nutrients and pollutants, having their origin in high traffic densities, usage of chemical fertilisers in private gardens and industrial activities (Li et al., 2001; Manta et al., 2002; Lorenz & Lal, 2009; Tresch et al., 2018). The urban atmosphere can be characterised by high amounts of pollutants and particulate matter (Coppalle et al., 2001; Li et al., 2001; Mazzei et al., 2008; Zhang et al., 2015) and, furthermore, by highly variable wind velocities and wind directions (Bornstein & Johnson, 1977).

Vascular plant biodiversity (in the following, the term 'plant' is used for vascular plants) of urban areas is strongly influenced by the specific climatic and environmental conditions as well as the high level of anthropogenic disturbances. Habitats available for plant colonization are reduced in urban areas due to soil sealing (Scalenghe & Marsan, 2009), and, furthermore, application of herbicides and mechanical destruction by authorities leads to a direct loss of single individuals of plants and vegetation cover. High amounts of nutrients and pollutants in the soil can favour nutrient-demanding or heavy metal resistant plant species, and, furthermore, thermophilic plant species can be promoted due to the urban heat island effect and missing frost periods in cities in winter. Annual plant species with short reproduction cycles and high seed production may be favoured by disturbance events (Grime, 1979; Wittig, 1996). Urbanisation is known to be a major cause of biotic homogenization (McKinney, 2006), and the level of urbanisation influences the total number of species found in cities with the highest plant species richness reported for moderate urbanisation levels (McKinney, 2008; Schmidt et al., 2014). On a broader scale, plant species richness is known to be higher in cites in Central Europe in comparison to the rural surrounding (Kühn et al., 2004; Knapp et al., 2008). Reasons for this are the concurrent occurrence of semi-natural habitats and novel, man-made habitats leading to high habitat heterogeneities and further, high numbers of non-native plant species, which were planted and/or unintentionally introduced to cities (Kühn et al., 2004; Lundholm & Marlin, 2006; Kowarik, 2011). Habitat destruction and increasing nutrient levels in the soil following urbanisation are major threats for plant species (Korneck et al., 1998). Species of bogs, nitrogen-poor habitats and plants with helomorphic leaves are known to become extinct in cities (Knapp et al, 2010). As a consequence, high proportions of threatened or extinct plant species are reported for cities (Duncan et al., 2011; Ives et al., 2016). For example, 25% of the plant species of Hamburg (Germany) are listed as threatened in the red list of plant species of Hamburg (red list categories 1, 2 and 3) and 11% of species are classified as extinct nowadays (red list category 0). Further, 24% of the plant species of Hamburg are listed as non-native species with their native range outside of Germany (1546 species in total; Poppendieck et al., 2010).

In urban areas, a large variability of semi-natural and man-made wetlands can be found on a small scale. This includes aquatic ecosystems, such as rivers, lakes, stormwater and retention ponds or harbour basins as well as semi-aquatic and more terrestrial habitats, such as disposal areas, soft and hardwood floodplain forests or small relicts of bogs and swamps. Further, ecosystems accidentally formed by human actions due to land-use change and/or impervious surfaces also belong to urban wetlands (Palta et al., 2017). Wetlands in urban areas have been directly modified by human actions or completely removed to meet different goals. Furthermore, actions in the catchment area of wetlands, such as soil sealing, have large impacts on these ecosystems as well (Chadwick et al., 2006; Patenaude et al., 2015). As a consequence, urban wetlands are characterised by altered hydrology, water and soil chemistry, geomorphology and trophic levels in comparison to non-urban wetlands (Ehrenfeld, 2000; Paul & Meyer, 2001). Thus, wetlands in urban areas are often of poor quality, degraded and reduced in their extent in comparison to wetlands in non-urban areas (Zedler & Leach, 1998; Kozlowski & Bondallaz, 2013; Noble & Hassall, 2015). In detail, urban rivers are often channelled, straightened or piped nowadays for recreational purposes, improved flood protection, water usage and shipping (Gurnell et al., 2007; Gurnell et al., 2012). In the past, bogs were drained for land-use and peat cutting (Chapman et al., 2003) and natural floodplain forests were cut for wood and agricultural land-use as effects of urbanisation (Scholz et al., 2005). As a consequence of diverse human actions, urban wetlands are often heavily polluted regarding nutrients, heavy-metals and pharmaceutical products (Adams et al., 2000; Waltham et al., 2014). Furthermore, human induced lowering of groundwater tables can have enormous effects on urban wetlands by influencing the hydrological regime (Groffman et al., 2003). Nevertheless, urban wetlands have been increasingly valued as important multifunctional ecosystems during the last years: They are used for recreational purposes, are important components for flood protection and in the drainage system, provide habitats for plants and animals and act as climate regulating systems (MEA, 2005; McInnes, 2014).

1.3 Ecosystem services of natural and urban wetlands

Wetlands are known to provide different ecosystem services to people and the importance as well as the economic value of selected ecosystem services is higher than in other ecosystems (Costanza et al., 1997; MEA, 2005; de Groot et al., 2012; ten Brink et al., 2013). In total, the monetary value of ecosystem services (provisioning, regulating, habitat and cultural services) of different types of wetlands ranges on average between 25,682 Int.$ ha^{-1} yr^{-1} for inland wetlands and 193,845 Int.$ ha^{-1} yr^{-1} for coastal wetlands (1 Int.$ = 1 US$; values in local currency units were converted by using purchasing power parity exchange rates; de Groot et al., 2012). These values are among the highest for monetary values of different ecosystems and, furthermore, are higher in comparison to terrestrial ecosystems, such as tropical forests or grasslands. However, only 4267 Int.$ ha^{-1} yr^{-1} are valued for freshwater rivers and lakes, which is mainly due to a lower valuation of regulating services. Globally, for all inland wetlands (including rivers and lakes), major provisioning and regulating services are food and freshwater supply, climate regulation, hydrological regulation as well as flood control and storm protection. Furthermore, cultural services such as recreational or educational usage and supporting services such as soil formation, nutrient cycling and biodiversity are also provided by wetlands (MEA, 2005).

In total, urban wetlands are estimated to provide more than 40 planned and unplanned ecosystem services (McInnes, 2014). The relevance of selected ecosystem services may differ spatially with regard to the urbanisation degree and the considered geographical region (Schneider et al., 2012; Radford & James, 2013). Major ecosystem services of wetlands in large cities in developed countries are the long-term storage of carbon, nutrient and pollutant retention, climate and hydrological regulation, flood protection, recreation and habitat provision (Bolund & Hunhammar, 1999; Haase, 2003; Lundy & Wade, 2011; Moore & Hunt, 2012; Völker & Kistemann, 2013; Voskamp & Van de Ven, 2014; Dorendorf et al., 2015; Völker & Kistemann, 2015; Säumel et al., 2016; Palta et al. 2017; Mehl et al., 2018).

1.4 Plant biodiversity and rhizosphere processes and their importance for ecosystem services

Relationships between plant biodiversity and ecosystem functions and processes have for a long time been studied in terrestrial and aquatic biodiversity experiments on different spatial and temporal scales (e.g. Engelhardt & Ritchie, 2002; Schmid et al., 2009; Fischer et al., 2010; Lange et al., 2015; Weisser et al., 2017). Numerous of these studies found a positive relationship between diversity of genes, species or functional traits and ecosystem functions (Cardinale et al., 2012; Mora et al., 2014). A freshwater mesocosm study showed that with increasing macrophyte species richness algae biomass increased as well as phosphorus concentrations in the water column decreased (Engelhardt & Ritchie, 2001). In another study, the increase in macrophyte species richness resulted in a promotion of ammonification by simultaneously inhibiting nitrification and denitrification in the sediment (Korol et al., 2016). Individual plant traits are known to influence ecosystem processes (García-Llorente et al., 2011). Grasses, and in particular reeds, are known to remove nutrients and pollutants very efficiently and are thus used as important components in retention ponds (Kao et al., 2003; Brisson & Chazarenc, 2009; Maltais-Landry et al., 2009; Hernández-Crespo et al., 2016). This is due to their ability to tolerate high amounts of organic compounds and nutrients in the sediment and their pronounced belowground and aboveground biomass for taking up and storing of nutrients and pollutants (Vymazal, 2011). Further, lowest methane emissions of flooded sediments in a freshwater mesocosm study were found when the functional richness of planted macrophyte species was highest (Bouchard et al., 2007). These studies highlight the importance of belowground plant traits for biogeochemical processes in wetlands, so that the transition zone between plant roots and the sediment should be taken more into account, when analysing biogeochemical processes in wetlands.

The rhizosphere of plants is the area of soil or sediment that is directly impacted by living roots. Here, biogeochemical processes are influenced by the release of exudates from the root, such as enzymes, oxygen or mucilages (Bais et al., 2006; Hinsinger et al., 2009). In wetland rhizospheres, various biogeochemical processes are affected by the release of oxygen from roots of macrophytes or hydrophytes (Brix, 1997; Gutknecht et al., 2006). Most aquatic plants are releasing oxygen only at the root tip into the sediment, whereas isoetid plants are leaching high amounts of oxygen along the entire root into the sediment (radial oxygen loss; ROL; Sand-Jensen et al., 1982; Smolders et al. 2002; Møller & Sand-Jensen, 2008), making them ideal model organisms for studies on rhizosphere oxygenation and coupled biogeochemical processes. Isoetids are small, evergreen hydrophyte or macrophyte species characterised by thick, stiff leaves or stems which form basal rosettes and a high proportion of belowground biomass (Smolders et al., 2002). By releasing oxygen along the entire root into the rhizosphere, isoetid plants preserve the oligotrophic conditions in their habitats and gain advantages over non-isoetid plants. Oxygenation of the rhizosphere promotes decomposition of organic compounds and the formation of insoluble iron-3-phosphates, which isoetids can take up via mycorrhiza, but which are not easily available for other macrophytes. Further, nitrification of ammonia to nitrate is supported by rhizosphere oxygenation, which is the main nitrogen source of most isoetid plant species (Pedersen et al., 1995; Christensen, 1997; Risgaard-Petersen & Jensen, 1997; Smolders et al. 2002; Vila-Costa et al., 2016). By influencing the rhizosphere environment, plants in terrestrial and aquatic ecosystems are affecting the structure and composition of the soil microbial community (Palmer et al., 2000; Scherber et al., 2010; Eisenhauer 2012), and, as a consequence, rhizospheres are known to be hotspots for plant-soil-microbe interactions (Pathan et al. 2020). Plant biodiversity in terms of species richness and functional richness should always be taken into account when analysing ecosystem functions and processes.

1.5 Objective of the thesis and chapter outline

Hamburg (Germany) is a good model region for analysing plant biodiversity of wetlands as the city contains different types of tidal and non-tidal freshwater wetlands (Fig. 1.3a). 8% of the city surface is classified as water bodies (Statistische Ämter des Bundes und der Länder, 2018). Furthermore, semi-natural wetlands, such as floodplains, relicts of bogs and wet meadows, as well as man-made wetlands, such as depositing sites and stormwater ponds, are present in Hamburg. The city is located in the northern part of Germany, has about 1.8 million inhabitants and covers an area of 755 km² (Statistische Ämter des Bundes und der Länder, 2018). The climate is temperate and oceanic with a mean annual temperature of 9.4 °C and an annual precipitation of 793 mm (DWD, 2019; reference period 1981-2010). Hamburg shows an average urban heat island of 1.1 °C, with more pronounced temperature differences during the night (Schlünzen et al., 2010).

Stormwater ponds are an important part of the flood protection strategy of Hamburg. The high proportion of sealed soil surfaces increases the risk of floods by increased surface runoff (Scalenghe & Marsan, 2009; Depietri et al., 2012), which can be temporarily stored in stormwater ponds. In this thesis, the term 'stormwater pond' is used in the context of describing all different types of ponds available for intermediate storage of water, regardless of the source of water (flood waters or rain waters) and the hydrological conditions of the stormwater pond (wet, moist and/or dry conditions). In addition to the primary function of water storage, urban stormwater ponds can also act as sediment and nutrient traps, they can be used by people for recreational purposes and provide habitat for plants and animals (Lundy & Wade, 2011; Moore & Hunt, 2012). Stormwater ponds are dynamic ecosystems characterized by changing water tables in time and space, and thus they may harbour diverse plant communities.

The Elbe River and its floodplains in Hamburg are highly influenced by tides. Frequency and duration of flooding determines the vegetation of floodplains, resulting in a characteristic zonation of pioneer zone (without trees), softwood forests and hardwood forests (Pott, 1996). Under tidal conditions, specific plant communities adapted to tolerate flooding up to two times a day, such as tidal reeds, can develop, which can be found along the Elbe River. River training as well as embankment of the floodplains has led to altered hydrological conditions, and, as a consequence, typical vegetation types of floodplains, such as hardwood forests, are threatened today (Finck et al., 2017). The Dove Elbe River is an anabranch of the Elbe, which was under tidal influence until 1951 when a sluice was built at its confluence with the Elbe River. Nowadays, the Dove Elbe River is embedded in a cultural landscape characterised mostly by floodplain grasslands. Relicts of characteristic floodplain vegetation, such as soft and hardwood forests, are scarce and can only be found on small scale along the Dove Elbe River. In urban areas, floodplain forests and floodplain grasslands are important semi-natural habitats, even though they are highly influenced by humans.

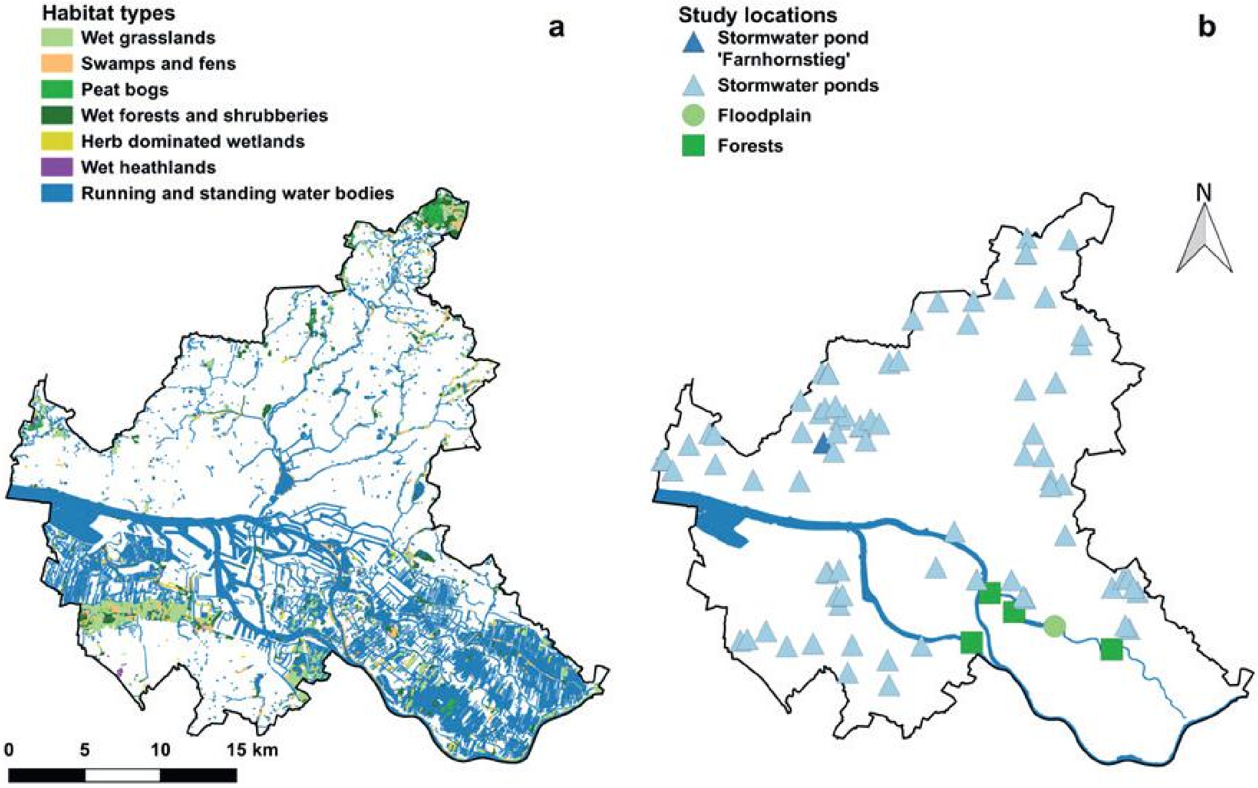

Fig. 1.3 a) Wetlands of Hamburg based on habitat types according to the biotope type mapping of the Ministry of Environment and Energy of Hamburg (BUE, 2018a). Habitat types with wet or flooded soils (wet grasslands, swamps and fens, peat bogs, wet forest and shrubberies, herb dominated wetlands, wet heathlands as well as running and standing water bodies) are shown in the map. The floodplain of the Elbe River contains a pronounced ditch system, but due to scaling of the map, these ditches pretend to cover most of the area of the floodplain. b) Study locations for analysing plant biodiversity of urban wetlands in Hamburg. The map shows the stormwater ponds, where spatial patterns were studied on small (stormwater pond 'Farnhornstieg'; Chapter 2) and larger scales (stormwater ponds, Box 1). Further, the study areas of the floodplain of the Dove Elbe River (floodplain; Chapter 3) and the softwood floodplain forests along the Elbe River and wet forests along the Dove Elbe River (forests; Box 2) are shown. The stormwater pond 'Farnhornstieg' was studied in the large scale survey on urban stormwater ponds as well. Additionally, the Elbe River and Dove Elbe River in Hamburg are shown in the map.

The objective of this thesis was to analyse patterns of vegetation composition and diversity of stormwater ponds, urban floodplains and different types of wet forests in the city of Hamburg (Fig. 1.3b). Further, processes of vegetation change were investigated focussing on initial successional processes of a reconstructed stormwater pond and on decadal vegetation change after de-embanking the Dove Elbe from tides. Finally, a method for studying rhizosphere processes (here O_2 and CO_2 fluxes) in wetlands using planar optodes is described. So far, experimental rhizosphere studies often focus on roots of single individuals when analysing rhizosphere processes and thus biodiversity effects are not considered (e.g. Koop-Jakobsen et al., 2018; Marzocchi et al., 2019). In future studies, interactions between different species and/or species with different functional traits should be considered when analysing belowground processes in the rhizospheres of plants (Fig. 1.4; Blossfeld et al., 2013). This thesis provides the base for future research focusing on plant biodiversity and their effects on rhizosphere processes of urban wetlands.

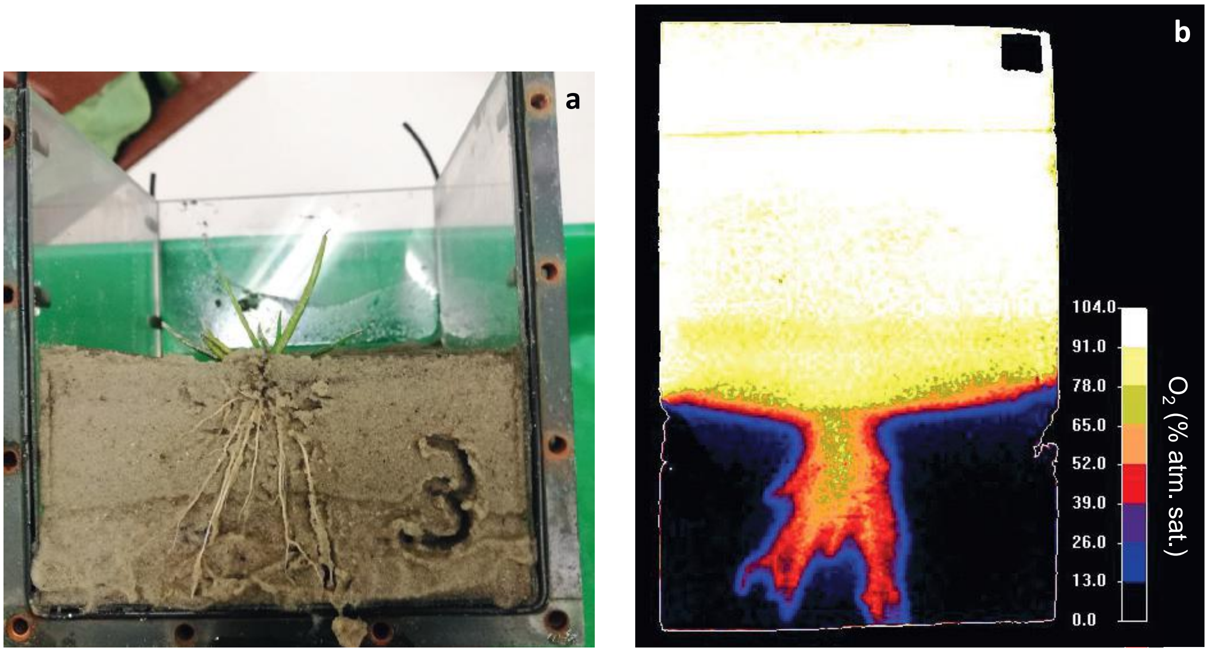

Fig. 1.4 (a) Water form of *Littorella uniflora* (L.) Asch. planted in a rhizobox and (b) O_2 concentration in the sediment around the roots of the water form of *Littorella uniflora* in darkness under emerged conditions. Work in progress by K. Koop-Jakobsen and N. Lenzewski.

The **main research questions** of this thesis are:

- What vegetation patterns are characteristic for urban wetlands in Hamburg?
- Which environmental factors determine these vegetation patterns?
- What processes drive vegetation change in stormwater ponds and urban floodplains?
- How can processes responsible for the delivery potential of ecosystem services be studied in rhizospheres of urban wetlands?

This thesis consists of five studies described in five chapters. In **chapter 2**, early vegetation change of an urban stormwater pond in Hamburg as a consequence of the reconstruction of the pond was studied. For a period of three years, the vegetation of the stormwater pond ‘Farnhornstieg’ was analysed once per year in different hydrological zones of the pond. Furthermore, the soil seed bank of the pond in the year before the reconstruction and in the year after the reconstruction was analysed. Changes in species richness and species composition were analysed and the role of the seed bank for recolonization processes was assessed. **Box 1** gives preliminary results of a large study on vegetation pattern and biodiversity of plants in stormwater ponds in Hamburg. The species composition of 80 stormwater ponds was analysed in 2017, and, furthermore, selected abiotic and biotic parameters of each stormwater pond were assessed. Plant species richness (total number and proportion of threatened species) of dry and wet stormwater ponds were compared and classification and regression trees (CART) were used to determine patterns in the total number of species and proportion of threatened species of stormwater ponds. **Chapter 3** deals with the long-term effects of the loss of tidal influence on vegetation patterns of an estuarine floodplain in Hamburg. In 2016, vegetation records were reassessed on selected plots along the Dove Elbe River, which were assessed first by Meyer (1954) in 1951 just before the tidal influence was lost by the installation of a sluice. Species richness and species composition of the plots as well as the mean weighted Ellenberg indicator values (EIV) for moisture and nutrition were compared between 1951 and 2016. **Box 2** gives results on vegetation differences of softwood forests along the tidal Elbe River and wet forests along the Dove Elbe River in Hamburg. Species richness and species composition of the herbaceous vegetation as well as abiotic and biotic parameters of four selected forests were compared. **Chapter 4** deals with rhizosphere processes of the submerged macrophyte *Lobelia dortmanna* L. (water lobelia), a characteristic plant species of soft water lakes of Northern and Central Europe. Due to the pronounced ability to release oxygen along the entire root, the isoetid plant is a suitable model organism for studying plant-soil-interactions. The recently developed technic of planar optodes in combination with O_2 and newly developed CO_2 sensitive foils was used for analysing the effects of light on the spatial and temporal dynamics of O_2 and CO_2 in the rhizosphere of *Lobelia dortmanna*. In **Chapter 5,** the main results of the studies are discussed in the context of the published literature.

For consistency throughout this thesis, the figures and tables of all published or submitted manuscripts were renumbered and all references were summarised at the end of the thesis.


Typha
latifolia

CHAPTER 2

Seed bank has the potential for re-colonizing urban stormwater ponds after reconstruction

Nikola Lenzewski, Kai Jensen and Kristin Ludewig

under revision

Abstract

Urban stormwater ponds are important for flood protection and provide habitat for plants and animals in heavily sealed cities. Little is known about the diversity of plants in urban stormwater ponds and the vegetation composition is often influenced by sowing and planting. We analysed the re-colonization of the vegetation in an urban stormwater pond, which was reconstructed to improve water retention. Specifically, we studied if the soil seed bank has the potential for re-colonizing the pond. We analysed the current vegetation from the year before until two years after reconstruction of a stormwater pond in Hamburg. Further, we analysed the soil seed bank in the year before and in the second year after reconstruction of the stormwater pond. We found 174209±70231 and 72050±13522 seedlings/m^2 (mean±standard error) in 2015 and 2017, respectively, of 74 species in the soil seed bank with *Juncus* spp. and *Epilobium* spp. being the most dominant taxa. We found only few species used in the mixtures for sowing in the current vegetation of the stormwater pond after reconstruction. Our results indicate that urban stormwater ponds have the potential for re-colonization out of seed bank and thus sowing is not a necessary management action in the construction process.

Keywords

Anthropogenic water body, Flood prevention, Plant species richness, Vegetation composition

1. Introduction

Land-use change is projected to be one of the major factors for biodiversity change in terrestrial and aquatic ecosystems worldwide by the year 2100 (Sala et al., 2000) with urbanisation being one specific process of it. Urban areas are characterized by altered environmental conditions in comparison to non-urban areas. For instance, in Hamburg, the so-called 'urban heat island effect' leads to higher mean temperatures up to 1.1 K in comparison to non-urban areas (Schlünzen et al., 2010). Even more important, the sealing of the soil surface leads to a direct loss of habitats for plants and to a loss of biodiversity. The soil available for plant colonization often contains high amounts of nutrients and pollutants. Hydrological conditions of soils in urban areas are also altered with a highly reduced infiltration capacity of the soil due to soil sealing. As a consequence, runoff is not able to seep away and the risk of floods increases with associated threats for human life and for physical damage of buildings and further infrastructure (Pickett et al., 2001; Scalenghe & Marsan, 2009; Depietri et al., 2012).

Stormwater ponds are usually of anthropogenic origin and an important part of flood protection strategies in heavily sealed areas due to their capacity for temporarily storage of runoff after heavy rainfalls. Here, the term 'stormwater pond' is used in the context of describing all different types of ponds available for intermediate storage of water, regardless of the source of water (flood waters or rain waters) and the hydrological conditions of the stormwater pond (wet, moist and/or dry conditions). In addition to the primary function of water storage, urban stormwater ponds can also act as sediment and nutrient traps, they can be used by people for recreational purposes and provide habitat for plants and animals (Lundy & Wade, 2011; Moore & Hunt, 2012). Overall, stormwater ponds are dynamic ecosystems characterized by changing water tables in time and space. The frequency and duration of flooding events as well as the elevation and groundwater level of a stormwater pond determine the composition of its flora (Casanova & Brock, 2000; Fan et al., 2013).

The importance of stormwater ponds for urban biodiversity of animals is well documented, mostly for aquatic animals or animals with a life cycle partly depending on aquatic conditions. Stormwater ponds can contain diverse odonate assemblages and promote a higher richness of threatened odonate species due to a higher habitat quality than water bodies without retention function (Scher & Thièry, 2005; Holtmann et al., 2018). Divers communities of other invertebrates (Briers, 2014; Hassall & Anderson, 2015) as well as amphibians (Hamer et al., 2012; Le Viol et al., 2012) are also documented for stormwater ponds. High bat activity levels above stormwater ponds in an agricultural landscape indicate the importance of stormwater ponds also for non-aquatic animals (Stahlschmidt et al., 2012). In general, the value of stormwater ponds for animal biodiversity depends on the abiotic and biotic conditions of the pond and the surrounding area as well as on the considered animal group (Le Viol et al., 2012; Gallagher et al., 2014; Holtmann et al., 2017). In contrast to animal biodiversity, surprisingly little is known about the importance of stormwater ponds for the biodiversity of wild plants.

Due to their dynamic and small scale heterogeneity, stormwater ponds can harbour plant species adapted to different environmental conditions, such as macrophytes in permanent flooded areas or plant species adapted to mesic water conditions in more dry parts of a stormwater pond. During flooding, sedimentation and erosion processes may disturb vegetation cover and in the following bare soil patches can develop. These areas can be recolonized by plants out of the soil seed bank or due to input via dispersal processes, mainly input via hydrochory (Henry et al., 1996; Abernethy & Willby, 1999; Barrat-Segretain & Bornette, 2000; Vogt et al., 2004). Therefore, stormwater ponds could be a secondary habitat for many wild plant species, ranging from aquatic to mesic conditions. This is especially promising in urban areas, where e.g. plant species adapted to aquatic conditions are at high extinction risk (Duncan et al., 2011). For bryophytes it is known, that species adapted to less shaded, bare soils as well as moist water conditions can be found in stormwater ponds. Furthermore, some of these bryophyte species are threatened and characterized by the ability to develop persistent spores or bulbils. As a consequence, these species are able to survive periods with unfavourable environmental conditions in the soil of stormwater ponds (Solga, 2001). Recent research show, that stormwater ponds may contain more aquatic and threatened vascular plant species than ponds without retention function due to their higher habitat heterogeneity, which highlights the importance of stormwater ponds as habitat for vascular plants (Holtmann et al., 2019). However, knowledge about the recolonization ability of vascular plant species in stormwater ponds is scarce.

In the city of Hamburg (Germany), seeds are usually sown on the soils of newly created or reconstructed stormwater ponds to facilitate fast re-colonization and, herewith, prevent soil erosion. Natural vegetation development cannot occur and a homogenous vegetation cover often develops in these stormwater ponds leading to low plant biodiversity. In other cities, such as Münster (Germany), sowing and planting of plants is not performed in stormwater ponds (Holtmann et al., 2019), and therefore, natural vegetation development can occur in these stormwater ponds. Knowledge about the re-colonization ability of seeds in the soils of stormwater ponds is important for decision-makers and the planning and construction of stormwater ponds to assess if this seed source would be significant for the colonization process.

The vegetation of an urban stormwater pond in Hamburg was studied for a period of three years. In 2016, the stormwater pond was reconstructed due to the development of a wet forest as a consequence of a missing management and flooding in the past. The soil of the stormwater pond was not completely replaced, which could allow the vegetation to recolonize out of the soil seed bank. We analysed the current aboveground vegetation of the stormwater pond over a period of three years, starting in the year before the reconstruction and furthermore, the seed bank was studied in the year before and in the second year after the reconstruction. For gaining information on the recolonization ability in the channel, plain, lower and upper shoreline of the stormwater pond, these four zones characterized by different hydrological conditions were studied. We aimed at answering the following research questions: Has the soil seed bank of the stormwater pond the potential for a natural re-colonization of the bare soil after reconstruction? Which species profit from the colonization from the seed bank and from sowing?

2. Materials and Methods

2.1 Study object

The stormwater pond is located in the city of Hamburg in northern Germany (Fig. 2.1). Hamburg has about 1.8 million inhabitants and covers an area of 755 km² (Statistische Ämter des Bundes und der Länder, 2018). The climate of Hamburg is temperate and oceanic with a mean annual temperature of 9.4 °C and an annual precipitation of 793 mm (DWD, 2019; reference period 1981-2010). The city is dominated by settlement (47%) and agricultural areas (23%) and furthermore, by traffic areas (12%), water bodies (8%) and woodlands (8%; Statistische Ämter des Bundes und der Länder, 2018).

The stormwater pond 'Farnhornstieg' (53°35'31"N, 9°54'30"E) is located in the urban district Eidelstedt in the north-western part of Hamburg (Fig. 2.1). Until 1998, the property was used for storage, but after demolition of the warehouse and soil remediation, the area was used for water retention of the nearby stream Mühlenau Due to a missing management of the vegetation, a wet forest composed of black alder (*Alnus glutinosa* L. Gaertn.) and different willow species (*Salix* spec.) established and the function for water retention was gradually reduced. In spring/summer 2016, the stormwater pond was reconstructed to improve the retention of stormwater from the Mühlenau. To prevent soil erosion, most of the bare soils of the stormwater pond were sown with different seed mixtures (grasses and weeds) in the beginning of 2016, dependent on the hydrological conditions of the soils. Furthermore, some species adapted to wetland conditions were planted in the channel and along the shorelines of the stormwater pond.

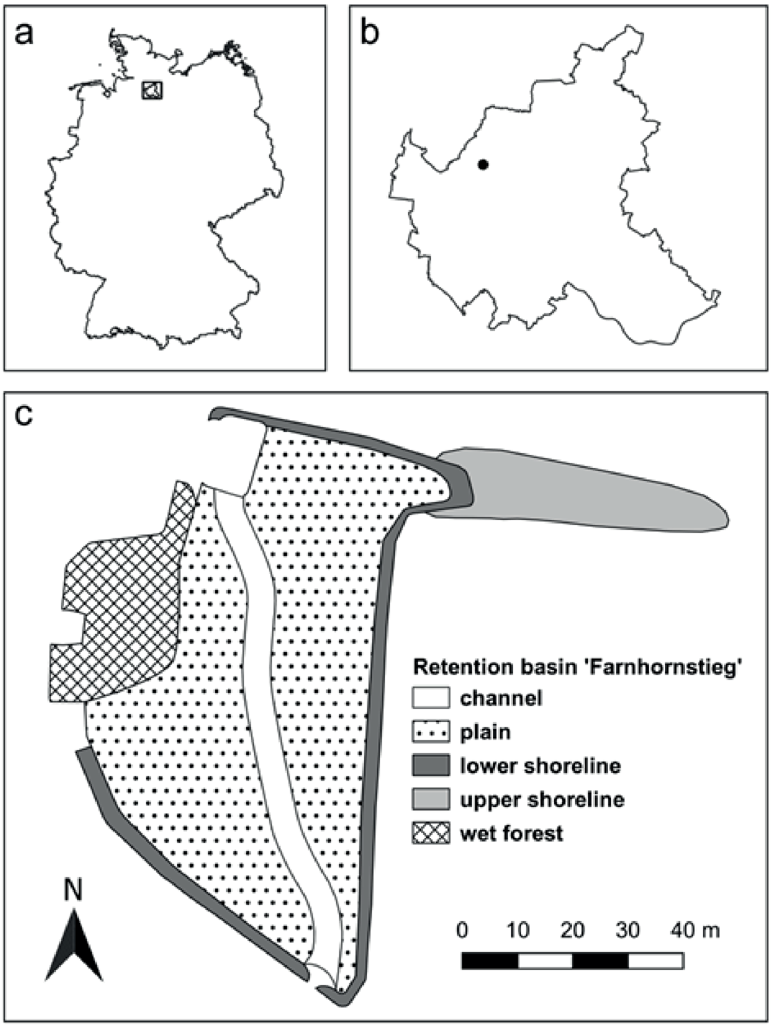

Fig. 2.1 Location of the studied stormwater pond Farnhornstieg' (53°35'31"N, 9°54'30"E) in the city of Hamburg in northern Germany (a, b) and zones (channel, plain, lower and upper shoreline, wet forest) of the stormwater pond based on the planning documents before the reconstruction of the stormwater pond (c).

2.2 Vegetation mapping and seed bank analysis

The vegetation of the stormwater pond was studied in late summer (August, September) 2015, 2016 and 2017. For each zone (channel, plain, lower and upper shoreline; Fig. 2.1c), five randomly distributed 1 m^2-plots were selected. The wet forest in the western part of the pond was not studied, due to the inaccessibility of this area and a missing herbaceous vegetation layer as a result of permanently standing water. All herbaceous vascular plant species rooting in the plots or reaching with their aboveground parts into the plots were recorded with their coverages according to a modified scale of Braun-Blanquet after Dierschke (1994; r =

0.1%, + = 0.5%, 1 = 2.5%, 2m = 2.5%, 2a = 8.8%, 2b = 20.0%, 3 = 37.5%, 4 = 62.5%, 5 = 87.5%, mean coverages, respectively).

On 11.08.2015 and 08.09.2017, mixed soil samples were collected from each study plot by using a soil steel corer (diameter: 50 mm, depth: 51 mm), combining five samples from the four corners and one from the centre of each plot. The soil samples were stratified in darkness for several weeks at 4 °C and afterwards processed according to Ter Heerdt et al. (1996). The soil samples were concentrated under running water using two soil sieves (mesh size: 4.0 mm and 0.212 mm). The remaining plant material in the 0.212 mm sieve was used for analysing the seed bank by spreading it into trays on a thin layer of a compost-sand-substrate (1:1 by volume). On 14.11.2015 and 18.01.2018, the trays were put in a greenhouse at 20/15 °C (day/night) and a light period of 12 h per day. Additional trays with only substrate as controls were put in the greenhouse to capture seeds included in the substrate and seed input through air. The samples were watered regularly and kept moist. All emerging seedlings were continuously counted, identified and afterwards removed from the trays. Plant determination was done using Csapody (1968), Raabe (1975), Hanf (1990), Christensen (1999) and Jäger (2017). Seedlings which could not be identified at this early life stage were transferred to pots and cultivated in the greenhouse for later identification. When no new seedlings occurred in the trays for seven days, the watering of the trays was suspended and the soil dried out. After 3 weeks, the hard soil layer was crumbled and again watered regularly for initiating additional germination of seeds. When no new seedlings emerged in the trays after this drying for seven days, the analysis was terminated. Seedlings which could not be identified to species level were identified to genus or family level. The nomenclature of plant species follows Jäger (2017).

2.3 Data preparation and statistical analysis

All analysis were performed with species groups like *Oenothera biennis* agg. or *Taraxacum* sect. *Ruderalia* Kirschner H. Øllg. & Štěpánek treated as species. Classification of species as endangered species for Hamburg was derived from Poppendieck et al. (2010) and the non-native status of species for Germany was taken from Wisskirchen & Haeupler (1998). Strategy types (c = competitors, r = ruderals, cr = competitive ruderals, cs = stress-tolerant competitors, sr = stress-tolerant ruderals and csr = competitive and stress-tolerant ruderals) according to (Grime, 1979) were derived from the BIOLFLOR database (Klotz et al., 2002) for the plant species found in the current aboveground vegetation of the pond. For the current aboveground vegetation, the total number of species and the number of ruderal species per plot and year were calculated. For the latter, the strategy types r, cr, sr and csr were considered.

Detrended correspondence analysis (DCA) was used to detect vegetation patterns of the seed bank and current vegetation of the study plots between the years. To be able to compare species composition between the current vegetation (cover) and the seed bank (number of seedlings), we transformed the data to relative abundance (vegetation: $\frac{\text{cover of each species}}{\text{cover sum of all species}} * 100$; seed bank: $\frac{\text{number of seedlings of each species}}{\text{sum of total number of seedlings}} * 100$) for each plot. In total, 117 species and 95 plots were considered in the DCA, while rare species were down-weighted in the analysis. Five plots could not be considered in the DCA as no vegetation was present in theses plots.

Epilobium hirsutum L. was excluded from further analysis of the seed bank due to its occurrence in the control trays in both years. The plant species used in the seed mixtures (Table 2.1) were derived from FLL (2016) and their occurrences in the soil seed bank in 2015 and in the current vegetation in 2017 were compared. As the actually used plant species in the seed mixtures is unknown, all pants listed in FLL (2016) for the used mixtures reported in the planning documents were considered. The species *Epilobium ciliatum* Raf. + *Epilobium obscurum* Schreb.+ *Epilobium montanum* L. + *Epilobium parviflorum* Schreb., *Juncus articulatus* L. + *Juncus bufonius* L. + *Juncus effusus* L. and *Persicaria lapathifolia* (L.) Delarbre + *Persicaria maculosa* Gray + *Persicaria mitis* (Schrank) Assenov were treated as one taxon (*Epilobium* spp., *Juncus* spp. and *Persicaria* spp., respectively) due to difficult determination of seedlings.

We used repeated measures ANOVAs (analysis of variance) to test for significant differences in the total number of species per plot and the number of ruderal species per plot between the zones and years. To meet the assumptions of normal distribution and homogeneity of variance, we performed a box-cox-transformation of data (total number of species: $\lambda = 0.32$, number of ruderal species: $\lambda = 0.02$). Normal distribution and homogeneity of variance were checked visually using QQ-plots. ANOVAs with significant results were followed by Tukey HSD post-hoc-tests to identify significant differences between the years for each zone.

Box-cox-transformation of data, QQ-plots, repeated measures ANOVAs and post-hoc-tests were carried out using STATISTICA 12.0 (StatSoft, 2014), while ordination was performed using PC-ORD 7.02 (McCune & Mefford, 2016).

3. Results

In the current aboveground vegetation, 95 herbaceous plant species were identified in the study plots in all three years (ESM Table 2.1). In the first year after reconstruction (2016), the total number of species of all plots was highest with 77 species, while the total number of species was considerably lower in the year before the reconstruction (2015: 37 species) and in the second year after reconstruction (2017: 57 species). *Hypericum tetrapterum* Fr. was found as endangered species for Hamburg in one study plot in the channel in 2017. Six non-native species were found, of which only *Oenothera biennis* agg. occurred frequently in the zones (except in the channel) and years (19 plots) with high coverages (up to 50%).

The DCA reveals a more homogeneous species compositions in the current vegetation of the study plots of the channel, plain and upper shoreline by clustering together in the ordination diagram in comparison to the plots of the lower shoreline (Fig. 2.2a,b). Species composition of the current vegetation of the plots of the channel and plain are grouped together. The study plots of the lower shoreline show different species compositions in the current vegetation indicated by a broad scattering in the diagram. The soil seed bank of the study plots contain part of the species found in the current vegetation and clusters in the middle of the plots of the current vegetation. The species are ordered along axis 1 indicating a moisture gradient of the study plots, with dry meadow species located in the left part of the diagram and hydrophytes and macrophytes located in the right part of the diagram.

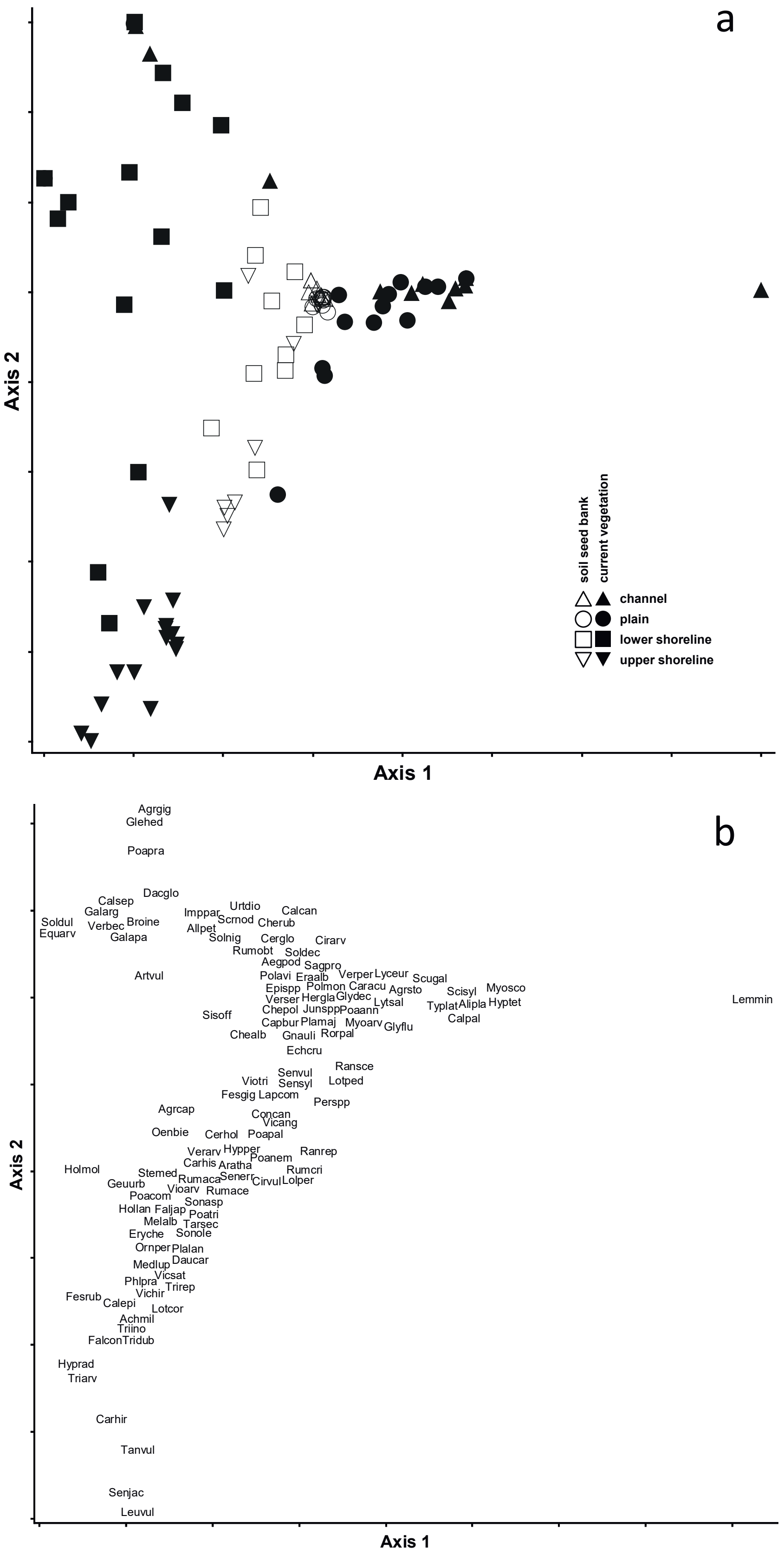

Fig. 2.2 Detrended correspondence analysis (DCA) of the studied stormwater pond based on 95 studied plots (a) and 117 herbaceous plant species (b) found in the soil seed bank and current aboveground vegetation. Study plots are differentiated after type of data (soil seed bank=open symbols, current vegetation=filled symbols) and zones (channel=triangle, plain=circle, lower shoreline=square, upper shoreline=reverse triangle). For species acronyms see ESM Table 2.1. Axis 1: eigenvalue 0.88, gradient length 12.01 SD; axis 2: eigenvalue 0.76, gradient length 5.15 SD.

In total, 74 species were found in the seed bank of all zones in both years, with more species (60 species) found in the second year after the reconstruction in comparison to the year before the reconstruction (51 species). The most frequent species were *Juncus* spp. (2015: 162995±69857 seedlings/m², 2017: 53069±11540 seedlings/m²) and *Epilobium* spp. (2015: 570±373 seedlings/m², 2017: 7553±3468 seedlings/m²; mean±standard error). 23 species were used in the seed mixtures in 2016 (Table 2.1). Only seven species of these were missing in the seed bank in 2015, but present in the current vegetation in 2017 (*Agrostis capillaris* L., *Agrostis stolonifera* L., *Daucus carota* L., *Festuca rubra* L., *Leucanthemum vulgare* (Vaill.) Lam., *Lotus corniculatus* L. and *Poa pratensis* L.). Three additional species sown in 2016 were already present in the seed bank in 2015 and also found in the current vegetation in 2017 (*Achillea millefolium* L., *Plantago lanceolata* L. and *Poa trivialis* L.). The remaining 13 species sown in 2016 were not identified in the current vegetation in 2017. Instead, 44 additional species were found in the current vegetation 2017, having their origin in the soil seed bank or in dispersal input.

Table 2.1 Vascular plant species found in the seed bank in 2015, sown plant species in 2016 and plant species found in the current vegetation in 2017. Data for the different zones were summarised. The species *Epilobium ciliatum* Raf. + *Epilobium obscurum* Schreb. + *Epilobium montanum* L. + *Epilobium parviflorum* Schreb., *Juncus articulatus* L. + *Juncus bufonius* L. + *Juncus effusus* L. and *Persicaria lapathifolia* (L.) Delarbre + *Persicaria maculosa* Gray + *Persicaria mitis* (Schrank) Assenov were summarised to *Epilobium* spp., *Juncus* spp. and *Persicaria* spp., respectively.

	2015	**2016**	**2017**
Scientific name	**seed bank**	**sown**	**vegetation**
Achillea millefolium L.	x	x	x
Aegopodium podagraria L.	x		
Agrostis canina L.		x	
Agrostis capillaris L.		x	x
Agrostis gigantea Roth			x
Agrostis stolonifera L.		x	x
Alisma plantago-aquatica L.			x
Alliaria petiolata (M.Bieb.) Cavara et Grande			x
Arabidopsis thaliana (L.) Heynh.	x		
Artemisia vulgaris L.	x		x
Bromus inermis Leyss.			x
Callitriche palustris agg.			x
Calystegia sepium (L.) R. Br.	x		
Cardamine hirsuta L.	x		
Centaurea jacea L. s. str.		x	
Cerastium holosteoides Fr.	x		x
Chenopodium album L.	x		

Table 2.1 (Continued)

	2015	2016	2017
Scientific name	**seed bank**	**sown**	**vegetation**
Chenopodium polyspermum L.	x		
Cirsium vulgare (Savi) Ten.	x		x
Conyza canadensis (L.) Cronquist	x		
Dactylis glomerata L.			x
Daucus carota L.		x	x
Epilobium spp.	x		x
Erysimum cheiranthoides L.	x		
Equisetum arvense L.			x
Festuca brevipila R. Tracey		x	
Festuca ovina L.		x	
Festuca rubra L.		x	x
Galeobdolon argentatum Smejkal			x
Galium album Mill.		x	
Galium aparine L.	x		x
Galium verum L. s. str.		x	
Geum urbanum L.			x
Glechoma hederacea L.	x		x
Glyceria fluitans (L.) R. Br.	x		x
Gnaphalium uliginosum L.	x		
Holcus lanatus L.	x		x
Hypericum perforatum L.	x		x
Hypericum tetrapterum Fr.			x
Impatiens parviflora Dc.	x		x
Juncus spp.	x		x
Lemna minor L.			x
Leontodon spec.		x	
Leucanthemum vulgare (Vaill.) Lam.		x	x
Lolium perenne L.		x	
Lotus corniculatus L.		x	x
Lotus pedunculatus Cav.			x
Lycopus europaeus L.	x		
Lythrum salicaria L.	x		x
Medicago lupulina L.		x	
Myosotis scorpioides L.			x
Oenothera biennis agg.	x		x
Persicaria spp.	x		
Pimpinella saxifraga L.		x	
Plantago lanceolata L.	x	x	x

Table 2.1 (Continued)

	2015	**2016**	**2017**
Scientific name	**seed bank**	**sown**	**vegetation**
Poa nemoralis L.	x	x	
Poa palustris L.	x		x
Poa pratensis L.		x	x
Poa trivialis L.	x	x	x
Poa supina Schrad.		x	
Polygonum aviculare L.	x		
Polypogon monspeliensis (L.) Desf.	x		
Ranunculus repens L.	x		x
Ranunculus sceleratus L.	x		
Rorippa palustris (L.) Besser	x		
Rumex acetosa L.	x		x
Rumex acetosella L.			x
Rumex crispus L.	x		
Rumex obtusifolius L.	x		x
Sagina procumbens L.	x		
Sanguisorba minor Scop.		x	
Scirpus sylvaticus L.	x		x
Scrophularia nodosa L.	x		x
Scutellaria galericulata L.			x
Senecio erraticus Bertol.	x		
Senecio jacobaea L.			x
Senecio sylvaticus L.	x		
Sisymbrium officinale (L.) Scop.	x		
Solanum dulcamara L.			x
Sonchus asper (L.) Hill			x
Tanacetum vulgare L.			x
Taraxacum sect. *Ruderalia* Kirschner, H. Øllg. & Štěpánek	x		x
Trifolium dubium Sibth.			x
Trifolium repens L.	x		x
Typha latifolia L.	x		x
Urtica dioica L.	x		x
Veronica arvensis L.	x		
Veronica beccabunga L.			x
Vicia angustifolia L.	x		
Viola arvensis Murray	x		

Except for the channel, the highest number of species and number of ruderal species were found in 2016, while the number of species and number of ruderal species decreased again in 2017 (Fig. 2.3a,b). In all these three zones, the lowest number of species and number of ruderal species were found in 2015. In contrast, in the channel, the lowest number of species (0±1, Mean±SE) and number of ruderal species (0±0) were found in 2016. In 2015 and 2017, equal values were found for the number of species and number of ruderal species in the channel. The number of species and number of ruderal species differed significantly between the zones (number of species: F = 57.8, p < 0.001; number of ruderal species: F = 47.8, p < 0.001) and years (F = 17.3, p < 0.001; F = 17.5, p < 0.001) and an interaction effect (F = 9.8, p < 0.001; F = 9.3, p < 0.001) was also detected (Table 2.2). While the number of species and number of ruderal species of the channel did not differ significantly between the years, in the other zones the significantly highest number of species and number of ruderal species was found in 2016 and the lowest in 2015 (Fig. 2.3a,b).

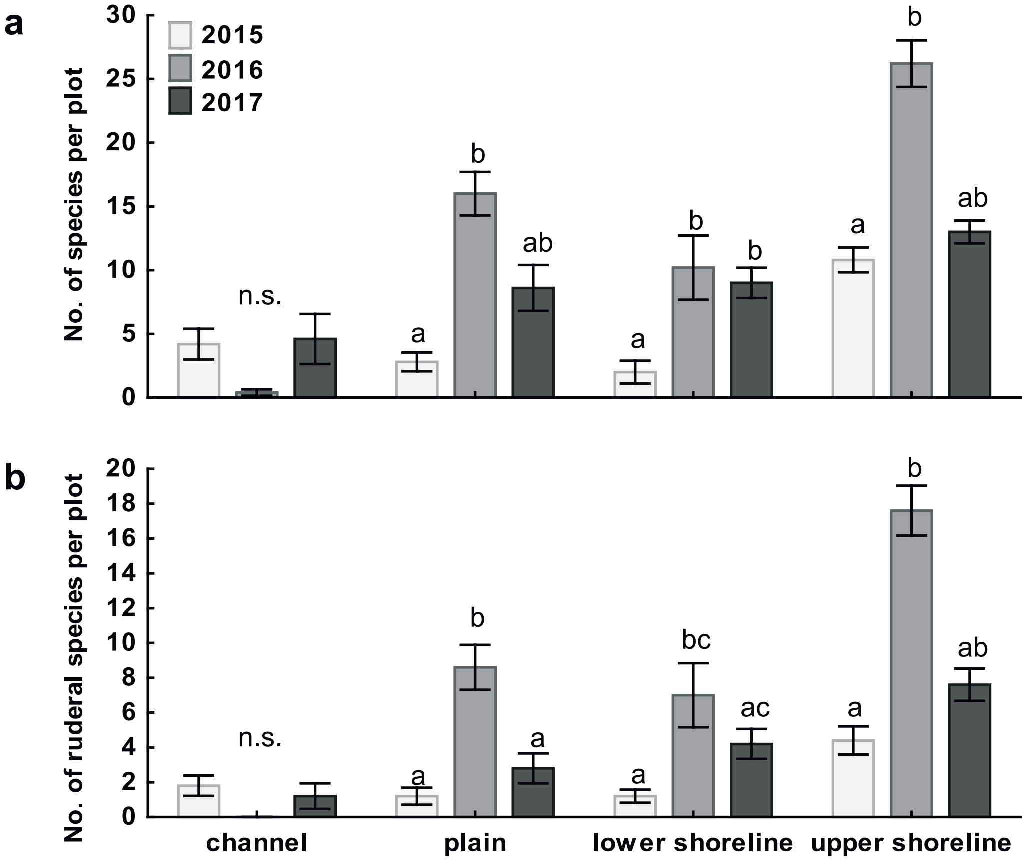

Fig. 2.3 Number of species (a) and number of ruderal species (b; Grime 1979) of the study plots of the current aboveground vegetation of the stormwater pond 'Farnhornstieg' in Hamburg, Germany, for the years 2015, 2016 and 2017, grouped according to the different zones of the stormwater pond (channel, plain, lower shoreline and upper shoreline). Letters indicate significant differences (p< 0.05) between the years for the different zones after Tukey HSD post-hoc-tests using box-cox-transformed data. For the number of ruderals, the strategy types r (ruderals), cr (competitive ruderals), sr (stress-tolerant ruderals) and csr (competitive and stress-tolerant ruderals) were considered. Mean and standard error of the original data are shown.

Table 2.2 Effects of zone (channel, plain, lower and upper shoreline), year (2015, 2016 and 2017) and their interaction on the number of species and number of ruderal species of the current aboveground vegetation. F- and p-values of repeated measures ANOVA are given. n.s. = no significant differences.

	No. of species		**No. of ruderal species**	
Effect	**F**	**P**	**F**	**P**
Zone	57.8	< 0.001	47.8	< 0.001
Year	17.3	< 0.001	17.5	< 0.001
Zone*Year	9.8	< 0.001	9.3	< 0.001

4. Discussion

Our study showed that the soil seed bank of an urban stormwater pond has the potential for natural re-colonization after reconstruction indicated by high seed numbers in the soil seed bank. The most dominant species group in the seed bank in both study years was *Juncus* spp. (*Juncus articulatus*, *J. bufonius*, *J. effusus*). *Juncus* species are known to have a high seed production leading to high seed rains and to build persistent seed banks (Thompson et al., 1997; Jensen, 1998; Ervin & Wetzel, 2001). The high number of *Juncus* seeds found in the seed bank of the stormwater pond in both study years is in accordance with other studies. *Juncus* species were found to be the most abundant species with high seed densities in the seed bank of different types of wet habitats (Jensen, 1998; Bissels et al., 2005; Bossuyt & Honnay, 2008). Therefore, the bare soils of the stormwater pond could be colonized quickly and, as vegetation dominated by *Juncus* species is known to not inhibit germination of further herbaceous species, a more heterogeneous vegetation could develop over time (Ludewig et al., 2015). For the second most abundant species group in our seed bank study, *Epilobium* spp. (*Epilobium ciliatum*, *E. obscurum*, *E. montanum*, *E. parviflorum*), persistent seed banks were reported as well (Thompson et al., 1997). Persistent seed banks determine how the vegetation will react to changing environmental conditions or disturbance events and thus persistent seed banks are an important feature in dynamic ecosystems with unpredictable conditions (Capon & Brock, 2006; Brock, 2011). In our study, the species composition of the soil seed bank is a subset of the species composition of the current vegetation with additional species not present in the current vegetation found in the soil seed bank. Similarity of the soil seed bank and the current vegetation can be low in wetland ecosystems (Jensen, 1998; Hopfensperger, 2007; Hopfensperger et al., 2009; Kimura & Tsuyuzaki, 2011). Before the reconstruction, no difference of the current vegetation was visible between the channel and plain and thus the zones contain similar species indicated by the DCA. The high amount of species in the soil seed bank not present in the current vegetation increases the potential of a successful recolonization of bare soil patches of the stormwater pond.

Species found in the seed bank were herbaceous as well as woody and, furthermore, these species can be classified into two main groups. Species of different types of wet habitats, such as reeds or wet meadows, were identified as well as ruderal species. Germination requirements of wetland species vary among species, but in general, wetland species are known to germinate under a variety of different environmental conditions. This includes hydrological conditions ranging from moist or flooded soils to dry soils, wide temperature ranges and different light conditions. Species also differ in their requirements for dormancy breaking (Keddy & Ellis, 1985; Schütz, 2000; Boedeltje et al., 2002; Brändel, 2006; Ludewig et al., 2014). When the species composition of wetland species in the seed bank is diverse, it could be assumed that the germination requirements of at least few species could be fulfilled. Further, we found ruderal species in the soil seed bank, which are able to recolonize rapidly after disturbance (Grime, 1979). The high coverages of *Juncus* and *Epilobium* species as well as the occurrence of ruderal species in the current vegetation in the first and second year after reconstruction indicate that these species benefit from natural recolonization. Only seven species used in the seed mixtures were found in the current vegetation in the second year after reconstruction but were absent in the seed bank in the year before the reconstruction. Except *Agrostis stolonifera*, these species are adapted to relatively dry soil conditions (Ellenberg indactor values for moisture between 4 and 6; Ellenberg et al., 1991) and were mainly found in the upper shoreline in the current vegetation in the second year after reconstruction. This indicates that species adapted to dry soil conditions benefit from sowing and that sowing was only successful in the drier meadow areas of the stormwater pond. However, the long-term establishment of the vegetation in the stromwater pond was not analysed in our study. It can be assumed that the composition of the current vegetation will change in the future, depending on the frequency and duration of flooding. When the hydrological conditions in the channel and plain will become drier in the future, germination and establishment of species adapted to drier conditions, such as *Arabidopsis thaliana* (L.) Heynh. or *Cardamine hirsuta* L., may occur. This resilience of the soil seed bank to react to changing environmental conditions is used in restoration projects to initiate former vegetation composition of wetlands. Nevertheless, the success of re-establishing former vegetation out of the seed bank depends on the initial conditions (Brouwer & Roelofs, 2001; Roelofs et al., 2002; Beas et al., 2013; Bauer et al., 2018).

5. Conclusion

Urban stormwater ponds can contain high numbers of seeds in the soil seed bank from diverse vascular plant species concerning lifeforms and preferred habitats, highlighting the potential for natural re-colonization after reconstruction and thus prevent soil erosion as a consequence of flooding. Therefore, sowing (and planting) of plant species is no necessary management action in the construction process. Sowing can initiate very homogenous vegetation covers, which should not be supported. Furthermore, natural re-colonization possibly promoting a higher habitat heterogeneity and thus higher biodiversity should be preferred and the construction of new stormwater ponds should be realised in areas, where soil seed banks are present (Holtmann et al., 2019).

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We thank Rudolf Hennemann from the planning office Plan.et and Stephan Schneider from the administrative district Eimsbüttel (Hamburg) for background information and the latter also for permission to work in the pond. We further thank Imke Bodendieck, Christian Pawlak and Thea Wahlers for field and lab assistance. Nikola Lenzewski was funded by the Federal Ministry of Education and Research (Germany) within the framework of the StucK-project (033W031B). Kristin Ludewig was financed within the MediAN-Project (01LC1601A) by the Federal Ministry of Education and Research (Germany).

Electronic Supplementary Material

ESM Table 2.1 Vascular plant species found in the current vegetation in the years 2015, 2016 and 2017. The species acronyms used in the DCA as well as the number of plots of the channel, plain, lower shoreline and upper shoreline are given. Maximum value per zone and year is five. Species acronyms are valid also for plant species in the soil seed bank. Further acronyms of species found in the seed bank are listed as a note below this table. The species *Epilobium ciliatum* Raf. + *Epilobium obscurum* Schreb. + *Epilobium montanum* L. + *Epilobium parviflorum* Schreb., *Juncus articulatus* L. + *Juncus bufonius* L. + *Juncus effusus* L. and *Persicaria lapathifolia* (L.) Delarbre + *Persicaria maculosa* Gray + *Persicaria mitis* (Schrank) Assenov were summarised to *Epilobium* spp., *Juncus* spp. and *Persicaria* spp., respectively.

Scientific name	**acronym**	**2015**	**2016**	**2017**
Achillea millefolium	Achmil	0/0/0/5	0/0/0/4	0/1/0/5
Agrostis capillaris	Agrcap	0/0/0/2	0/0/1/0	0/0/4/1
Agrostis gigantea	Agrgig	0/0/0/0	0/0/0/0	0/0/1/0
Agrostis stolonifera	Agrsto	3/2/1/0	0/2/1/0	1/3/0/1
Alisma plantago-aquatica	Alipla	0/0/0/0	0/1/0/0	2/0/0/0
Alliaria petiolata	Allpet	0/0/0/0	0/0/2/0	0/0/1/0
Artemisia vulgaris	Artvul	0/0/0/2	0/1/1/4	0/0/1/0
Bromus inermis	Broine	0/0/0/1	0/0/0/0	0/0/1/0
Calamagrostis canescens	Calcan	1/1/0/0	0/0/0/0	0/0/0/0
Calamagrostis epigejos	Calepi	0/0/0/2	0/0/0/2	0/0/0/0
Callitriche palustris agg.	Calpal	0/0/0/0	0/0/0/0	1/0/0/0
Calystegia sepium	Calsep	1/1/0/0	0/0/1/0	0/0/0/0
Capsella bursa-pastoris	Capbur	0/0/0/0	0/0/0/1	0/0/0/0
Carex hirta	Carhir	0/0/0/2	0/0/0/0	0/0/0/0
Cerastium holosteoides	Cerhol	0/0/0/4	0/0/0/4	0/0/0/3
Chenopodium album	Chealb	0/0/0/0	0/0/0/2	0/0/0/0
Cirsium arvense	Cirarv	0/0/0/0	0/1/1/0	0/0/0/0
Cirsium vulgare	Cirvul	0/0/0/0	0/0/0/3	0/1/0/0
Conyza canadensis	Concan	0/0/0/0	0/1/0/3	0/0/0/0

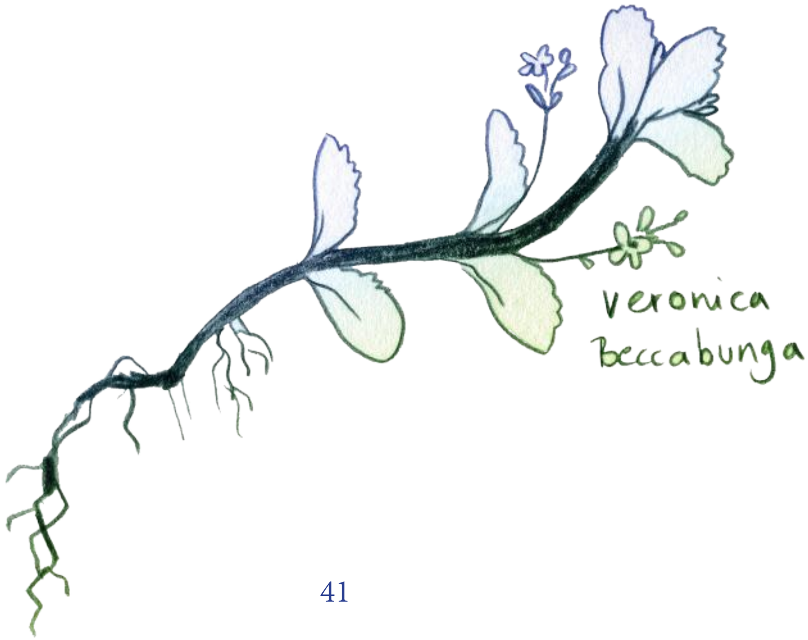
ESM Table 2.1 (Continued)

Scientific name	**acronym**	**2015**	**2016**	**2017**
Dactylis glomerata	Dacglo	0/0/0/0	0/0/0/0	0/1/1/0
Daucus carota	Daucar	0/0/0/0	0/1/0/0	0/0/0/1
Epilobium ciliatum	Epicil	1/0/0/0	0/5/1/1	1/2/1/0
Epilobium hirsutum	Epihir	0/0/0/0	0/0/0/1	0/0/0/0
Epilobium montanum	Epimon	1/0/0/0	0/0/0/0	0/1/0/0
Equisetum arvense	Equarv	3/2/2/1	0/1/4/5	0/0/3/1
Erysimum cheirantheoides	Eryche	0/0/0/0	0/0/1/1	0/0/0/0
Fallopia convolvulus	Falcon	0/0/0/0	0/0/0/1	0/0/0/0
Festuca rubra	Fesrub	0/0/1/5	0/0/1/5	0/0/1/3
Galeobdolon argentatum	Galarg	0/0/0/0	0/0/1/0	0/0/1/0
Galium aparine	Galapa	0/0/1/1	0/0/3/0	0/0/1/0
Geum urbanum	Geuurb	0/0/0/0	0/0/0/0	0/0/1/0
Glechoma hederacea	Glehed	2/1/2/0	0/0/3/1	0/0/3/0
Glyceria fluitans	Glyflu	0/0/0/0	0/5/0/1	2/1/0/0
Gnaphalium uliginosum	Gnauli	0/0/0/0	0/3/0/2	0/0/0/0
Holcus lanatus	Hollan	0/0/1/4	0/1/2/5	0/1/2/4
Holcus mollis	Holmol	0/0/0/0	0/0/1/0	0/0/0/0
Hypericum perforatum	Hypper	0/0/0/4	0/0/1/2	0/0/3/2
Hypericum tetrapterum	Hyptet	0/0/0/0	0/0/0/0	1/0/0/0
Hypochaeris radicata	Hyprad	0/0/0/1	0/0/0/0	0/0/0/0
Impatiens parviflora	Imppar	1/1/0/0	0/0/1/0	0/0/1/0
Juncus articulatus	Junart	0/0/0/0	0/5/0/0	1/2/0/0
Juncus bufonius	Junbuf	0/0/0/0	0/3/0/5	0/1/0/0
Juncus effusus	Juneff	2/2/0/0	0/5/0/2	1/5/2/3
Lemna minor	Lemmin	0/0/0/0	1/2/0/0	2/0/0/0
Leucanthemum vulgare	Leuvul	0/0/0/0	0/0/0/1	0/0/0/1
Lolium perenne	Lolper	0/0/0/0	0/1/0/0	0/0/0/0
Lotus corniculatus	Lotcor	0/0/0/0	0/0/0/0	0/0/1/2
Lotus pedunculatus	Lotped	0/0/0/0	0/2/0/0	0/2/0/0
Lycopus europaeus	Lyceur	0/1/0/0	0/0/0/0	0/0/0/0
Lythrum salicaria	Lytsal	2/2/0/0	1/5/0/0	2/5/0/0
Medicago lupulina	Medlup	0/0/0/0	0/0/0/4	0/0/0/0
Melilotus albus	Melalb	0/0/0/0	0/1/0/4	0/0/0/0
Myosotis scorpioides	Myosco	0/0/0/0	0/0/0/0	1/0/0/0
Oenothera biennis agg.	Oenbie	0/0/0/3	0/1/4/4	0/0/3/4
Ornithopus perpusillus	Ornper	0/0/0/0	0/0/0/1	0/0/0/0
Persicaria lapathifolia	Perlap	0/0/0/0	0/2/1/2	0/0/0/0
Persicaria maculosa	Permac	0/0/0/0	0/5/1/3	0/0/0/0
Phleum pratense	Phlpra	0/0/0/0	0/0/0/4	0/0/0/0
Plantago lanceolata	Plalan	0/0/0/3	0/1/2/5	0/0/1/5

ESM Table 2.1 (Continued)

Scientific name	acronym	2015	2016	2017
Poa compressa	Poacom	0/0/0/0	0/0/0/2	0/0/0/0
Poa palustris	Poapal	0/0/0/0	0/1/0/1	0/1/0/1
Poa pratensis	Poapra	0/0/0/1	0/0/0/0	0/0/1/0
Poa trivialis	Poatri	0/0/0/0	0/0/1/3	0/1/1/5
Polygonum aviculare	Polavi	0/0/0/0	0/1/1/0	0/0/0/0
Ranunculus repens	Ranrep	0/0/0/0	0/1/0/2	0/1/0/2
Ranunculus sceleratus	Ransce	0/0/0/0	0/4/0/0	0/0/0/0
Rorippa palustris	Rorpal	0/0/0/0	0/1/0/0	0/0/0/0
Rumex acetosella	Rumace	0/0/0/0	0/0/2/3	0/0/0/1
Rumex crispus	Rumcri	0/0/0/0	0/1/0/0	0/0/0/0
Rumex obtusifolius	Rumobt	1/0/0/0	0/1/1/1	0/2/0/1
Scirpus sylvaticus	Scisyl	1/1/0/0	0/5/0/0	3/5/1/1
Scrophularia nodosa	Scrnod	0/0/0/0	0/0/1/1	0/0/2/0
Scutellaria galericulata	Scugal	0/0/0/0	0/0/0/0	0/1/0/0
Senecio jacobaea	Senjac	0/0/0/1	0/0/0/0	0/0/0/2
Sisymbrium officinale	Sisoff	0/0/0/0	0/0/1/1	0/0/0/0
Solanum dulcamara	Soldul	0/0/0/0	0/0/1/0	0/0/1/0
Solanum nigrum	Solnig	0/0/0/0	0/0/1/0	0/0/0/0
Sonchus asper	Sonasp	0/0/0/0	0/0/0/1	0/0/0/1
Sonchus oleraceus	Sonole	0/0/0/1	0/0/0/1	0/0/0/0
Stellaria media	Stemed	0/0/0/0	0/0/0/1	0/0/0/0
Tanacetum vulgare	Tanvul	0/0/0/0	0/0/0/2	0/0/0/1
Taraxacum sect. *Ruderalia*	Tarsec	0/0/0/0	0/2/3/4	0/1/1/5
Trifolium arvense	Triarv	0/0/0/1	0/0/0/0	0/0/0/0
Trifolium dubium	Tridub	0/0/0/1	0/0/0/2	0/0/0/1
Trifolium repens	Trirep	0/0/0/2	0/5/1/5	0/1/0/5
Tripleurospermum perforatum	Triper	0/0/0/0	0/0/0/2	0/0/0/0
Typha latifolia	Typlat	0/0/0/0	0/3/0/0	4/4/0/0
Urtica dioica	Urtdio	2/0/1/0	0/0/3/1	0/0/4/1
Veronica arvensis	Verarv	0/0/0/0	0/0/0/1	0/0/0/0
Veronica beccabunga	Verbec	0/0/1/0	0/0/0/0	1/0/0/0
Vicia hirsuta	Vichir	0/0/0/2	0/0/0/5	0/0/0/0
Vicia sativa	Vicsat	0/0/0/0	0/0/0/2	0/0/0/0
Viola arvensis	Vioarv	0/0/0/0	0/0/0/2	0/0/0/0

Note: Species acronyms of additional species found in the soil seed bank: *Aegopodium podagraria* L. (Aegpod), *Arabidopsis thaliana* (L.) Heynh. (Aratha), *Cardamine hirsuta* L. (Carhis), *Carex acuta* L. (Caracu), *Cerastium glomeratum* Thuill. (Cerglo), *Chenopodium polyspermum* L. (Chepol), *Chenopodium rubrum* L. (Cherub), *Echinocloa crus-calli* (L.) P. Beauv. (Echcru), *Eragrostis albensis* H. Scholz (Eraalb), *Festuca gigantea* (L.) Vill. (Fesgig), *Glyceria declinata* Bréb (Glydec), *Herniaria glabra* L. (Hergla), *Lapsana communis* L. (Lapcom), *Myosotis arvensis* Hill (Myoarv), *Plantago major* L. (Plamaj), *Poa annua* L. (Poaann), *Poa nemoralis* L. (Poanem), *Polypogon monspeliensis* (L.) Desf. (Polmon), *Sagina procumbens* L. (Sagpro), *Senecio erraticus* Bertol. (Senerr), *Senecio sylvaticus* L. (Sensyl), *Senecio vulgaris* L. (Senvul), *Solanum decipiens* Opiz (Soldec), *Veronica peregrina* L. (Verper), *Veronica serpyllifolia* L. (Verser), *Vicia angustifolia* L. (Vicang), *Viola tricolor* L. (Viotri)


veronica
Beccabunga

Ranunculus
repens

BOX 1

Plant biodiversity of urban stormwater ponds

Nikola Lenzewski, Kai Jensen and Kristin Ludewig

Unpublished manuscript

Keywords

Flood protection, Hamburg (Germany), Species richness, Vascular plants

1. Introduction

Stormwater ponds in urban areas are important habitats for flora and fauna due to poor availability of aquatic and semi-aquatic habitats and strong degradation of remaining wetlands in these areas (see Poppendieck et al. (2010) for Hamburg). The importance of urban stormwater ponds for biodiversity of amphibians, odonates and other invertebrates is well studied (Scher & Thièry, 2005; Hamer et al., 2012; Le Viol et al., 2012; Briers, 2014; Hassall & Anderson, 2015; Holtmann et al., 2017; Holtmann et al., 2018). Solga (2001) studied the bryophyte diversity of urban stormwater ponds in the city of Münster (Germany) and identified a diverse species composition with a high proportion (30%) of threatened species for North Rhine-Westphalia. Further, Holtmann et al. (2019) analysed the diversity of vascular plants in stormwater ponds in Münster. However, Holtmann et al. (2019) did not analysed the entire plant diversity of stormwater ponds but focused on target species groups, such as threatened species or aquatic species. So far, little is known about the entire vascular plant biodiversity of urban stormwater ponds.

We conducted a large survey on vascular plant biodiversity of 80 stormwater ponds in Hamburg in 2017. All vascular plant species were recorded differentiated after bottom and shoreline of the stormwater pond and, further, additional abiotic and biotic parameters of the stormwater pond and the near surrounding were gained. The aim of the study was to analyse plant biodiversity of wet and dry stormwater ponds. Wet and dry stormwater ponds are characterised by different hydrological conditions, and therefore plant biodiversity can be different between these two types of stormwater ponds.

We tested the following hypotheses:
Number of species is higher and proportion of threatened species is lower in the bottom of dry stormwater ponds in comparison to wet stormwater ponds (i), number of species and proportion of threatened species in the shoreline is not different between dry and wet stormwater ponds (ii) and the hydrological conditions indicated by the classification as dry or wet stormwater pond and the Ellenberg indicator values (EIV) for moisture are the main factor differentiating the number of species and proportion of species of wet and dry stormwater ponds (iii).

2.1 Material and Methods

2.1 Study objects and vegetation mapping

In Hamburg, 80 stormwater ponds (Fig. B1.1) were randomly selected from a list of stormwater ponds, which was created after Hagemann (2009), BUE (2016) and further information on stormwater ponds by the agency of roads, bridges and water Hamburg.

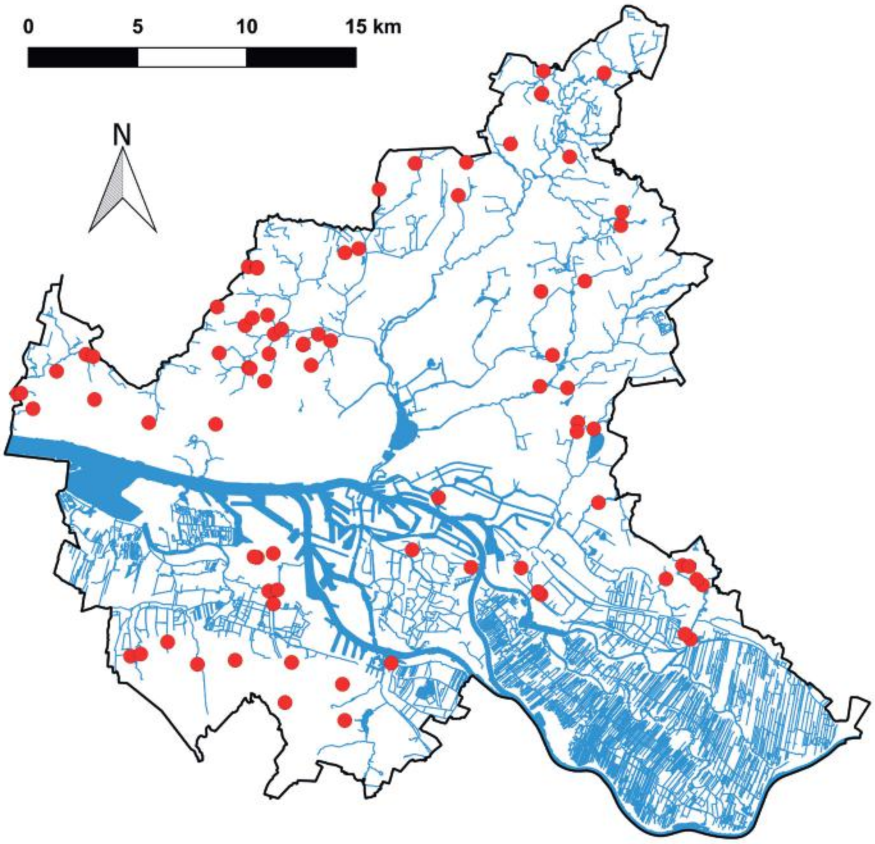


Fig. B1.1 Locations of the 80 studied stormwater ponds in Hamburg (Germany). Running and standing water bodies are additionally shown in the map.

In summer 2017, the stormwater ponds were surveyed twice and all vascular plant species were recorded with their coverages differentiated after the zones bottom and shoreline. Coverage was estimated in classes: <1% (mean 0.5%), 1-5% (3%), 5-25% (15%), 25-50% (37.5%), 50-75% (62.5%) and 75-100% (87.5%). Plants were identified using Raabe (1975), Christensen (1999), Jäger (2017) and van de Weyer et al. (2011). All plants were identified on species level, except for *Aquilegia vulgaris* agg., *Callitriche palustris* agg., *Carex muricata* agg., *Nasturtium officinale* agg., *Oenothera biennis* agg., *Rubus fruticosus* agg. and *Taraxacum* sect. *Ruderalia* KIRSCHNER, H. ØLLG. & ŠTĚPÁNEK, which were identified on aggregate level. Nomenclature of species follows Jäger (2017). Further, the slope of the shoreline of each stormwater pond and shading by woody species of each zone were estimated.

2.2 Data preparation and statistical analysis

For each stormwater pond, the location in the seven districts of Hamburg was derived; the distance to the town hall (53°33′1″N, 9°59′31″E) and a mean weighted soil sealing value in a puffer area of 50 m around each stormwater pond were calculated by using QGis. The latter was derived from the calculation of mean weighted Ellenberg Indicator values (EIV) after Diekmann (2003) using soil sealing data of Hamburg (BUE, 2017). Stormwater ponds were classified as dry and wet stormwater ponds, following the main hydrological characteristic of each stormwater pond. When the permanently flooded area of a stormwater pond exceeded half of the total area, the stormwater pond was classified as wet stormwater pond. All analysis were performed with species groups such as *Carex muricata* agg. or *Taraxacum* sect. *Ruderalia* treated as species. The number of species and the proportion of threatened species in percent of Hamburg were calculated for each stormwater pond differentiated after bottom and shoreline. Red list status of species was derived from Poppendieck et al. (2010). Further, mean weighted EIVs for moisture, reaction and nutrients of the bottom and shoreline were calculated after Diekmann (2003) and the area in m² of the bottom and shoreline was calculated in QGis.

The number of species and proportion of threatened species in % were analysed for significant differences with two-way ANOVAs with the factors type of stormwater pond (dry and wet) and zone (bottom and shoreline). Significant ANOVAs were followed by HSD test for unequal n. Classification and regression tree (CART) analysis were calculated for detecting patterns in the number of species and proportion of threatened species in % of the stormwater ponds. As variables, district, distance to town hall, soil sealing, type of stormwater pond, area, shading, slope of shoreline and the mean EIVs for moisture, reaction and nutrients were considered (Table B1.1). The minimum number of stormwater pond per node was set to five and the 'V-fold cross validation' was set to five. Statistical analyses were computed using Statistica (StatSoft Inc., 2014).

Table B1.1 Variables considered in the classification and regression trees (CART) for the number of species and proportion of threatened species in %. Further, a description and for ordinal data the parameter classes are given.

Parameter	Description
district	1=Altona, 2=Bergedorf, 3=Eimsbüttel, 4=Harburg, 5=HH-Mitte, 6=HH-Nord, 7=Wandsbek
distance to town hall	Distance of SP to the town hall of Hamburg
sealing	mean weighted soil sealing value in a puffer area of 50 m around SP
type of SP	dry SP, wet SP
area	area in m²
shading	Coverage of shading by woody species; 0=0%, 1=<5%, 2=5-25%, 3=25-50%, 4=50-75%, 5=75-100%
slope of shoreline	estimated mean slope of shoreline in °; only considered when analysing shoreline data
EIV m	mean weighted Ellenberg Indicator Value for moisture (EIV m)
EIV r	mean weighted Ellenberg Indicator Value for reaction (EIV r)
EIV n	mean weighted Ellenberg Indicator Value for nutrients (EIV n)

3. Results

503 plant species (including species groups) were found in the 80 stormwater ponds and 83 of these species are listed as threatened species for Hamburg. Covering less than 0.03% of the area of Hamburg, 32.5% of the species of the local flora of Hamburg were recorded in the stormwater ponds. A wide range of species, such as macrophytes and hydrophytes, wet meadow and dry grassland species, nitrophytes and ruderal species or species used as ornamental plants were found in the stormwater ponds.

The lowest number of species was found in the bottom of wet stormwater ponds with 18±2 (mean±standard error) species (Fig. B1.2a). Higher numbers of species were found in the bottom of dry stormwater ponds with 48±3 species and in the shorelines of dry and wet stormwater ponds with 56±4 and 56±3 species, respectively. The number of species differed significantly between type ($F=24.5$; $p<0.001$) and zone ($F=55.1$; $p<0.001$; two-way ANOVA) of stormwater pond, while the number of species in the bottom of the wet stormwater ponds was significantly different from the other values (HSD test for unequal n).

The highest proportion of threatened species was found in the bottom of wet stormwater ponds with 8.1±1.0% (Fig. B1.2b) and the lowest proportions were found in the shoreline of dry and wet stormwater ponds with 1.9±0.5% and 2.6±0.3%, respectively. Significant differences in the proportion of threatened species were found between type ($F=6.6$; $p<0.05$) and zone ($F=22.9$; $p<0.001$; two-way ANOVA) of stormwater ponds. The proportion of threatened species in the bottom of wet stormwater ponds differed significantly from the other values (HSD test for unequal n).

The number of species in the shoreline was with 71 species significantly higher in stormwater ponds with an area of shoreline >862 m^2 in comparison to stormwater ponds with smaller shorelines with a mean of 48 species (Fig. B1.3). In the larger stormwater ponds, the number of species was further derived by EIV for nutrients and EIV for reaction with a higher number of species in shorelines with an EIV for nutrients ≤7.0 (81 species) and an EIV for reaction >6.0 (93 species). Stormwater ponds with an area of shoreline ≤862 m^2 were further grouped by area, district, sealing and EIV for moisture. The number of species in the shoreline was with 62 species significantly higher in stormwater ponds with a mean weighted soil sealing value ≤4.9 in comparison to stormwater ponds with a mean weighted soil sealing value >4.9 (49 species). Further, the shoreline of stormwater ponds with an EIV for moisture ≤6.4 (54 species) contained a significantly higher number of species in comparison to stormwater ponds with an EIV for moisture >6.4 in the shoreline (35 species). CART revealed no significant differences in the number of species in the shoreline between dry and wet stormwater ponds as already shown (compare Fig. B1.2) and further, CART revealed no splitting variables for the proportion of threatened species in the shoreline of stormwater ponds.

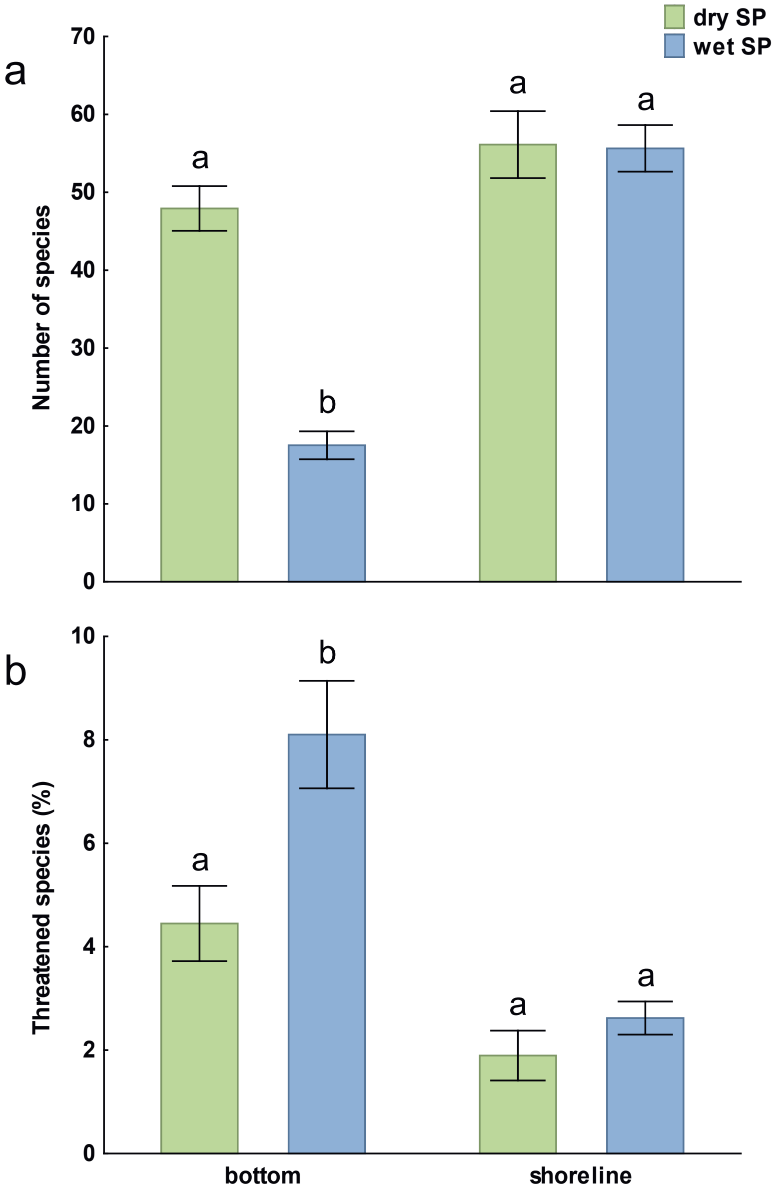


Fig. B1.2 Number of vascular plant species (a) and proportion of threatened species in % (b) of the studied stormwater ponds (SP), grouped according to type of SP (dry and wet) and zone (bottom and shoreline). Red list status of Hamburg was derived from Poppendieck et al. (2010). Mean and standard error are shown. Different letters indicate significant differences after HSD test for unequal n.

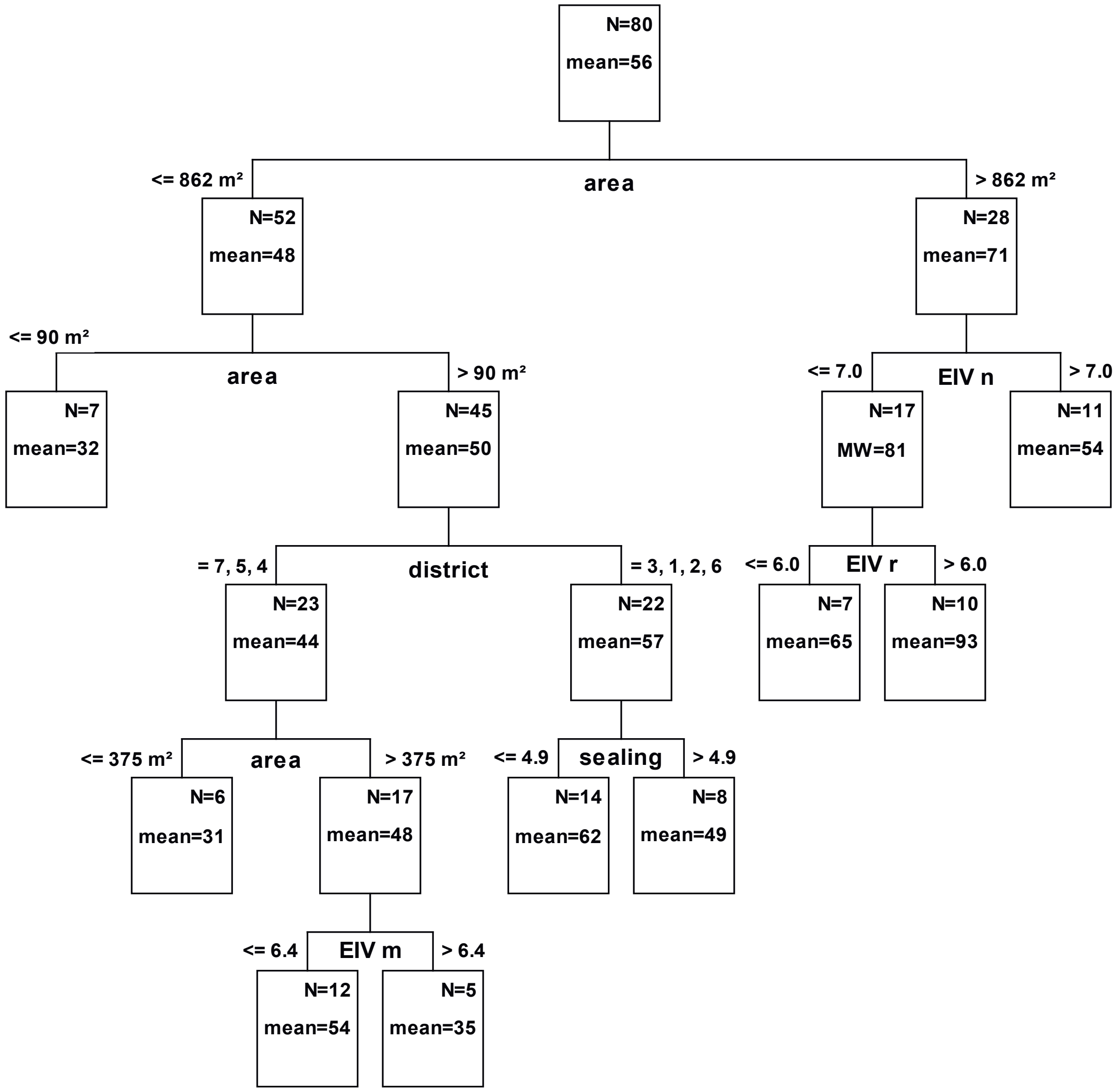


Fig. B1.3 Classification and regression tree (CART) for number of species in the shoreline of the studied stormwater ponds in Hamburg. For calculation of CART, the variables district, distance to town hall, sealing, type of SP, area, shading, slope of shoreline, Ellenberg Indicator value for moisture (EV m), Ellenberg Indicator value for reaction (EIV r) and Ellenberg Indicator value for nutrients (EIV n) were considered. For more information about predicator variables, see Table B1.1. For each node (rectangle), the number of SP (N) and mean number of species are given. The minimum number of SP per node was set to five and the 'V-fold cross validation' was set to five.

In CART, the first splitting variable for the number of species in the bottom was type of stormwater pond (Fig. B1.4). Dry stormwater ponds contained a significantly higher number of species (48 species) in the bottom in comparison to wet stormwater ponds (18 species). Further splitting variables for the number of species in the bottom of dry stormwater ponds were shading and EIV for nutrients. Bottoms of stormwater ponds with shading ≤25% contained a higher number of species with 58 species in comparison to more shaded bottoms and further, in bottoms with an EIV for nutrient ≤6.7 (64 species) a higher number of species was found in comparison to bottoms with an EIV for nutrient >6.7 (50 species). In wet stormwater ponds, bottoms with an EIV for moisture ≤9.5 contained a higher number of species (24 species) in comparison to bottoms with an EIV for moisture >9.5 (14 species). Further, the number of species in the bottom of wet stormwater ponds was derived by shading, EIV for moisture and soil sealing. Stormwater ponds with soil sealing values in the environment ≤4.5 contained a higher number of species in the bottom (24 species) in comparison to stormwater ponds with higher soil sealing values in the environment (12 species). In CART, the proportion of threatened species in the bottom of stormwater ponds was only derived by EIV for moisture (Fig. B1.5). A significantly higher proportion of threatened species was found in bottoms with EIV for moisture >9.1 (9.3%) in comparison to bottoms with an EIV for moisture ≤9.1 (4.4%).

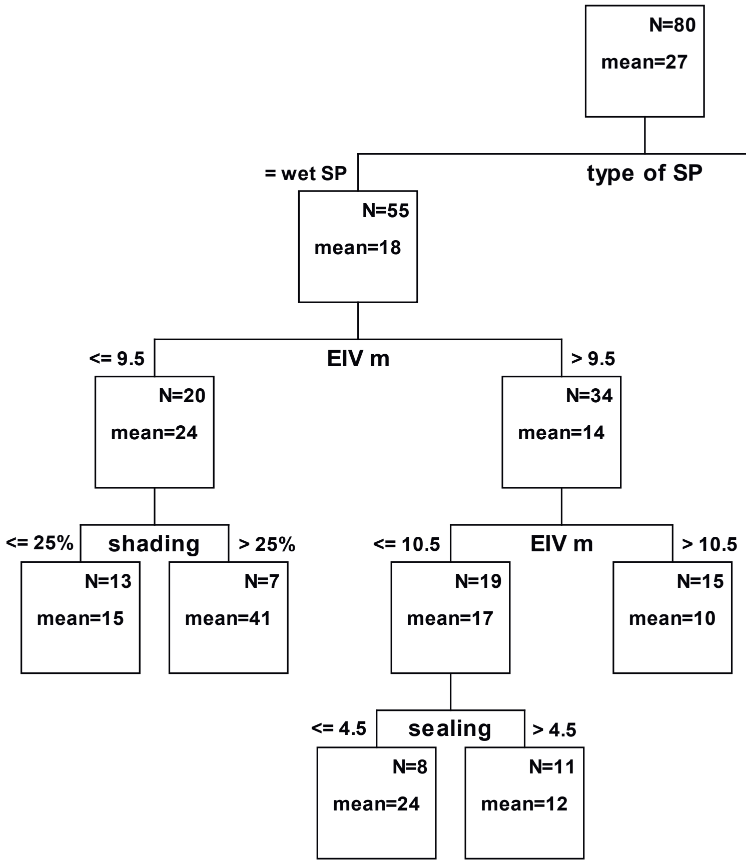


Fig. B1.4 Classification and regression tree (CART) for number of species in the bottom of the studied stormwater ponds in Hamburg. For calculation of CART, the predicator variables district, distance to town hall, sealing, type of SP, area, shading, EIV m, EIV r and EIV n were considered. For more information about the predicator variables, see Table B1.1. For each node (rectangle), the number of SP (N) and mean number of species are given. The minimum number of SP per node was set to five and the 'V-fold cross validation' was set to five.

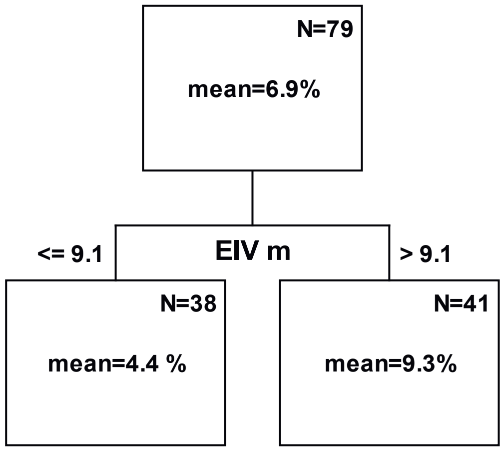


Fig. B1.5 Classification and regression tree (CART) for proportion of threatened species in % in the bottom of the studied stormwater ponds in Hamburg. For calculation of CART, the predicator variables district, distance to town hall, sealing, type of SP, area, shading, EIV m, EIV r and EIV n were considered. For more information about predicator variables, see Table B1.1. For each node (rectangle), the number of SP (N) and mean proportion of threatened species in % are given. The minimum number of SP per node set to five and the 'V-fold cross validation' was set to five. One stormwater pond was excluded from analysis due to missing EIVs.

4. Discussion

In accordance with the first hypothesis, a significantly higher number of species and lower proportion of threatened species was found in the bottom of dry stormwater ponds in comparison to wet stormwater ponds. It is well known that macrophyte species often develop dominant, dense stands, in which only few other species can establish (Wiegleb et al., 2014). In contrast to this, grasslands are known to be especially species-rich due to variability in environmental conditions leading to different types of microhabitats (Reitalu et al., 2008). Further, due to strong diffusion processes in water, microhabitats can be less available in aquatic ecosystems, which can lead to more uniform environmental conditions in water in comparison to terrestrial ecosystems. The higher proportion of threatened species in the bottom of wet stormwater ponds in comparison to dry stormwater ponds can be explained by the high proportion of macrophytes listed as threatened species especially in urban areas due to degradation of wetlands and availability of suitable habitats (see Poppendieck et al. (2010) for Hamburg).

In accordance with the second hypothesis, no differences in the number of species and proportion of threatened species in the shoreline of dry and wet stormwater ponds were found. Shorelines of both types of stormwater ponds were highly diverse regarding species composition and coverage of woody species, so that there is no clear differentiation of the shoreline of both types concerning species number and proportion of threatened species.

The third hypothesis that the hydrological conditions are the main factor differentiating the number of species and proportion of species of wet and dry stormwater ponds can be partly confirmed. Hydrological variables were displayed as main variables in CART for the number of species and proportion of threatened species in the bottom of stormwater ponds. Further, additional variables were displayed in CART for the number of species in the bottom. For dry stormwater ponds, a higher number of species in the bottom was found in less shaded stormwater ponds with low nutrient conditions. This can be explained by the negative relationship between species richness and nutrient depositions in grasslands reported by numerous studies (e.g. Cornwell & Grubb, 2003; Duprè et al., 2010; Dickson et al., 2014; Gross & Mittelbach, 2017). For wet stormwater ponds, the number of species was influenced by shading and soil sealing in the near environment as well as EIVs for moisture. In contrast to dry stormwater ponds, more shaded wet stormwater ponds contained a higher number of species. The hydrological conditions in the shoreline of stormwater ponds were only for a few stormwater ponds a significant factor. Here, the main factor for the number of species was area, with large stormwater ponds contained a higher number of species, which can be explained by the species-area-relationship (Dengler et al., 2020). Further, variables, such as nutrient and pH conditions of the soil or the location of the stormwater ponds in Hamburg, were additionally important for the number of species and proportion of threatened species of urban stormwater ponds.

The results of this study indicate that stormwater ponds play an important role in preserving plant diversity under heavy anthropogenic pressures by covering less than 0.03% of the area of Hamburg, but containing 32.5% of the species of the local flora of Hamburg (Poppendieck et al., 2010). Additional to the hydrological conditions, local and landscape variables are also important for the number of species and proportion of threatened species of stormwater ponds in Hamburg.

Acknowledgments

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Angelica
archangelica

CHAPTER 3

Diversity decrease due to loss of tidal influence at the Dove Elbe River between 1951 and 2016

Mareike Asdonk*, Nikola Lenzewski*, Kai Jensen and Kristin Ludewig

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*These authors contributed equally to this work

Abstract

Anthropogenic influence on riverine ecosystems has caused a drastic decline of natural floodplain ecosystems. Estuarine floodplains with their tidal influence are highly dynamic and harbour many rare and threatened plant species in Central Europe. This study focuses on the Dove Elbe River, which is an anabranch of the Elbe Estuary in Northwest Germany. In 1951, a sluice was built to disconnect the Dove Elbe River from the tidal influence of the Elbe River. This study aims to analyse changes in vegetation and environmental variables from 1951 to 2016. Therefore, 98 plots with vegetation records from 1951 along the Dove Elbe River were reassessed in 2016. 45 of the original plots were inventoried again, as 53 of the original plots were under water or majorly transformed, e.g. used as arable fields. Changes in vegetation type, diversity measures, species composition, and Ellenberg Indicator Values (EIV) for moisture and nutrition were analysed. The most remarkable outcome was the almost complete loss of wet pioneer vegetation types. While willows and other woody species were established on several plots with the former reed, *Angelica archangelica* community or *Phalaris arundinacea* community vegetation type, the intensification of agricultural land use caused a strong decline in species richness on grasslands. Overall, species richness per plot also decreased, and some threatened species were lost. The weighted average EIV for moisture clearly declined on all plots, which indicates drier conditions today compared to the mid-20th century. Our results reinforce the argument to restore the tidal influence along the Dove Elbe River.

Keywords

Degradation, Elbe Estuary, Floodplain, Land-use intensification, Restoration, Species richness

1. Introduction

Anthropogenic disturbances result in a severe decline of biodiversity on the global scale (Sala et al., 2000; Butchart et al., 2010). Recent research projects that land use changes will have the largest negative effect on biodiversity of terrestrial and freshwater ecosystems, followed by climate change and other factors by the year 2100 (Sala et al., 2000). Globally, the biodiversity of freshwater ecosystems is especially threatened by human activities such as river shore obstructions and river training, as well as intensive land use which results in ever increasing inputs of nutrients, contaminants, sediments and sewage (Ricciardi & Rasmussen, 1999; Sala et al., 2000). Due to increasing human impacts, intact freshwater habitats with natural conditions are scarce today (Nilsson et al., 2005; Dudgeon et al., 2006). In Germany, two thirds of the morphological river floodplains are now located behind dikes, and thus are no longer exposed to flooding, while 90% of the regularly flooded floodplains are degraded by anthropogenic disturbances (Brunotte et al., 2009). As a result, most freshwater and especially tidal freshwater habitats in Germany are classified as threatened ecosystems (Ellwanger et al., 2012).

Freshwater ecosystems such as river floodplains are often considered to be hotspots of biodiversity (Naiman et al., 1993; Tockner & Stanford, 2002), which can provide essential ecosystem services such as flood protection, food supply or recreation (Scholz et al., 2012; Schindler et al., 2014). Although the Elbe Estuary in Germany may not be especially species rich in comparison to other ecosystems, its floodplains provide diverse habitats and hosts rare species that are highly adapted to dynamic tidal conditions (Preisinger, 2005). One prominent example is *Oenanthe conioides*, an endemic plant species occurring only in tidal freshwater wetlands of the Elbe River (Preisinger, 2005; Elbe estuary working group, 2012).

The ecological value of freshwater ecosystems provides strong reasons to prevent the degradation of freshwater ecosystems. International strategies such as the European Water Framework Directive were negotiated for the development of sustainable water management (European Commission, 2000). On a national scale, the Integrated Elbe River Management Plan provides specific recommendations for more sustainable water management along the Elbe Estuary (Elbe estuary working group, 2012). A major recommendation of this plan is to restore natural flooding dynamics (Elbe estuary working group, 2012). Overall, restoration efforts aim to restore lost biodiversity from former times. Therefore, in order to evaluate the necessity for restoring a freshwater ecosystem and to develop suitable measures for restoration, it is essential to know how anthropogenic impacts have altered riverine biodiversity over a long period of time.

Since the mid-20th century, floodplain grasslands in Central Europe were majorly transformed due to land-use change and intensification followed by an increase in soil nitrogen (Prach, 2008; Krause et al., 2011; Wesche et al., 2012). Wet grasslands and species-rich mesic grasslands strongly declined (Krause et al., 2011). Furthermore, re-sampling studies document the decline of plant species richness and the loss of characteristic plant species in wet grasslands (Krause et al., 2015; Prach, 2008; Wesche et al., 2012). Competitive plant species adapted to high mowing frequencies (e.g. *Elymus repens*) and nitrogen contents in the soil (e.g. *Urtica dioica*) increased in their abundance. In contrast, ruderal and weedy species as well as threatened plant species decreased, while the latter were already not common in the mid-20th century (Prach, 2008; Wesche et al., 2012). However, long-term studies on changes of vegetation due to ceased or altered tidal influence are rare.

Analyses of changes in biodiversity over long periods are often impossible due to a lack of data. In this study, we used a vegetation dataset of an estuarine floodplain from the 1950s as a reference (Meyer, 1954). Here, vegetation along the Dove Elbe River in Hamburg (Germany), an anabranch of the upper Elbe Estuary was analysed just before the tidal influence at the Dove Elbe River was lost by the installation of a sluice. We conducted a new vegetation survey along the Dove Elbe River, 65 years after the first survey, to determine to which extent the former vegetation types, plant diversity, species composition and the environmental conditions changed after the tidal influence was lost. We expected an overall decline in soil moisture due to the loss of the tidal influence, and increases in soil nutrition due to an intensification of land use with increased use of fertilizer.

We tested the following hypotheses:
Loss of tidal influence led to (i) a lower number of plots with non-cultural vegetation types (semi-aquatic pioneer vegetation, reed, or *Angelica archangelica* community) and a higher number of plots with vegetation types of the cultural landscape (pastures and meadows), (ii) more generalist and non-native species, less threatened species, less typical floodplain species and decreased species diversity, and (iii) lower soil moisture and higher soil nutrient content 65 years after loss of the tidal influence.

2. Material and Methods

2.1 Study area and vegetation sampling

The study was conducted in the floodplain of the Dove Elbe River in the city of Hamburg, Germany (Fig. 3.1). The climate is temperate and oceanic with a mean annual temperature of 9 °C and annual precipitation of 730 mm (DWD, 2017a, reference period 1981–2016). Fluvisols form the dominant soil type near water, while Gleysols are present at higher elevations. Technosols can be found in places with anthropogenic deposits (Kalinski, unpublished data).

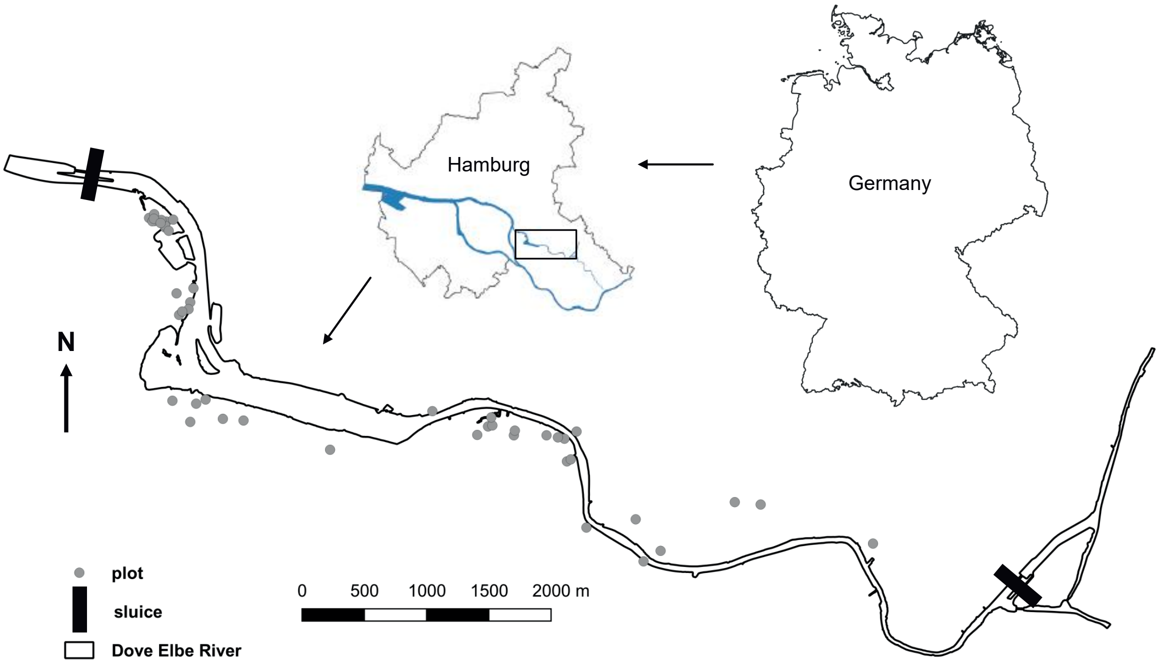

Fig. 3.1 Study area with study plots along the Dove Elbe River in Hamburg, Germany, between the sluices Krapphofschleuse in the East (53.47 °N, 10.19 °E) and Tatenberger Schleuse in the West (53.50 °N, 10.08 °E). Shown are the 45 plots, on which the vegetation was analysed in 1951 and 2016. Within the area of Hamburg, the main streams of the Elbe and the Dove Elbe Rivers are plotted.

As an anabranch of the Elbe River, the Dove Elbe River is part of the Elbe Estuary. In the 15th century, the Dove Elbe River had been separated from the Elbe River by a dam at its upstream end (Gammer Ort; Behre, 2008; BSU, 2017), leaving the tidal regime intact from the downstream confluence of the Dove Elbe River and the Elbe River until the construction of a sluice in 1951. The sluice disconnected the Dove Elbe River completely from its tidal regime. The ecology of the Dove Elbe River was further altered by gravel quarrying and the construction of a regatta course combined with the expansion of agricultural lands and increased recreation on the water body and floodplain (BUE, 2018b). Today, the Dove Elbe River is embedded in a cultural landscape characterized mostly by floodplain grasslands.

In 1951, Meyer (1954) recorded the vegetation along the Dove Elbe River on 98 plots (between today's Krapphofschleuse (53.47 °N, 10.19 °E) and Tatenberger Schleuse (53.50 °N, 10.08 °E; Fig. 3.1)) to characterize vegetation composition and diversity immediately before the loss of tidal influence. Meyer (1954) sampled his vegetation records using the Braun-Blanquet approach and classified them into vegetation types following Tüxen (1937). However, he used names roughly based on the dominant species. The vegetation records from 1951 were classified into the vegetation types *Limosella aquatica* community, *Ranunculus repens* community (including the species *Ranunculus reptans*), reed, *Angelica archangelica* community, *Phalaris arundinacea* community, wet meadow and nutrient rich pasture. Meyer (1954) documented his study plots as dots in hand-drawn maps without the information of the plot-size except for one plot, which was 20 m^2. These maps were georeferenced based on persistent landscape structures, such as dikes, using QGIS 2.8.4 (QGIS Development Team, 2018) for receiving the exact locations of the plots. For the 98 plots from 1951, the current vegetation types were determined according to the habitat mapping of Hamburg (BUE, 2016), and on 45 plots, which were not under water or majorly transformed in 2016 (as arable field, horticulture or recreational park), we recorded vegetation on 20 m^2 (app. 4.47 m x 4.47 m) between May and September 2016. We approached the plots with a handheld GPS device with an error of 3-7 meters depending on the weather conditions. We identified all vascular plant species and estimated their abundance according to the scale of Braun-Blanquet (Tremp, 2005; r=0.1%, +=0.2%, 1=2.5%, 2=15%, 3=37.5%, 4=62.5%, 5=87.5%). All plants were identified on species level, except for *Taraxacum* sp., which were identified on section level. Meyer (1954) identified all plants on species level, except for *Alchemilla vulgaris* and *Ranunculus auricomus*, which were identified on aggregate level. Nomenclature of plant species follows Jäger (2011), and the nomenclature of the former vegetation data used by Meyer (1954) was adjusted accordingly, except for *Alchemilla vulgaris*, for which we kept the aggregate (Table 3.A1). We classified the vegetation types of the study plots in 2016 (floodplain forest, meadow, pasture, tall forb community without *Angelica archangelica* and wet meadow) after Tüxen (1937).

2.2 Statistical analysis

We calculated the number of threatened plant species of Hamburg (Poppendieck et al., 2010: category 1 (critically endangered), 2 (endangered), 3 (vulnerable) and NT (near threatened)), non-native species of Germany (NN; Poppendieck et al., 2010), the overall number of species, and Shannon's evenness ($E = H/\ln(S)$, were H is the value of Shannon index; Tremp, 2005) per plot and year. As proxies for environmental conditions, we calculated the weighted mean Ellenberg indicator values (EIVs; Ellenberg & Leuschner, 2010) for moisture and nitrogen following Diekmann (2003) for each plot and year. For calculating the EIVs, we used the corresponding percentage cover values from the Braun-Blanquet cover classes. As proxies for typical floodplain species, we calculated the number of species indicating dynamic hydrological conditions (˜), the number of species indicating flooding (=) and the number of hydrophytes (Ellenberg & Leuschner, 2010). Differences in the number of species, evenness and EIVs per plot were analysed with repeated-measures ANOVAs according to the former vegetation type. To meet the assumptions of normal distribution and homogeneity of variance, we used a Box-Cox transformation of the data (species number: $\lambda = 0.63$; evenness: $\lambda = 4.60$; moisture value: $\lambda = 0.29$; nutrition value: $\lambda = 0.93$). Normal distribution and homogeneity of variance were verified visually using Q-Q-plots of the residuals. The data structure did not allow for an analysis of variance for the number of threatened and non-native species between 'former vegetation type' and 'year'. Therefore, differences in the number of threatened and non-native species per plot between the years were analysed with a Wilcoxon-signed-rank-test. ANOVAs with significant results were followed by Bonferroni post-hoc tests. The number of species indicating dynamic hydrological conditions, the number of species indicating flooding and the number of hydrophytes were not tested statistically due to insufficient species numbers.

To reveal vegetation patterns in the study area in 1951 and 2016, we used the species´ percentage cover values from the Braun-Blanquet cover classes in a detrended correspondence analysis (DCA). To reduce the disproportional influence of rare species in this analysis, plant species that were recorded in the data set only once were excluded from the analysis. Finally, 115 plant species and 90 plots were included in the ordination. EIVs for moisture and nutrition were plotted as vector arrows with the length of each arrow indicating the importance of the variable. Pearson correlations were calculated for the correlation of the EIVs for moisture and nutrition with the first DCA axis. Further, we calculated a PERMANOVA testing whether the overall species composition changed from 1951 to 2016.

The bar chart, ANOVAs, Box-Cox transformations and Bonferroni post-hoc tests were calculated using STATISTICA 12.0 (StatSoft, 2014). Boxplot diagrams were plotted using the packages “ggplot2” (Wickham, 2009) and “grid” in R (R Core Team, 2016). The Wilcoxon-signed-rank-test was conducted using the package “stats” and the PERMANOVA by using the package “vegan” in R (R Core Team, 2016). The DCA was performed using PC-ORD 7.04 (McCune & Mefford, 2016).

3. Results

The vegetation on the 98 plots surveyed by Meyer changed drastically from 1951 to 2016. More than one third (37 plots) of the original 98 plots from 1951 were under water in 2016, containing all plots with the vegetation types *Limosella aquatica* community and *Ranunculus repens* community.

On the 45 plots surveyed in 2016, the vegetation types reed, *Angelica archangelica* community and *Phalaris arundinacea* community could no longer be found in 2016 (Fig. 3.2). Instead, on some of these plots (ten plots in total), the new vegetation type floodplain forest with typical soft- and hardwood species developed, some characterized by high coverages of the non-native species *Rubus armeniacus*. Furthermore, a tall forb community without *Angelica archangelica* appeared on plots of all former vegetation types (12 plots in total). Here, the dominant species *Urtica dioica* occurred together with other tall forbs, such as *Senecio sarracenicus*. Additionally, a drier meadow vegetation type without species indicating moisture developed on some plots. The grassland vegetation types meadow (four plots in total), pasture (12 plots in total) and wet meadow (seven plots in total) were found on plots of all former vegetation types.

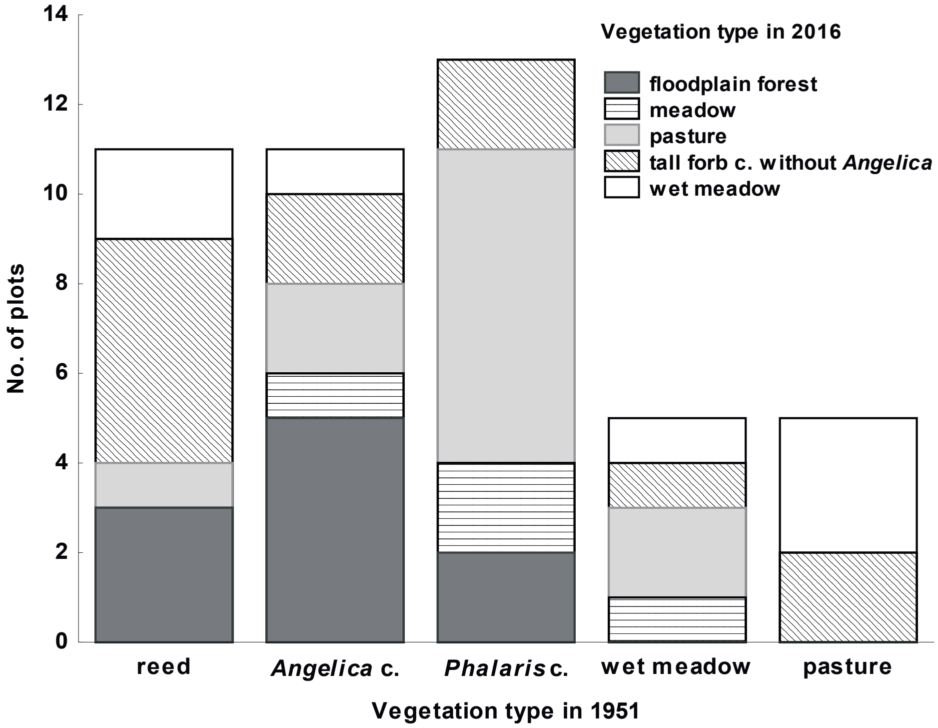

Fig. 3.2 Number of plots of the current vegetation types found along the Dove Elbe River in the year 2016 (floodplain forest, meadow, pasture, tall forb community without *Angelica archangelica* and wet meadow). The number of plots for each vegetation type in 2016 were grouped according to the former vegetation types in 1951 (reed, *Angelica archangelica* community, *Phalaris arundinacea* community, wet meadow and pasture).

On the 45 plots for which the vegetation was recorded in 2016, significantly more threatened species were found in 1951 (16 in total, 1.4 ± 1.1 (mean ± standard deviation) per plot) than in 2016 (4, 0.2 ± 0.4; Wilcoxon-test, $p < 0.001$; Fig. 3.3 A). Only the threatened species *Senecio sarracenicus* and *Cynosurus cristatus* were recorded in both years. The number of non-native plant species was significantly lower in 1951 (4, 0.2 ± 0.4) than in 2016 (6, 0.4 ± 0.6; Wilcoxon-test, $p < 0.01$, Fig. 3.3 B). Some vegetation types differed in numbers of species between 1951 and 2016: In 1951, reed was species poor while *Phalaris arundinacea* communities and nutrient rich pastures were species rich. In 2016, however, the number of species was equally low for all five former vegetation types (Fig. 3.3 C). The number of species per plot in all vegetation types declined from 1951 to 2016, except for the reed vegetation type (ANOVA, interaction: F 4, 40=7.38, $p < 0.001$; Fig. 3.3 C). The differences between the years were significant for the plots containing the *Angelica archangelica* community, the *Phalaris arundinacea* community and the nutrient rich pasture in 1951 (all $p < 0.05$). Evenness was lowest for reed vegetation in 1951 (Fig. 3.3 D). Evenness did not show any significant differences according to the interaction of vegetation type and year (ANOVA, F 4, 40=1.12, p=0.36). The number of species indicating dynamic hydrological conditions, the number of species indicating flooding and the number of hydrophytes declined between 1951 and 2016 within the vegetation types (data not shown).

The EIV for moisture differed significantly according to the interaction of vegetation types and years (ANOVA, F 4, 40=15.17, $p < 0.001$; Fig. 3.3 E). The EIV for moisture of the vegetation types reed, *Angelica archangelica* community and *Phalaris arundinacea* community were significantly higher in 1951 than in 2016 ($p < 0.01$). The EIV for moisture of the wet meadow and nutrient rich pasture vegetation types did not differ between the years. Most importantly, while the EIV for moisture largely varied between the vegetation types in 1951, with the most significantly highest value belonging to reed, the moisture value was about equally low in all plots in 2016 (Fig. 3.3 E). The EIV for nutrition did not differ according to the interaction between vegetation type and year (ANOVA, F 4, 40=1.11, p=0.37; Fig. 3.3 F).

The DCA diagram of the study plots shows a clear separation between years, except for the five plots of pastures from 1951 (Fig. 3.4 A; gradient length of the first and second DCA axis: 11.8 and 5.6; eigenvalue of the first and second DCA axis: 0.9 and 0.7; total inertia: 15.9). This separation between the years is also supported by a PERMANOVA (F 1, 89=40.15, $p < 0.001$). Species most abundant in 1951 were *Phalaris arundinacea*, *Filipendula ulmaria* and *Anthriscus sylvestris* (Fig. 3.4 B), and all were found on 28 of the 45 plots. Species most abundant in 2016 were *Poa trivialis* (found on 25 of the 45 plots), *Urtica dioica* (24), *Dactylis glomerata* (23) and *Glechoma hederacea* (23). The separation of the plots according to year roughly follows the gradient of the weighted mean EIV for moisture and nutrition. However, EIV moisture shows a stronger correlation (r=0.87) to the DCA axes values of the plot than EIV nutrition (r=0.44) indicating that the moisture value is of greater importance to explain differences in the vegetation patterns of the plots along the first axis.

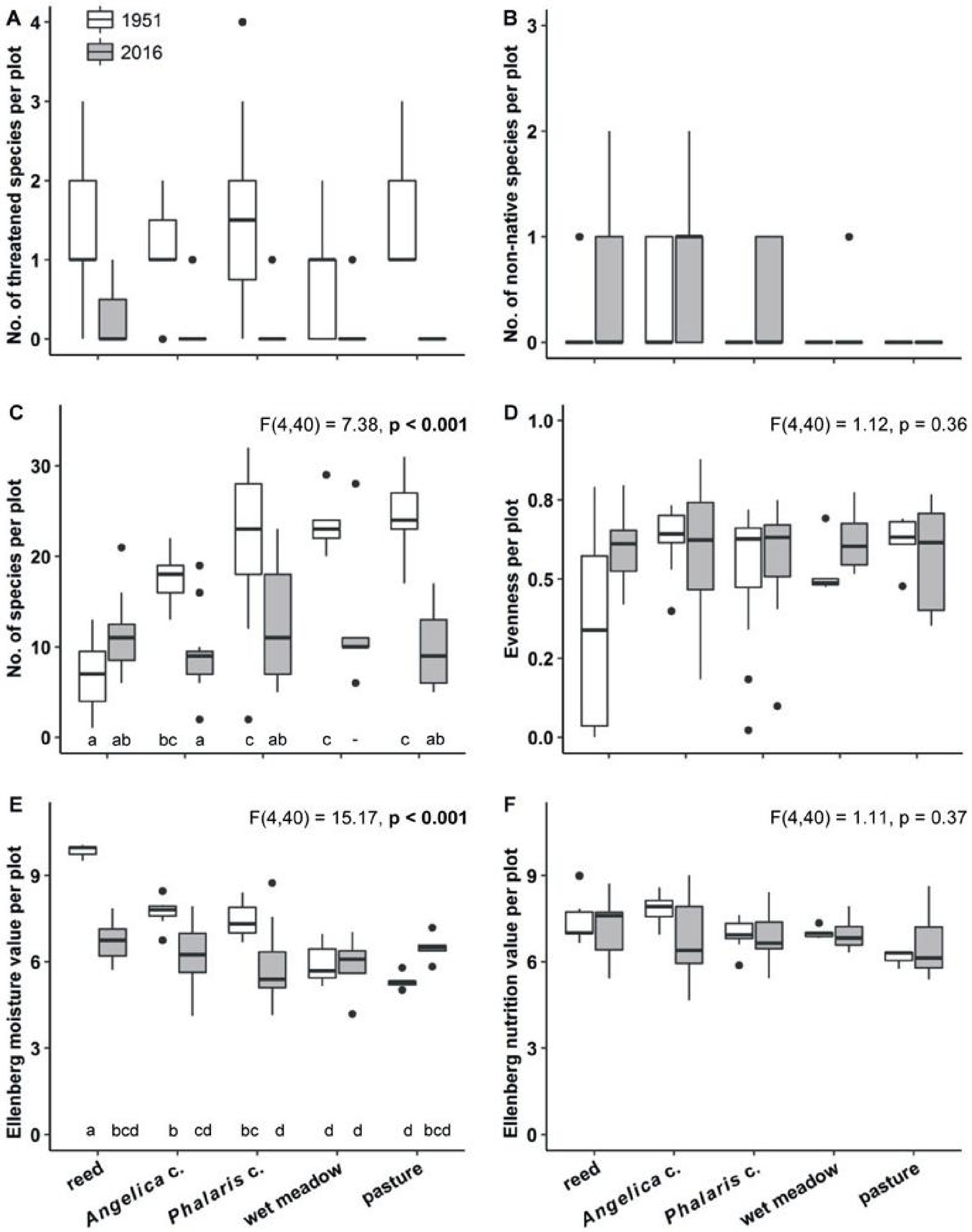

Fig. 3.3 A - F: Number of threatened species (A), number of non-native species (B), number of species (C), evenness (D), Ellenberg moisture value (E) and Ellenberg nutrition value (F) found per plot along the Dove Elbe River in Hamburg, Germany for the years 1951 and 2016, grouped according to the former vegetation type in 1951 (reed, *Angelica archangelica* community, *Phalaris arundinacea* community, wet meadow and pasture). Median, 25th and 75th percentile as well as outliers are shown. Results of the repeated-measures ANOVA analysis for the interaction between year and vegetation type with Box-Cox transformed data are given. Letters indicate differences according to post-hoc tests (Bonferroni, $p < 0.05$).

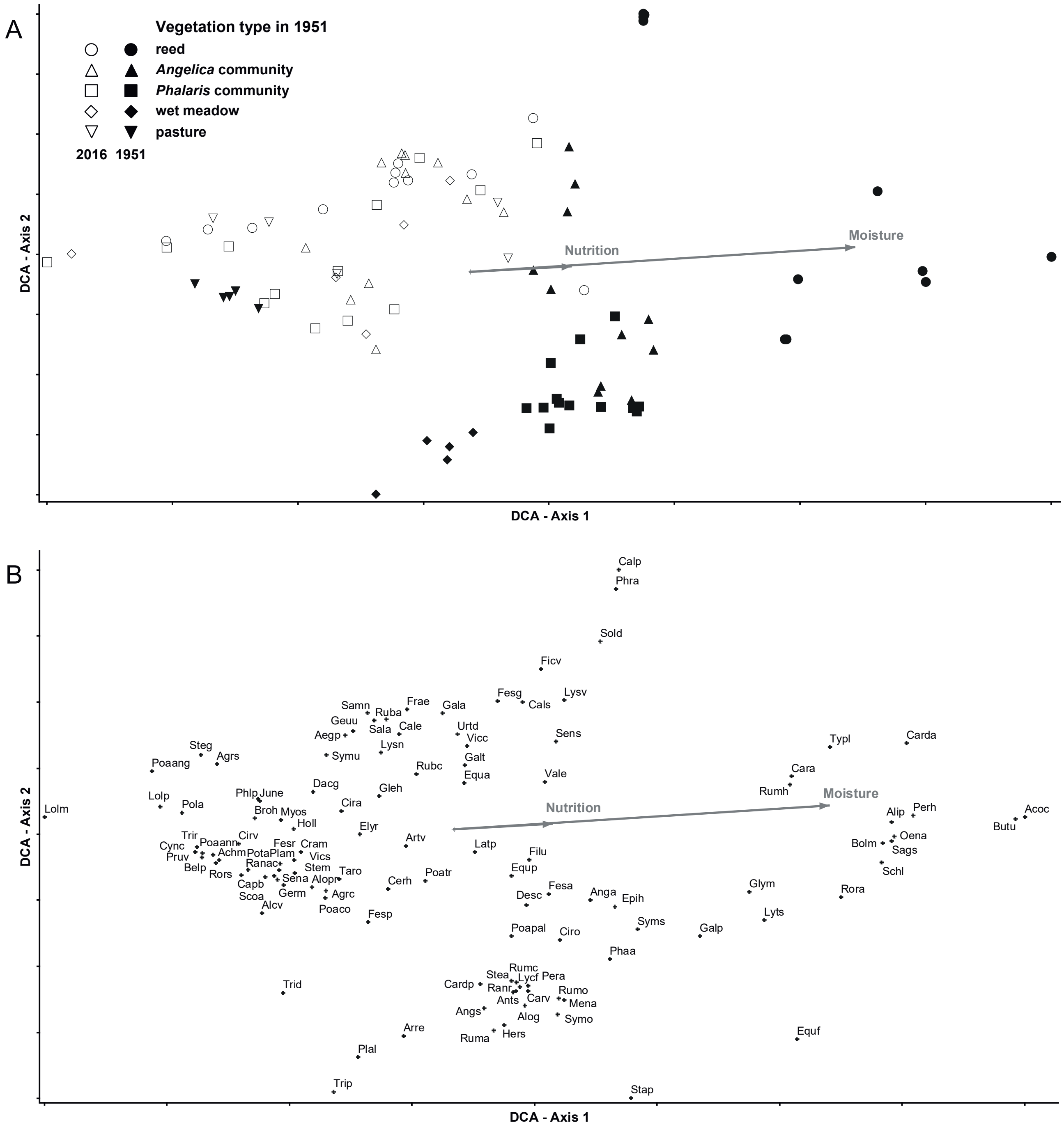

Fig. 3.4 A+B: DCA ordination of the 45 studied plots classified according to the former vegetation type (reed, *Angelica archangelica* community, *Phalaris arundinacea* community, wet meadow and pasture) in 1951 (A) and the found plant species (B) along the Dove Elbe River in Hamburg, Germany. Furthermore, the study plots were differentiated according to the year of survey (1951: filled symbols; 2016: open symbols). Gradient length of the first and second DCA axis: 11.8 and 5.6; eigenvalue of the first and second DCA axis: 0.9 and 0.7; total inertia: 15.9. Plant species that were recorded in the data set only once were excluded from the analysis. In total, 115 plant species and 90 plots (45 per year) were included in the ordination and additional, the correlation with the weighted mean Ellenberg indicator values for moisture and nutrition of the study plots are shown. For acronyms of species, see Table 3.A1.

4. Discussion

The vegetation types *Limosella aquatica* community and *Ranunculus repens* community (including the species *Ranunculus reptans*) at the wet end of the hydrological gradient were lost completely after construction of the sluice. This finding is further supported by a floristic mapping of Hamburg, which demonstrates the absence of the species *Limosella aquatica* and *Ranunculus reptans* from the dammed Dove Elbe River in recent years (Poppendieck et al., 2010). In fact, the last occurrence of *Limosella aquatica* at the Dove Elbe River is just in front of the sluice, where the tidal influence is still facilitating the mudflat zone. In the case of the dammed Dove Elbe River, the loss of the tidal influence led to stable water tables, where the reduction of mudflats may have prevented the growth of semi-aquatic pioneer vegetation. Furthermore, the river bed of the Dove Elbe River has been altered so that some of the former plots of the pioneer vegetation are now completely submerged. Overall, this indicates that these vegetation types of the pioneer zone are especially vulnerable to reduced hydrological dynamics. The vegetation on the 45 plots studied in 2016 changed from reeds, *Angelica archangelica* community and *Phalaris arundinacea* community to more productive vegetation types, such as floodplain forests, tall forb community without *Angelica archangelica* and different grassland types. The decline in EIV for moisture in almost all vegetation types reveals a homogenization in the hydrological conditions of the floodplain along the Dove Elbe River. Meyer (1954) predicted that the loss of the tidal influence will lead to a complete loss of amphibious habitats. This research confirms Meyer's prediction as several vegetation types which were adapted to dynamic water level changes and wet soil moisture conditions such as *Limosella aquatica* communities or *Angelica archangelica* communities are shown to be lost. Overall, we can confirm our first hypothesis that the introduction of the sluice led to a lower number of plots with non-cultural vegetation types than plots with vegetation types of the cultural landscape. As another major change, some vegetation types newly developed on some of the 45 investigated plots. As an example, floodplain forests developed in the course of succession on plots with former reed, *Angelica archangelica* community and *Phalaris arundinacea* community. As another example, former *Angelica archangelica* community, *Phalaris arundinacea* community and wet meadow plots developed towards meadows with drier conditions.

In line with the second hypothesis, threatened species were lost, floodplain species declined and generalist and non-native species increased in abundance from 1951 to 2016, while species diversity decreased by approximately six species over all 45 plots. To be more specific, the species number per plot was significantly higher in 1951 than in 2016 in three vegetation types, while the evenness per plot did not differ. These results are in accordance with other studies focusing on the diversity changes of grasslands since the mid-20th century, in which the decline of plant species richness and characteristic species were documented (Prach, 2008; Wesche et al., 2012; Krause et al., 2015). The plots with former grasslands underwent a greater decline in species richness than the other vegetation types. As the EIV for moisture did not decline on the plots of former grasslands, the loss of tidal influence has probably had no effect on the soil moisture of the grasslands.

It has to be kept in mind that former grasslands were located on higher elevations and, therefore, inhabited the drier parts of the former moisture gradient. Moreover, the intensification of land-use (seed sowing and use of herbicides) might be the most important factor for species loss in grasslands. This is supported by numerous studies which state that besides changes in hydrological conditions, increasing anthropogenic land use must also be taken into account to explain species loss in river floodplains (Nilsson et al., 2005; Dudgeon et al., 2006; Ellwanger et al., 2012).

In our third hypothesis we expected lower soil moisture after the loss of the tidal influence and higher soil nutrient content due to increased fertilizer use as part of an overall intensified land use. Supporting this, the weighted mean EIV for moisture per plot significantly decreased from 1951 to 2016 (Fig. 3.3 E). The importance of tidal influence for the vegetation patterns is also indicated by the DCA (Fig. 3.4). Several studies concluded that with decreasing soil moisture, (agricultural) land use increasingly had an influence on the species composition and diversity in floodplain vegetation (Haacks, 1998; Leyer, 2002). Therefore, the loss of the tidal influence causing lower soil moisture was probably followed by growing agricultural land-use, leading to further changes in species diversity and composition. In contrast to our second hypothesis, the weighted mean EIV for nutrition did not increase between the years. We expected a higher weighted mean EIV for nutrition due to land-use intensification of the floodplain grasslands as proved by a resampling study of floodplains in Northern Germany (Krause et al., 2015). A reason for the stable EIV for nutrition between the years could be less nutrient input due to lower fertilisation than expected. Furthermore, the lost tidal influence could have led to a reduced nutrient input to the soil and maintained stable nutrient conditions in the soil. Another reason could be that the species from 1951 were replaced by other species adapted to lower soil moisture, but equally high EIV for nutrition. It has to be kept in mind that the species of vegetation under tidal influence already have relatively high nutrient values, which are in the same range as those of species from pastures and meadows.

5. Conclusion

Our results reveal a significant decline in species diversity along the Dove Elbe River over the past 65 years after the loss of tidal influence. This study shows how important floodplains under tidal influence are for protecting the characteristic species of this ecosystem. We conclude that the remaining areas with tidal influence need strict conservation and that restoration measures should be carried out to increase the 'ecological integrity' of the Dove Elbe River. As river training is one of the main reasons for river degradation in Germany, i.e. the building of dikes and sluices (Ellwanger et al., 2012), restoration of the Dove Elbe River should be based on an (at least partial) opening of the sluice and reintroduction of the tidal influence. This would restore the lost dynamics responsible for characteristic ecosystems of estuarine landscapes with their characteristic species composition (Ward et al., 2002; Biswas & Mallik, 2010).

Declaration of competing interest

None.

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Appendix A

Table 3.A1 List of all plant species found along the Dove Elbe River in 1951 (Meyer, 1954) and in 2016. The table presents the scientific names (nomenclature follows Jäger (2011), except for *Alchemilla vulgaris* agg.), the acronyms of the species in the ordination, the classification as threatened species according to the Red List of Hamburg (RL-HH; 1: critically endangered, 2: endangered, 3: vulnerable, NT: near threatened, DD: data deficient, NE: not evaluated; Poppendieck et al., 2010) and the classification as non-native species in Germany (NN: non-native, DD: data deficient; Poppendieck et al., 2010) and the number (#) of plots on which a species was found in 1951 and 2016 (on 45 plots).

No.	Scientific names	Acronyms of species in ordination	RL-HH	Non-native	# plots 1951	# plots 2016
1	*Achillea millefolium* L.	Achm			2	2
2	*Acorus calamus* L.	Acoc		NN	2	0
3	*Aegopodium podagraria* L.	Aegp			1	5
4	*Agrostis capillaris* L.	Agrc			0	4
5	*Agrostis stolonifera* L.	Agrs			3	14
6	*Alchemilla vulgaris* agg.	Alcv	DD		5	0
7	*Alisma plantago-aquatica* L.	Alip			4	0

Table 3.A1 (Continued)

No.	Scientific names	Acronyms of species in ordination	RL-HH	Non-native	# plots 1951	# plots 2016
8	*Alliaria petiolata* (M. Bieb.) Cavara et Grande	-			0	1
9	*Alnus glutinosa* (L.) Gaertn.	-			0	1
10	*Alopecurus geniculatus* L.	Alog			4	3
11	*Alopecurus pratensis* L.	Alopr			9	7
12	*Angelica archangelica* L.	Anga			20	0
13	*Angelica sylvestris* L.	Angs	NT		8	0
14	*Anthriscus sylvestris* (L.) Hoffm.	Ants			28	1
15	*Arctium lappa* L.	-			0	1
16	*Arctium tomentosum* Mill.	-	2		1	0
17	*Arrhenatherum elatius* (L.) J. Presl et C. Presl	Arre			8	13
18	*Artemisia vulgaris* L.	Artv			1	2
19	*Ballota nigra* L.	-	2		0	1
20	*Bellis perennis* L.	Belp			5	3
21	*Berula erecta* (Huds.) Coville	-			1	0
22	*Betula pendula* Roth	-			0	1
23	*Betula pubescens* Ehrh.	-			0	1
24	*Bolboschoenus maritimus* (L.) Palla	Bolm	NT		3	0
25	*Bromus hordeaceus* L.	Broh			0	6
26	*Bromus sterilis* L.	-			0	1
27	*Bunias orientalis* L.	-		NN	1	0
28	*Butomus umbellatus* L.	Butu			2	0
29	*Calamagrostis canescens* (F. H. Wigg.) Roth	-			0	1
30	*Calamagrostis epigejos* (L.) Roth	Cale			0	6
31	*Callitriche hamulata* W. D. J. Koch	-	DD		1	0
32	*Caltha palustris* L.	Calp	3		9	0
33	*Calystegia sepium* (L.) R. Br.	Cals			8	17
34	*Capsella bursa-pastoris* (L.) Medik.	Capb			0	2
35	*Cardamine amara* L.	Carda	NT		6	0
36	*Cardamine pratensis* L. s. str.	Cardp			8	3
37	*Carex acuta* L.	Cara			2	0
38	*Carex vulpina* L.	Carv	2		3	0
39	*Cerastium holosteoides* Fr.	Cerh			8	8
40	*Cirsium arvense* (L.) Scop.	Cira			13	13
41	*Cirsium vulgare* (Savi) Ten.	Ciro			25	0
42	*Cirsium oleraceum* (L.) Scop.	Cirv			2	1
43	*Corylus avellana* L.	-			0	1
44	*Crataegus monogyna* Jacq.	Cram			0	3
45	*Crepis paludosa* (L.) Moench	-	3		1	0
46	*Cynosurus cristatus* L.	Cync	NT		5	2
47	*Dactylis glomerata* L.	Dacg			3	23
48	*Daucus carota* L.	-			0	1

Table 3.A1 (Continued)

No.	Scientific names	Acronyms of species in ordination	RL-HH	Non-native	# plots 1951	# plots 2016
49	*Deschampsia cespitosa* (L.) P. Beauv.	Desc			4	0
50	*Draba verna* L.	-			0	1
51	*Elymus repens* (L.) Gould	Elyr			1	22
52	*Epilobium angustifolium* L.	-			0	1
53	*Epilobium hirsutum* L.	Epih			10	0
54	*Epilobium lamyi* F. W. Schultz	-			0	1
55	*Equisetum arvense* L.	Equa			1	4
56	*Equisetum fluviatile* L.	Equf			5	0
57	*Equisetum palustre* L.	Equp			11	1
58	*Festuca arundinacea* Schreb.	Fesa			5	0
59	*Festuca gigantea* (L.) Vill.	Fesg			1	1
60	*Festuca pratensis* Huds.	Fesp			8	0
61	*Festuca rubra* L.	Fesr			0	7
62	*Ficaria verna* Huds.	Ficv			7	1
63	*Filipendula ulmaria* (L.) Maxim.	Filu			28	2
64	*Forsythia* x *intermedia* Zabel	-	NE		0	1
65	*Fraxinus excelsior* L.	Frae			0	5
66	*Galeopsis tetrahit* L.	Galt			0	2
67	*Galium aparine* L.	Gala			8	20
68	*Galium palustre* L. s. str.	Galp			7	0
69	*Geranium dissectum* L.	-			0	1
70	*Geranium molle* L.	Germ			0	2
71	*Geum urbanum* L.	Geuu			0	5
72	*Glechoma hederacea* L.	Gleh			11	23
73	*Glyceria maxima* (Hartm.) Holmb.	Glym			24	1
74	*Heracleum sphondylium* L.	Hers			8	1
75	*Holcus lanatus* L.	Holl			8	16
76	*Impatiens parviflora* DC.	-		NN	0	1
77	*Iris pseudacorus* L.	-			1	0
78	*Juglans regia* L.	-		DD	0	1
79	*Juncus effusus* L.	June			4	2
80	*Lathyrus pratensis* L.	Latp			8	2
81	*Lolium multiflorum* Lam.	Lolm		NN	1	3
82	*Lolium perenne* L.	Lolp			5	14
83	*Lotus corniculatus* L.	-			0	1
84	*Lotus pedunculatus* Cav.	-			1	0
85	*Lychnis flos-cuculi* L.	Lycf			3	0
86	*Lycopus europaeus* L.	-			1	0
87	*Lysimachia nummularia* L.	Lysn			2	1
88	*Lysimachia vulgaris* L.	Lysv			2	0
89	*Lythrum salicaria* L.	Lyts			18	0

Table 3.A1 (Continued)

No.	Scientific names	Acronyms of species in ordination	RL-HH	Non-native	# plots 1951	# plots 2016
90	*Medicago lupulina* L.	-			0	1
91	*Mentha aquatica* L.	Mena			5	0
92	*Myosotis scorpioides* L.	Myos			4	1
93	*Oenanthe aquatica* (L.) Poir.	Oena	NT		2	0
94	*Persicaria amphibia* (L.) Delarbre	Pera			15	1
95	*Persicaria hydropiper* (L.) Delarbre	Perh			8	0
96	*Persicaria lapathifolia* (L.) Delarbre	-			0	1
97	*Phalaris arundinacea* L.	Phaa			28	6
98	*Phleum pratense* L.	Phlp			7	6
99	*Phragmites australis* (Cav.) Steud.	Phra			14	10
100	*Pilosella aurantiaca* (L.) F. W. Schultz et Sch. Bip.	-		DD	0	1
101	*Plantago lanceolata* L.	Plal			14	5
102	*Plantago major* L.	Plam			12	3
103	*Poa angustifolia* L.	Poang	DD		0	14
104	*Poa annua* L.	Poan			2	3
105	*Poa compressa* L.	Poac			0	7
106	*Poa palustris* L.	Poap			4	2
107	*Poa pratensis* L.	-			0	1
108	*Poa trivialis* L.	Poatr			18	25
109	*Polygonum aviculare* L.	Pola			1	1
110	*Populus* x *canadensis* Moench	-		NN	0	1
111	*Potentilla anserina* L.	Pota			9	0
112	*Potentilla reptans* L.	-			0	1
113	*Prunella vulgaris* L.	Pruv			5	0
114	*Ranunculus acris* L.	Ranac			12	8
115	*Ranunculus auricomus* agg.	-	3		1	0
116	*Ranunculus repens* L.	Ranr			17	0
117	*Rorippa amphibia* (L.) Besser	Rora			4	0
118	*Rorippa sylvestris* (L.) Besser	Rors			2	0
119	*Rubus armeniacus* Focke	Ruba		NN	0	9
120	*Rubus caesius* L.	Rubc			0	5
121	*Rumex acetosa* L.	Ruma			19	2
122	*Rumex crispus* L.	Rumc			8	1
123	*Rumex hydrolapathum* Huds.	Rumh			2	0
124	*Rumex obtusifolius* L.	Rumo			23	2
125	*Rumex sanguineus* L.	-			0	1
126	*Sagittaria sagittifolia* L.	Sags			2	0
127	*Salix alba* L.	Sala			0	10
128	*Salix caprea* L.	-			0	1
129	*Salix fragilis* L.	-	DD		0	1
130	*Sambucus nigra* L.	Samn			0	4

Table 3.A1 (Continued)

No.	Scientific names	Acronyms of species in ordination	RL-HH	Non-native	# plots 1951	# plots 2016
131	*Schoenoplectus lacustris* (L.) Palla	Schl	2		2	0
132	*Scorzoneroides autumnalis* (L.) Moench	Scoa			11	0
133	*Scrophularia nodosa* L.	-			1	0
134	*Senecio aquaticus* Hill	Sena	2		6	0
135	*Senecio paludosus* L.	-	2		1	0
136	*Senecio sarracenicus* L.	Sens	3		10	3
137	*Sisymbrium officinale* (L.) Scop.	-			0	1
138	*Solanum dulcamara* L.	Sold			3	2
139	*Stachys palustris* L.	Stap			4	2
140	*Stellaria alsine* Grimm	Stea	3		2	0
141	*Stellaria graminea* L.	Steg			0	2
142	*Stellaria media* (L.) Vill.	Stem			0	2
143	*Symphyotrichum* x *salignum* (Willd.) G. L. Nesom	Syms		NN	5	0
144	*Symphytum officinale* L. s. str.	Symo			23	0
145	*Symphytum* x *uplandicum* Nyman	Symu		NN	0	2
146	*Taraxacum* sect. *Ruderalia* Kirschner, H. Øllg. et Štěpánek	Taro	DD		16	13
147	*Thalictrum flavum* L.	-	3		1	0
148	*Torilis japonica* (Houtt.) DC.	-			0	1
149	*Trifolium dubium* Sibth.	Trid			1	1
150	*Trifolium pratense* L.	Trip			6	2
151	*Trifolium repens* L.	Trir			9	12
152	*Typha angustifolia* L.	-			1	0
153	*Typha latifolia* L.	Typl			4	0
154	*Ulmus minor* Mill.	-	3		0	1
155	*Urtica dioica* L.	Urtd			21	24
156	*Valeriana excelsa* subsp. *excelsa* Poir.	Vale			21	0
157	*Veronica arvensis* L.	-			0	1
158	*Veronica beccabunga* L.	-			0	1
159	*Veronica chamaedrys* L. s. str.	-			1	0
160	*Viburnum opulus* L.	-			0	1
161	*Vicia cracca* L.	Vicc			4	2
162	*Vicia parviflora* Cav.	-	NE		0	1
163	*Vicia sepium* L.	Vics			1	2
164	*Vicia tetrasperma* (L.) Schreb.	-			0	1

Oenanthe
conioides

BOX 2

Effects of loss of tidal influence on the herbaceous vegetation of softwood forests in Hamburg

Nikola Lenzewski, Luca A. Schebesch, Kai Jensen and Kristin Ludewig

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Shortened, English version is given here

Abstract

The effect of loss of tidal influence on softwood forests along the tidal Elbe River and non-tidal Dove Elbe River in Hamburg was analysed in two tidal softwood forest and two non-tidal forests. The vegetation composition and diversity of vascular plants was analysed in 20 study plots, five study plots in each forest. Tidal-influenced floodplain forests at the tidal Elbe River are different from non-tidal forests at the Dove Elbe River by containing a higher total number of species as well as a higher number of herbaceous species. Further, threatened species of Hamburg and river corridor plants were nearly found only in the tidal-influenced floodplain forests and the species composition was more heterogeneous in comparison to non-tidal floodplain forests. Reasons for these differences may be the different hydrological conditions at the tidal Elbe River.

Keywords

Dove Elbe River, Elbe River, Species composition, Species richness, Vascular plants

1. Introduction

Tidal-influenced softwood forest are a specific type of floodplain forests and can be found at tidal-influenced estuaries. Floodplain forests are characterised by fluctuating water levels and are therefore highly dynamic ecosystems (Ward, 1998; Patt, 2016). Frequency of flooding and associated sediment and erosion processes as well as mechanical stress by water and ice determine vegetation of floodplain forests (Glenz et al., 2006; Kofalk et al., 2016). Softwood forests under tidal influence are flooded up to two times a day, so that plant species occurring in these habitats have to be adapted to this condition. Tidal-influenced floodplain forests develop in freshwater or oligohaline bank sites (Engels & Jensen, 2009; Markus-Michalczyk, 2014) and are habitat for highly adapted plant species, such as *Oenanthe conoides* LANGE along the tidal Elbe River in Germany (Preisinger, 2005).

The extent of tidal-influenced softwood forests decreased dramatically worldwide in the last century (Miller, 2002; Pereira et al., 2002; Sharpe & Baldwin, 2013), so that today, tidal-influenced softwood forests are classified as threatened ecosystems (Red list status in Germany: 1; Finck et al., 2017). Reason for this is river training, which was conducted with beginning of the industrialisation. Loss of tidal influence had dramatic effects on the flora and fauna of rivers and their floodplains (Meyer 1954; Ferguson & Wolff, 1984; Asdonk et al., 2019), so that today, only relicts of tidal-influenced softwood forests exists (Ellwanger et al., 2012; Kofalk et al., 2016).

The effects of loss of tidal influence on the floodplain vegetation along the Elbe River were studied by Meyer (1954; 1957), Preisinger (1991) and Asdonk et al. (2019). Nowadays, restoration of the tidal influence at the Dove Elbe River is discussed, so that the effect of loss of tidal influence on vegetation composition of softwood floodplain forests can be questioned. In this study, the vegetation of tidal-influenced floodplain forests and non-tidal forests in Hamburg was compared. In the study region, two softwood floodplain forests at the tidal Elbe River and two non-tidal forests at the Dove Elbe River were selected. The forests at the Dove Elbe River are not under tidal influence since 1951. The vegetation composition and the diversity of vascular plants (total number of species and number of herbaceous species) were investigated and compared between the tidal-influenced floodplain forest and the non-tidal forests. Further, abiotic and biotic parameters determining differences in the species composition of the forests were identified.

In this study, the following hypotheses were tested:
(I) Tidal-influenced softwood forests contain more species in total and more herbaceous species in comparison to non-tidal forests,
(II) tidal-influenced softwood forests are characterised by a more heterogeneous vegetation composition in the herb layer in comparison to non-tidal forests and,

(III) the species composition in the herb layer of tidal-influenced softwood forests is mainly affected by flooding parameters, in contrast to the vegetation composition in the herb layer of non-tidal forests, which is mainly affected by other parameters, such as the soil nutrient conditions.

2. Material and Methods

2.1 Study areas and vegetation mapping

Four forests along the tidal Elbe River and Dove Elbe River in Hamburg were selected (Fig. B2.1). The study areas Spadenland and Heuckenlock are located at the tidal Elbe River and both, are parts of nature reserves. The study areas Tatenberg and Krapphofschleuse are located along the Dove Elbe River and both areas are cut-off from the tidal-influence since 1951 due to the installation of the sluice Tatenberger Schleuse.

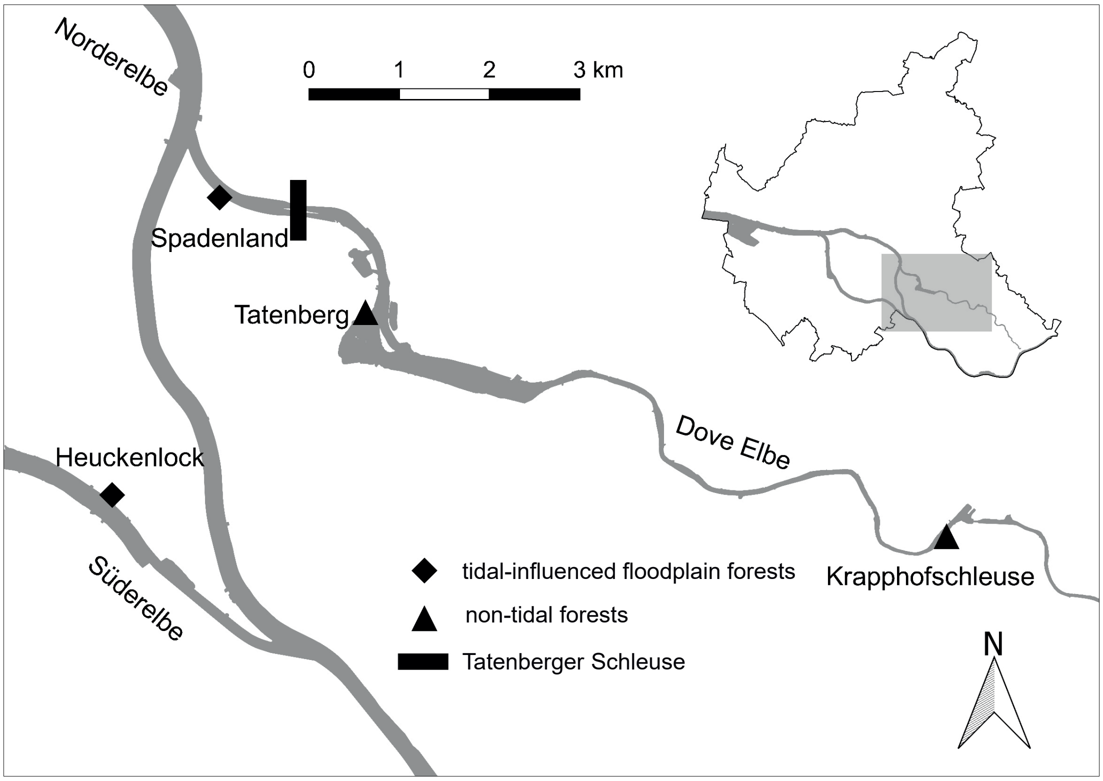

Fig. B2.1 Location of the study area with the tidal-influenced floodplain forests Heuckenlock and Spadenland at the tidal Elbe River and the non-tidal forests at the Dove Elbe River in Hamburg.

Vegetation of the four forests was surveyed from June to August 2018 in areas of different sizes (Spadenland: 23 ha, Heuckenlock: 50 ha, Tatenberg: 33 ha and Krapphofschleuse: 16 ha). Five randomly selected 10 m²-plots were chosen in each area and all vascular plant species in these plots were recorded with their coverages after a modified Braun-Blanquet scale (cited in Dierschke, 1994). Plant determination followed Raabe (1975) and Jäger (2017). All plants were identified on species level, except for *Taraxacum* sect. *Ruderalia* Kirschner, H. Øllg. & Štěpánek, which was identified on aggregate level. Nomenclature followed Jäger (2017). Additional parameters, coverage herb layer, coverage total vegetation, coverage litter, coverage woody debris and proportion of bare soil in percent, were estimated for each study plot (Table B2.1).

2.2 Data preparation

Red list status of Hamburg was derived from Poppendieck et al. (2010) for each species and further, classification as river corridor plant was derived from Burkart (2001). The number of species and number of herbaceous species were calculated for each study plot. Furthermore, weighted mean Ellenberg indicator values (EIV) for light, moisture, reaction and nutrient (Ellenberg & Leuschner, 2010) were calculated following Tremp (2005) and only herbaceous plant species were considered for calculation (Table B2.1). As hydrological parameters, the number of days with flooding in 2017, the total duration of flooding in 2017 and the total duration of flooding in the vegetation period in 2017 were calculated for each study plot (Table B2.1). For calculation, the digital terrain model for Hamburg (LGV, 2014) and water level data from the stations 'Hamburg-Harburg' (N 53°28.360020', E 9°59.509980'; Heuckenlock), 'Schöpfstelle' (N 53°30.499980', E 10°3.690000'; Spadenland) and 'Allermöher Deich' (N 53°29.102167', E 10°5.737000'; Tatenberg and Krapphofschleuse) were used (HPA, 2017; LSBG, 2017). Time of the vegetation period in 2017 was defined from beginning of flowering of *Forsythia* x *intermedia* Zabel until leaf fall in autumn of *Quercus robur* L. and data for this calculation were taken from the phenological station 'Reinbek' in Hamburg (DWD, 2017b). The vegetation period in 2017 was therefore from March 28th until November 9th. For the calculation of flooding parameters, a study plot was counted as flooded when the water level exceeded the elevation of the study plot. All flooding parameters are given in days. The total duration of flooding in 2017 and the total duration of flooding in the vegetation period in 2017 are given in whole days. In contrast, for the calculation of number of days with flooding in 2017, each day with a flooding event of at least one minute was considered.

Table B2.1 Characteristic data of the four areas Krapphofschleuse, Tatenberg, Spadenland and Heuckenlock: Ellenberg indicator value (EIV) for light, moisture, reaction and nutrient, coverage herb layer, total vegetation, litter, woody debris and proportion of bare soil (in %, respectively) as well as total duration of flooding, number of days with flooding and total duration of flooding in the vegetation period. Further, the acronyms used in the DCA as well as the mean and standard error of values for the four areas are given.

		non-tidal		**tidal-influenced**	
Parameter	**Acronym in DCA**	**Krapphofschleuse**	**Tatenberg**	**Spadenland**	**Heuckenlock**
EIV for light	light	6.2 ± 0.3	5.4 ± 0.2	6.9 ± 0.1	6.3 ± 0.2
EIV for moisture	moisture	7.0 ± 0.5	5.8 ± 0.1	7.5 ± 0.4	7.2 ± 0.4
EIV for reaction	reaction	6.9 ± 0.2	6.8 ± 0.2	6.7 ± 0.1	6.9 ± 0.4
EIV for nutrient	nutrient	7.1 ± 0.2	7.2 ± 0.2	7.1 ± 0.2	7.2 ± 0.3
coverage herb layer (%)	I	87.0 ± 2.6	77.8 ± 5.4	72.0 ± 6.8	73.8 ± 7.8
coverage total vegetation (%)	II	96.0 ± 1.7	95.2 ± 3.8	99.0 ± 0.0	93.6 ± 2.2
coverage litter (%)	III	39.0 ± 15.4	56.0 ± 14.1	49.8 ± 12.8	29.0 ± 15.5
coverage woody debris (%)	IV	21.0 ± 12.7	30.0 ± 5.2	25.0 ± 11.4	11.8 ± 5.6
proportion bare soils (in %)	V	11.2 ± 3.8	7.4 ± 2.3	19.0 ± 7.9	47.0 ± 12.2
total duration of flooding (days per year)	VI	0 ± 0	0 ± 0	34 ± 02	22 ± 05
number of days with flooding (days per year)	VII	0 ± 0	0 ± 0	255 ± 07	180 ± 34
total duration of flooding in the vegetation period (days per vegetation period)	VIII	0 ± 0	0 ± 0	20 ± 01	12 ± 03

2.3 Statistical analysis

The number of species and the number of herbaceous species was tested for significant differences between the four study areas with one-way ANOVAs. Significant results were followed by Tukey HSD post-hoc-tests. To reveal vegetation patterns between the four study areas, a detrended correspondence analysis (DCA) was conducted. 20 study plots and 51 herbaceous species were considered in the DCA and rare species were down weighted in the analysis. The parameters shown in Table B2.1 were also considered in the DCA.

3. Results

In total, 74 vascular plant species were recorded, with 51 species being herbaceous (Table B2.2). 40 species were only identified in the tidal-influenced floodplain forests. Eight threatened species for Hamburg, *Caltha palustris* L. (Red list category 3), *Peucedanum palustre* (L.) Moench (3), *Populus nigra* L. (2), *Scrophularia umbrosa* Dumort. (3), *Senecio aquaticus* Hill (2), *Senecio paludosus* L. (2), *Ulmus laevis* Pall. (3) and *Veronica maritima* L. (1), were identified in the survey, but these species were only found in the tidal-influenced floodplain forests. Further, *Acer campestre*, *Angelica archangelica* L., *Populus nigra*, *Senecio paludosus* and

Veronica maritima, were identified as river corridor plants, which, except for *Acer campestre*, were found only in the tidal-influenced floodplain forests. Frequent plant species in the study plots were *Urtica dioica* L. (in 16 study plots), *Glechoma hederacea* L. (ten plots), *Calystegia sepium* (L.) R. Br. (eight plots), *Galium aparine* L. (eight plots), *Phragmites australis* (Cav.) Steud. (eight plots) and *Salix alba* L. (eight plots), which were mostly characterised by EIVs for nutrient between 7 and 9.

Table B2.2 Species list of all in the study plots recorded taxa (Nomenclature follows Jäger (2017)). Acronyms used in the DCA, red list status of Hamburg and occurrence of species in the four study areas are given. * = least concern, 1 = critically endangered, 2 = endangered, 3 = vulnerable, D = data deficient, nb = not evaluated. H = Heuckenlock, SP = Spadenland, Kr = Krapphofschleuse, T = Tatenberg.

Scientific name	**Acronym in DCA**	**Red list status**	**H**	**Sp**	**Kr**	**T**
Acer campestre L.		*			x	x
Acer platanoides L.		*				x
Acer pseudoplatanus L.		*			x	x
Aegopodium podagraria L.	Aegpod	*	x			x
Agrostis gigantea Roth	Agrgig	*	x			
Alliaria petiolata (M. Bieb.) Cavara et Grande	Allpet	*	x			
Alnus glutinosa (L.) Gaertn.		*			x	
Angelica archangelica L.	Angarc	*		x		
Anthriscus sylvestris (L.) Hoffm.	Antsyl	*	x	x		
Arctium lappa L.	Arclap	*		x		
Betula pendula Roth		*			x	x
Calamagrostis epigejos (L.) Roth	Calepi	*			x	
Caltha palustris L.	Calpal	3	x			
Calystegia sepium (L.) R. Br.	Calsep	*	x	x	x	
Cardamine pratensis L.	Carpra	*	x			
Carex acutiformis Ehrh.	Caracu	*			x	
Cirsium oleraceum (L.) Scop.	Cirole	*	x	x		
Crataegus monogyna Jacq.		*	x		x	x
Dryopteris filix-mas (L.) Schott	Dryfil	*			x	x
Equisetum fluviatile L.	Equflu	*		x		
Euonymus europaeus L.		*	x			
Festuca gigantea (L.) Vill.	Fesgig	*	x		x	
Festuca rubra L.	Fesrub	*	x	x		
Filipendula ulmaria (L.) Maxim.	Filulm	*	x			
Fraxinus excelsior L.		*	x		x	x
Galeopsis tetrahit L.	Galtet	*				x
Galium aparine L.	Galapa	*	x	x	x	x
Galium palustre L.	Galpal	*		x		
Geum urbanum L.	Geuurb	*	x		x	x

Table B2.2 (Continued)

Scientific name	Acronym in DCA	Red list status	H	Sp	Kr	T
Glechoma hederacea L.	Glehed	*	x		x	x
Heracleum sphondylium L.	Hersph	*	x			
Humulus lupulus L.	Humlup	*	x		x	
Impatiens glandulifera Royle	Impgla	*	x			
Impatiens parviflora Dc.	Imppar	*				x
Lolium perenne L.	Lolper	*	x			
Lycopus europaeus L.	Lyceur	*		x		
Malus pumila Mill.		nb			x	
Mentha aquatica L.	Menaqu	*		x		
Myosotis scorpioides L.	Myosco	*		x		
Nasturtium officinale W. T. Aiton	Nasoff	*	x	x		
Persicaria hydropiper (L.) Delarbre	Perhyd	*	x	x		
Peucedanum palustre (L.) Moench	Peupal	3		x		
Phalaris arundinacea L.	Phaaru	*			x	
Phragmites australis (Cav.) Steud.	Phraus	*	x	x	x	
Poa palustris L.	Poapal	*			x	
Poa trivialis L.	Poatri	*		x	x	
Populus nigra L.		2	x			
Quercus robur L.		*			x	x
Ranunculus repens L.	Ranrep	*	x	x		
Ribes rubrum L.		*			x	
Robinia pseudoacacia L.		*				x
Rorippa amphibia (L.) Besser	Roramp	*	x	x		
Rubus caesius L.		*	x		x	
Rubus armeniacus Focke		*			x	x
Rumex obtusifolius L.	Rumobt	*	x	x		
Rumex sanguineus L.	Rumsan	*		x		
Salix alba L.		*	x	x	x	x
Salix caprea L.		*				x
Salix cinerea L.		*		x		
Salix viminalis L.		*	x	x		
Salix x *rubens* Schrank		*	x			
Sambucus nigra L.		*	x		x	x
Scrophularia umbrosa Dumort.	Scrumb	3		x		
Scutellaria galericulata L.	Scugal	*		x		
Senecio aquaticus Hill	Senaqu	2	x	x		
Senecio paludosus L.	Senpal	2		x		
Silene latifolia subsp. *alba* (Mill.) Greuter et Burdet	Sillat	*		x		
Solanum dulcamara L.	Soldul	*		x		
Symphoricarpos albus (L.) S. F. Blake		*				x
Taraxacum sect. *Ruderalia* Kirschner, H. Øllg. & Štěpánek	Tarsec	D	x	x		

Table B2.2 (Continued)

Scientific name	Acronym in DCA	Red list status	H	Sp	Kr	T
Ulmus laevis Pall.		3	x			
Urtica dioica L.	Urtdio	*	x	x	x	x
Valeriana excelsa Poir.	Valexc	*		x		
Veronica maritima L.	Vermar	1	x			

The highest number of species per plot was found in the study area Spadenland with 15.4±1.2 species (mean±standard error), while the lowest number of species was found in the study area Tatenberg with 9.0±1.3 species (Fig. B2.2a). The study areas Heuckenlock and Krapphofschleuse had values in between (11.8±1.2 and 10.4±0.2, respectively). The number of species per plot differed significantly between the study areas (ANOVA: F=6.9; p<0.01), with the values of Spadenland being significantly different from the values of Krapphofschleuse und Tatenberg (Tukey HSD post-hoc-test). The same pattern was found for the number of herbaceous species per plot, where the highest values were found for the study area Spadenland (14.0±1.3) and the lowest values were found for the study area Tatenberg (4.8±0.2; Fig. B2.2b). The number of herbaceous species per plot differed significantly between the study areas (ANOVA: F=23.9; p<0.001), with the values of Tatenberg, Spadenland and Heuckenlock being significantly different from each other (Tukey HSD post-hoc-test).

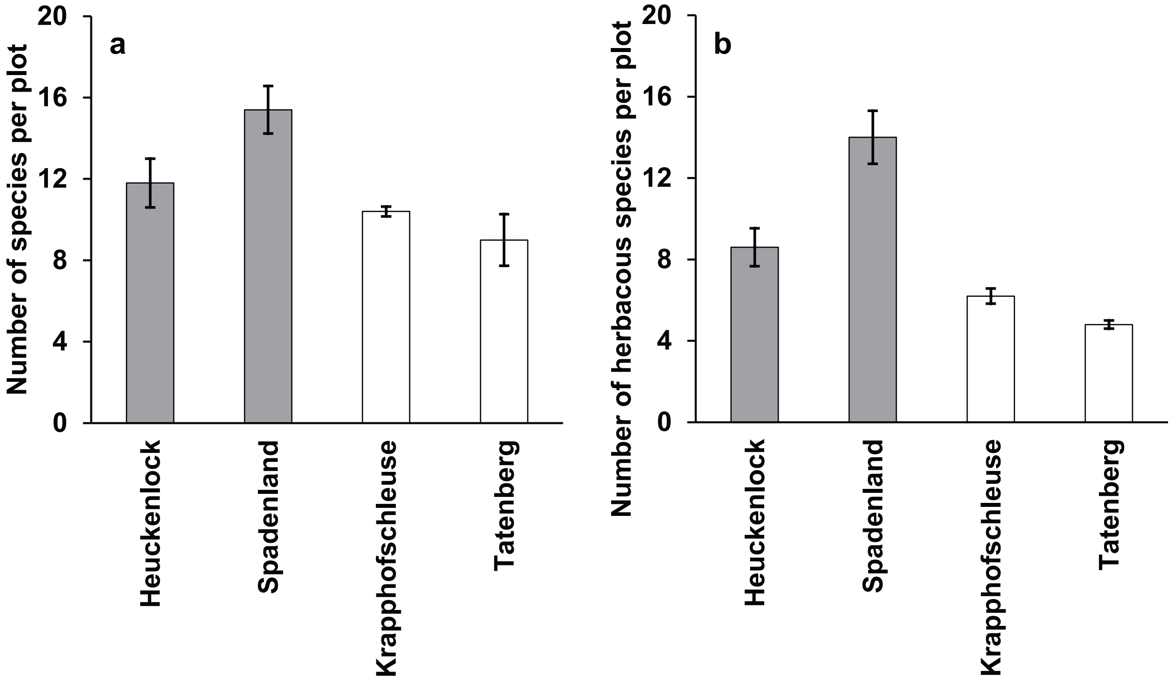

Fig. B2.2 Total number of species (a) and number of herbaceous species (b) per 10 m²-plot of the tidal-influenced floodplain forests Heuckenlock and Spadenland at the tidal Elbe River (grey columns) and the non-tidal forests Krapphofschleuse and Tatenberg at the Dove Elbe River (white columns). Mean and standard error are shown. n=5.

The study plots of the non-tidal forests are arranged together in the DCA and are separated from the study plots of the tidal-influenced floodplain forests (Fig. B2.3). The latter spread wide in the DCA and are therefore characterised by a more heterogeneous vegetation composition in comparison to the study plots of the non-tidal forests. The EIVs for light and moisture as well as the proportion of bare soil and the flooding parameters are displayed in the DCA and all parameters are arranged in the direction of the study plots of the tidal-influenced floodplain forests. The arrows show correlative relationships between the parameters and the species composition of the study plots.

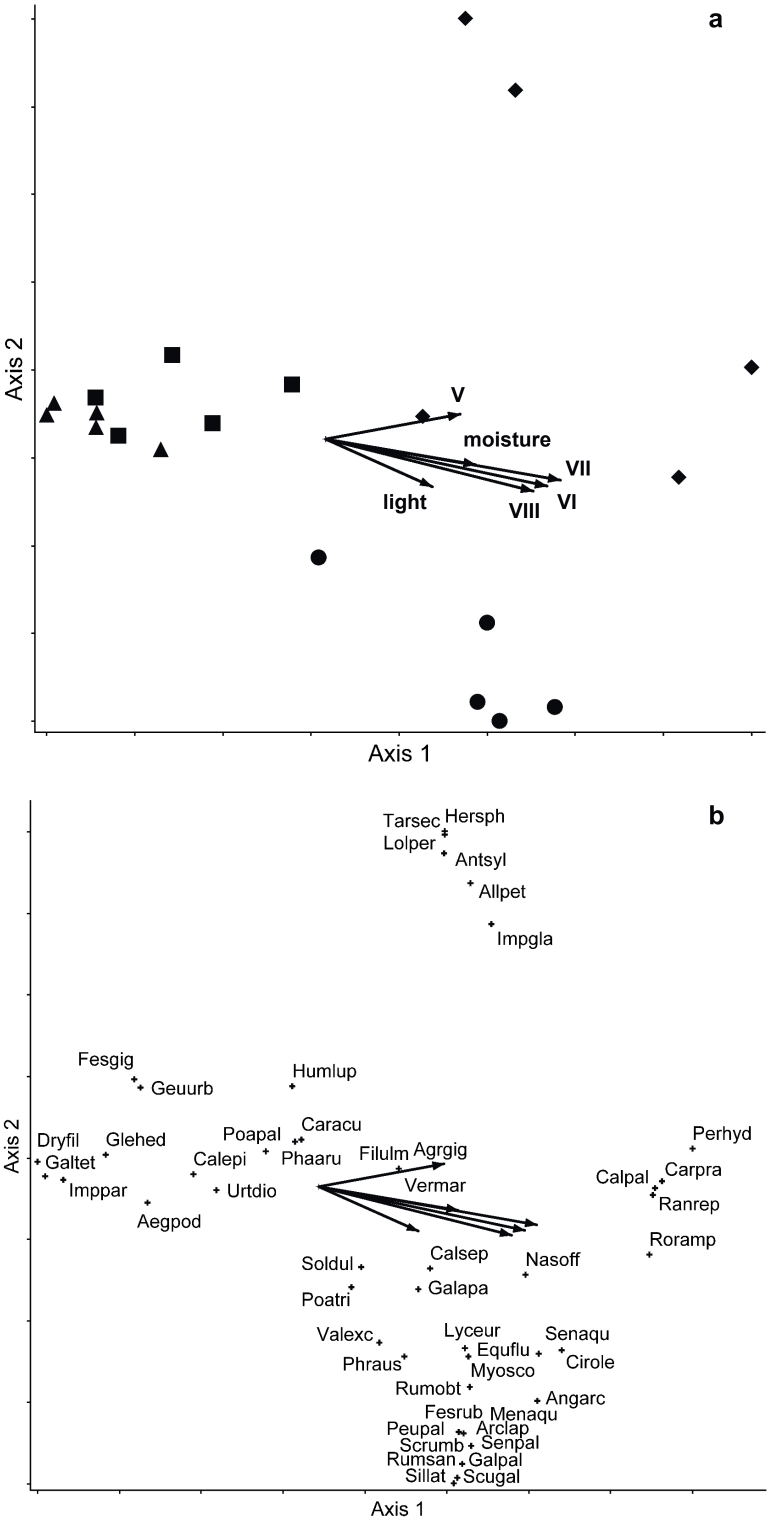

Fig. B2.3 DCA ordination of the 20 study plots classified according to the study area (◆ = Heuckenlock, ● = Spadenland, ■ = Krapphofschleuse, ▲= Tatenberg) along the Dove Elbe River (a) and plant species found in the study plots along the Dove Elbe River (b). Gradient length of the first and second DCA axis: 6.2 and 5.5; eigenvalue of the first and second DCA axis: 0.9 and 0.7; total variance: 6.7. In total, 51 herbaceous plant species and 20 plots were included in the ordination and additional, the correlation with the weighted mean Ellenberg indicator values for light and moisture as well as the proportion of bare soil (V), the total duration of flooding in 2017 (VI), the number of days with flooding in 2017 (VII) and the total duration of flooding in the vegetation period in 2017 (VIII) are shown. For acronyms of species, see Table B2.2.

4. Discussion

The tidal-influenced softwood floodplain forests at the tidal Elbe River contained more threatened species and river corridor plants in comparison to the non-tidal forests at the Dove Elbe River. This is in accordance with Asdonk et al. (2019), which found a decrease of threatened species in selected plots in the floodplain of the Dove Elbe River since loss of tidal influence in 1951. The river corridor plants identified in the tidal-influenced softwood forests were also found in other studies on vegetation of softwood forests (Preisinger, 1991; Klepgen, 2008; Struyf et al., 2009). The occurrence of hardwood floodplain forest species, such as *Fraxinus excelsior* L. or *Ulmus leavis*, in the study area Heuckenlock, indicate the transition to this type of floodplain forest, which is caused by the higher elevation of study plots and as a consequence, a lower frequency of flooding.

The higher number of species in the study plots of the tidal-influenced floodplain forests at the tidal Elbe River in comparison to the non-tidal forests at the Dove Elbe River confirmed results of Asdonk et al. (2019), which found a decreased number of species in reassessed study plots 65 years after loss of tidal influence. Intermediate disturbance is known to favour habitat heterogeneity by building microhabitats, which can be colonized by different plant species (Hobbs & Huenneke, 1992). This is in accordance with the results of this study that tidal-influenced softwood forests contained more herbaceous plant species in comparison to non-tidal forests. Further, a regularly occurring disturbance can prevent the establishment of dominant stands of species (Preisinger, 2002). This is supported by high coverages of *Glechoma hederacea* and *Urtica dioica* in the study plots of the non-tidal forests. The first hypothesis that tidal-influenced softwood forests contain more species in total and more herbaceous species in comparison to non-tidal forests can therefore be assumed.

In the DCA, the study plots of the non-tidal forests were grouped more together in comparison to the study plots of the tidal-influenced softwood forests. This confirmed the vegetation zonation in tidal ecosystems because of abiotic conditions and regular disturbance (Preisinger, 2002; Struyf et al., 2009). As a consequence, microhabitat availability leads to a heterogeneous vegetation composition. The second hypothesis that tidal-influenced softwood forests are characterised by a more heterogeneous vegetation composition in the herb layer in comparison to non-tidal forests can therefore be assumed.

The results of the DCA reinforce the importance of flooding and its associated processes such as sedimentation and erosion, for tidal-influenced softwood forests. Duration and frequency of flooding are relevant parameters for the vegetation zonation in floodplains. As shown by the vectors in the DCA, hydrology is a stronger factor influencing the vegetation composition of the study plots of the tidal-influenced softwood forests in comparison to the study plots along the Dove Elbe River. The proportion of bare soil was higher in the study plots of the tidal-influenced softwood forests in comparison to the study plots along the Dove Elbe River, which can be explained by sedimentation and erosion as a consequence of frequent flooding. The third hypothesis can be confirmed partly: The species composition in the herb layer of tidal-influenced softwood forests is mainly affected by flooding parameters. However, no parameters influencing the vegetation composition in the herb layer of non-tidal forests could be identified.

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veronica maritima

Lobelia dortmanna

CHAPTER 4

Dynamics of oxygen and carbon dioxide in rhizospheres of *Lobelia dortmanna* – a planar optode study of belowground gas exchange between plants and sediment

Nikola Lenzewski*, Peter Mueller*, Robert Johannes Meier, Gregor Liebsch, Kai Jensen and Ketil Koop-Jakobsen

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*These authors contributed equally to this work

Summary

- Root-mediated CO_2 uptake, O_2 release and their effects on O_2 and CO_2 dynamics in the rhizosphere of *Lobelia dortmanna* were investigated.
- Novel planar optode technology, imaging CO_2 and O_2 distribution around single roots, provided insights into the spatiotemporal patterns of gas exchange between roots, sediment and microbial community.
- In light, O_2 release and CO_2 uptake were pronounced, resulting in a distinct oxygenated zone (radius: *c.* 3 mm) and a CO_2-depleted zone (radius: *c.* 2 mm) around roots. Simultaneously, however, microbial CO_2 production was stimulated within a larger zone around the roots (radius: *c.* 10 mm). This gave rise to a distinct pattern with a CO_2 minimum at the root surface and a CO_2 maximum *c.* 2 mm away from the root. In darkness, CO_2 uptake ceased, and the CO_2-depleted zone disappeared within 2 h. By contrast, the oxygenated root zone remained even after 8 h, but diminished markedly over time.
- A tight coupling between photosynthetic processes and the spatiotemporal dynamics of O_2 and CO_2 in the rhizosphere of *Lobelia* was demonstrated, and we suggest that O_2-induced stimulation of the microbial community in the sediment increases the supply of inorganic carbon for photosynthesis by building up a CO_2 reservoir in the rhizosphere.

Keywords

Freshwater lakes, Isoetids, Plant-soil interaction, Radial oxygen loss, Rhizobox, Rhizosphere imaging, Soil biogeochemistry

1. Introduction

Lobelia dortmanna (Campanulaceae; *Lobelia* in the following) is a common representative of isoetid plants, a group of small and slow-growing amphibious or submerged macrophytes. *Lobelia* is native to Northern and Central Europe, and North America, where it inhabits shallow parts (<2 m) of oligotrophic soft water lakes with sandy sediments and low organic content (Farmer & Spence, 1987; Farmer, 1989; Pedersen & Sand-Jensen, 1992; Smolders et al., 2002).

The soft water lakes inhabited by *Lobelia* are characterized by their limited availability of inorganic carbon. As resistance at the boundary layer is higher, and diffusivity of gases is lower, in water than in air, submerged living plants usually require high concentrations of CO_2 to saturate their photosynthetic demand (Maberly & Spence, 1989; Madsen, 1993). Furthermore, *Lobelia* exclusively utilizes CO_2 as an inorganic carbon source, whereas bicarbonate cannot be utilized (Wium-Andersen, 1971; Raun et al., 2010). However, the amount of CO_2 in the sediment of soft water lakes is markedly higher than in the water column, and many isoetids have the ability to utilize this plentiful reservoir of inorganic carbon via root uptake (Wium-Andersen, 1971; Boston et al., 1987; Winkel & Borum, 2009). The leaves of *Lobelia* have a thick cuticle lacking stomata that prevents gas loss through the leaves and promotes O_2 and CO_2 exchange across the rhizodermis, which has significantly higher gas permeability (Pedersen & Sand-Jensen, 1992). This causes a tight coupling of aboveground photosynthesis and belowground gas exchange between the plant and sediment.

CO_2 is taken up by the roots and transported, via a pronounced lacunae system in the roots and the two large lacunae in every leaf (Wium-Andersen, 1971; Madsen et al., 2002; Winkel & Borum, 2009), to the chloroplasts in the leaves, which are located close to the lacunae (Raven et al., 1988). In this way, *Lobelia* acquires the majority of its inorganic carbon for photosynthesis, recovering > 98% of its CO_2 requirements by sediment uptake (Richardson et al., 1984; Winkel & Borum, 2009). In contrast with several other isoetid species, *Lobelia* does not carry out its assimilation of inorganic carbon via a CAM (Crassulacean acid metabolism)-like mechanism (Boston & Adams, 1983; Raven et al., 1988).

O_2 produced in the leaves is transported via the lacunae system to the roots, where it is released into the surrounding sediment along the entire root (Sand-Jensen & Prahl, 1982; Møller & Sand-Jensen, 2008), promoting aerobic decomposition and thereby higher CO_2 concentrations at depth in the sediment (Sand-Jensen et al., 1982). The extent of the oxygenated zone is dependent on the O_2 demand of the microbial community in the sediment and decreases with increasing concentrations of sediment organic matter (Sand-Jensen et al., 2005a; Raun et al., 2010; Møller & Sand-Jensen, 2011).

O_2 and CO_2 dynamics in the rhizosphere of *Lobelia* are strongly affected by diurnal cycles as *Lobelia* roots absorb CO_2 for photosynthesis and release O_2 in the light. This leads to a distinct diel pattern in the rhizosphere pore-water chemistry with low CO_2 concentrations in the light, as a result of root-facilitated CO_2 uptake, and high CO_2 concentrations in the dark, as the uptake ends and CO_2 from root and sediment respiration is released (Pedersen et al., 1995). By contrast, the O_2 concentration in the rhizosphere increases in light as a result of plant-mediated sediment oxygenation resulting from photosynthesis. In darkness, less O_2 is released as no O_2 is produced by photosynthesis (Pedersen et al., 1995; Sand-Jensen et al., 2005a,b; Møller & Sand-Jensen, 2011; Ribaudo et al., 2017).

The investigation of O_2 and CO_2 dynamics inside *Lobelia* rhizospheres without exerting damage to the belowground biomass or disturbing the spatial gradients in the pore-water chemistry arising from root-sediment interactions is challenging. Consequently, most studies in *Lobelia* rhizospheres rely on micro- and mini-electrode profiling or point measurements at different depths over time (Pedersen et al., 1995; Risgaard-Petersen & Jensen, 1997; Sand-Jensen et al., 2005b; Møller & Sand-Jensen, 2008). These measurements demonstrate CO_2 removal and O_2 enrichment in the isoetid rhizosphere in light. However, information on the direct connection between the roots and sediment processes as well as the spatial and temporal impact of the individual roots is sparse.

The use of planar optode technology, in combination with rhizoboxes, facilitates the quantitative monitoring of temporal and spatial dynamics of O_2 and CO_2 around individual roots with minimal disturbance of the biomass and biogeochemical gradients (Blossfeld & Gansert, 2012). In the last two decades, planar O_2 optodes have rendered possible the recording of O_2 distribution in sediments and soils (Glud et al., 1996; Holst et al., 1998), and planar optode technology is slowly gaining a foothold in research on rhizosphere O_2 dynamics (Jensen et al., 2005; Frederiksen & Glud, 2006; Askaer et al., 2010; Minett et al., 2013; Jovanovic et al., 2015; Koop-Jakobsen & Wenzhöfer, 2015; Larsen et al., 2015; Han et al., 2016; Koop-Jakobsen et al., 2017). In comparison, planar optode investigations of CO_2 are still in their infancy (Santner et al., 2015), and studies on CO_2 dynamics in rhizospheres are still very sparse. Blossfeld et al. (2013) investigated the CO_2 dynamics in the rhizosphere of *Viminaria juncea* (Fabaceae), showing that growing roots exhibit a large zone of influence (millimeter-scale) on soil CO_2 content, thereby demonstrating the usefulness of the technology to assess CO_2 dynamics in terrestrial rhizospheres.

The current study investigated the root-sediment interactions in the rhizosphere of *Lobelia* using a novel planar optode system: the VisiSens TD optode system from PreSens GmbH, Regensburg, Germany. The spatial variation of O_2 and CO_2 around roots of *Lobelia* was recorded as two-dimensional images, and the impact of light exposure of the leaves was investigated.

We hypothesized, first, large fluctuations in plant-mediated sediment oxygenation between light and dark periods, as the low gas permeability of *Lobelia* leaves makes photosynthesis the primary O_2 source for belowground O_2 transport. Second, we hypothesized a high spatial and temporal variability in the sediment CO_2 levels of *Lobelia* rhizospheres as a result of active root uptake of CO_2 for photosynthesis combined with O_2-stimulated CO_2 production.

2. Material and Methods

2.1 Plant and sediment material

Lobelia dortmanna L. plants and sediments for this study were collected from the Ihlsee near Bad Segeberg in Schleswig-Holstein, Germany. The mesotrophic lake has a surface area of 29 ha, a mean depth of 7.4 m and a maximum depth of 21.5 m. Ihlsee has a catchment area of 89 ha, which is dominated by forests in the western and southern parts and by single detached houses with private gardens in the northern and eastern parts. As a former oligotrophic lake, typical isoetid plant species, such as *Isoetes lacustris* (Isoetaceae), *Littorella uniflora* (Plantaginaceae) and *Lobelia*, colonize the shallow water zones of the Ihlsee. Samples of *Lobelia* were collected from the northern, shallow water zones during the summer of 2016 (53°57'036″N, 10°18'00″E). Sediments of the sampling sites are sands with < 2% contributions of silt and clay, and a low organic matter content of *c.* 1%. The sediment pH of the site was pH 6.3 during sampling. The samples were placed in plastic bags filled with lake water and transported to the laboratory, where they were planted in aquaria with sediment and water collected at the field site. The samples were cultured for 3 months in a climate chamber (12 h : 12 h, light : dark; *c.* 200 µmol m^{-2} s^{-1}; 18°C) until the start of the measurements. Sediment pH was checked after the measurements and remained within a range of pH 6.3-6.7, close to *in situ* conditions.

2.2 Preparation of a rhizobox for optode investigations

A rhizobox (Fig. 4.1), an aquarium for the visualization of rhizosphere processes (Neumann et al., 2009), was custom-made from Makrolon® plates, a transparent polycarbonate sheet material. Rhizoboxes consisted of a U-shaped inner frame (10-mm Makrolon®) with detachable front and back plates (5-mm Makrolon®), making a cubic aquarium (10 x 10 x 10 cm^3). Front and back plates were attached with 10 screw threads, and a 2-mm neoprene round cord was mounted along the edges of the U-shaped inner frame (Fig. 4.1). This made the front and back plates detachable, and yet water tight when attached.

Fig. 4.1 Experimental set-up: *Lobelia dortmanna* in an opened and drained rhizobox with multiple roots placed for optode analysis. Part of the corresponding O_2 optode image is inserted as an overlay image showing the O_2 distribution relative to the location of the roots under submerged conditions during measurements. This study reports on the results of measurements conducted on single roots of individual plants; in this photograph, the effect of several roots of a single plant is shown.

2.3 Preparation of *Lobelia* samples for optode investigations

To prepare the *Lobelia* samples for planar optode studies, the rhizobox was filled halfway with sediment, and water was added to fill the rhizobox. The sediment was mixed and subsequently allowed to settle, ensuring a uniform distribution. Subsequently, the rhizobox was slowly drained, placing it on its side. The rhizobox was moved to an upright position, and a small hole was dug in the sediment at a 1-cm distance from the front plate. The *Lobelia* sample for investigation was selected and planted in the hole. Roots selected for measurements remained on the sediment surface, facing the front plate. Subsequently, the rhizobox was placed at a 45° angle, and the front plate was detached. The selected roots were placed on the sediment in a position lining up with the front plate (Fig. 4.1). An optode foil (O_2 or CO_2 sensitive) was attached to the front plate. Under water, the optode foil was slowly pressed against the front plate, and both items were gently lifted out of the water. This generated a uniform and air-bubble-free water film between the foil and front plate, holding the foil in place. The front plate with the foil attached in a position covering the root was mounted on the rhizobox, and the rhizobox was slowly filled with water, adding water along the back plate, whilst the box was still at a 45° angle. In this way, the sediment was slowly saturated with water, preventing the entrapment of air bubbles along the optode foil. This approach was only possible because of the high permeability of the sandy substrate, which allowed rapid percolation of the added water, and the high stability of the sediment, which allowed it to be placed at an angle without collapsing. Finally, for measurements, the rhizobox was placed in an upright position and completely filled with water.

2.4 Optode investigation of O_2 and CO_2 in *Lobelia* rhizospheres

Planar optode investigations of O_2 and CO_2 dynamics in *Lobelia* rhizospheres were conducted using the planar optode system VisiSens TD (a novel optode system for two-dimensional mapping of O_2, pH and CO_2 from PreSens – Precision Sensing GmbH). The VisiSens TD system is a fluorescence imaging-based optode system. For a detailed description of the planar optode imaging principles and the theoretical background behind the VisiSens optode system, the reader is referred to Wang et al. (2010), Tschiersch et al. (2011, 2012) and Kumari & Gupta (2017). The VisiSens TD system is an integrated system with image acquisition hardware and software (VisiSens ScientifiCal) for image processing. It facilitates the read-out of optode sensor foils with a high spatial resolution of up to 25 µm. The optode investigations were conducted with O_2-sensitive optode foils (PreSens GmbH product code: SF-RPSu4; size, 4 x 4 cm^2 and 10 x 10 cm^2; range, 0-100% O_2 atm. sat.) and CO_2-sensitive optode foils (PreSens GmbH product code: SF-CD1R; 4 x 4 cm^2; 1-25% CO_2).

Image acquisition was conducted with a camera resolution of 1292 x 964 pixels. The camera and LED light sources were positioned at a distance of *c.* 20 cm from the rhizobox. The acquired optode images had a resolution of eight to nine pixels per millimeter. Optode measurements were conducted continuously over a light-dark cycle with a temporal resolution of one image per 10 min, resulting in time series of > 200 images. To facilitate optode recordings during illumination of the plants, the light illuminating the aboveground biomass was set on a timer, turning off the light for a 3-min period every 30 min, synchronized with the time of image acquisition. Consequently, the actual temporal resolution was one image per 10 min during darkness and one image per 30 min during light.

Calibration and initial image processing were conducted using the integrated VisiSens ScientifiCal software. Further quantitative data acquisition of specific features in the optode images, such as measurements of profiles across the roots, was performed using the image processing software ImageJ (version: Fiji).

To visualize the exact position of the root relative to the O_2 and CO_2 distribution shown in the optode images, the georeferencing tool in Qgis v.2.18.1 was used for the generation of overlap images of a root photograph of the selected root in the rhizobox with the associated optode image. Subsequently, the root was made visible in the optode image using the software Gimp v.2.8.18.

2.5 Calibrations and units of measurement

In this study, O_2 measurements are expressed as the percentage O_2 saturation in freshwater at atmospheric equilibrium (% atm. sat.). The O_2 optode foils were calibrated by the application of a two-point calibration with anoxic sediment for 0% O_2 and air-bubbled water for 100% atmospheric equilibrium O_2. CO_2 is measured as CO_2 partial pressure (pCO_2) and is expressed here as percentage CO_2 at atmospheric pressure (abbreviated as % CO_2 in the following). For CO_2 optode foils, the calibrations were conducted using four concentrations between 0.01 and 17% CO_2 in water-saturated air, in accordance with the manufacturer's guidelines. CO_2 foils were calibrated in a closed chamber with a small inlet and outlet, and the flow-through gas stream was controlled by a high-precision air pump (ADC, Hoddesdon, Hertfordshire, UK). The foil was exposed to each CO_2 concentration until the read-out stabilized (5-15 min). Calibrations were conducted at the same temperature as the actual measurements. Planar CO_2 optode foils are sensitive only for CO_2. The other components of the carbonic acid equilibrium (i.e. carbonate and bicarbonate) are not measured, but can be calculated if the pH and temperature are known. However, as *Lobelia* exclusively utilizes CO_2 as an inorganic carbon source (Wium- Andersen, 1971), the direct measurement of CO_2 is sufficient for the present study on the belowground CO_2 dynamics in the *Lobelia* rhizosphere.

2.6 Experimental design and spatial and temporal analysis

This study investigates the interaction between individual roots of *Lobelia* and their immediate environment. In order to investigate the spatial and temporal variation of O_2 and CO_2 around the roots of *Lobelia*, planar optode measurements were conducted on single roots of five individual plants ($n = 5$). Selected roots were manually placed on the sediment, lining up the front plate to allow for direct contact with the optode foil (Figs 4.1, Supporting Information 4.S1). Optode measurements were conducted continuously for three 8-h periods, alternating between dark and light conditions (dark-light-dark).

The spatial extent of the effect exerted by the roots on the O_2 and CO_2 concentration in the surrounding sediment was demonstrated in optode images. The extent of the spatial variation was quantified by measurement of the pore-water concentration profiles of O_2 and CO_2. Concentration profiles were measured perpendicular to the roots at the location at which the root-affected zone was widest. Data were extracted from these profiles to account for the extent of the affected zones and the maximum and minimum concentrations of O_2 and CO_2 in the pore-water. The radii of the root-affected zones were measured in the profiles as the distance from the root surface to the point at which an effect on O_2 or CO_2 could no longer be detected. To account for the effect of light exposure of the leaves, the spatial variation was recorded at the end of the light phase and at the end of the second dark phase.

The temporal variation of the O_2 and CO_2 concentrations in the sediment surrounding the roots was measured continuously over time during alternating light and dark periods. After the sample had been prepared for analysis in the rhizobox, it was first exposed to an 8-h dark period (dark 0-8 h). This preparatory period was introduced in order to re-equilibrate the sediment condition after sample preparation, and to generate a starting point without any effects of light exposure. This period is not shown in the results. Subsequently, the samples were analyzed during subsequent dark (8-16 h)-light (16-24 h)-dark (24-32 h) periods.

Average O_2 and CO_2 concentrations were followed within a designated area around the roots, which was manually determined on the basis of the O_2 and CO_2 patterns in the respective optode images. The area was selected as the whole affected area, which was visually different from the bulk sediment in optode images. The area was selected from the optode image showing the largest area affected in the recorded time series. This method to measure temporal variation is a feature included in the VisiSens SCIENTIFICAL 1.0 image processing software. In addition, for CO_2, there is a distinct area in the immediate vicinity of roots in which CO_2 uptake affects the CO_2 concentration patterns in the sediment surrounding the roots. The temporal variation of CO_2 within this area was also recorded as described above. To test for effects of illumination (light vs dark period) on the size and O_2 or CO_2 concentrations of the designated areas, paired *t*-tests with size and concentration values measured at the end of light vs dark periods were conducted.

3. Results

3.1 Spatial rhizosphere O_2 and CO_2 distribution

The spatial O_2 and CO_2 distribution around the roots of *Lobelia* under light and dark conditions is shown by example for one root in Fig. 4.2. Altogether, five roots of individual plants were investigated. The optode images of all replicates under light and dark conditions are shown in Fig. 4.S1. Measures of the spatial distribution of O_2 and CO_2, as well as maximum and minimum concentrations, are given in Table 4.1. *Lobelia* roots affected the O_2 and CO_2 content of the sediment surrounding the roots, which is clearly shown in the optode images. Three distinct rhizosphere zones can be identified: the oxic root zone (O_2 release from the root to the sediment results in an oxygenated zone in the immediate vicinity of the root; Fig. 4.2a–d); the CO_2-enhanced zone (respiratory processes are stimulated by root presence, which is demonstrated by an enhanced CO_2 concentration in a wider area around the root; Fig 4.2e-h); and the CO_2 uptake zone (CO_2 uptake via the roots results in a CO_2-depleted zone in the immediate vicinity of the root inside the CO_2-enhanced zone; this zone is only present in light; Fig. 4.2e,g).

Table 4.1 Radius, maximum and minimum concentration of oxic root zones in light and dark, the CO_2 uptake zone (CO_2 is depleted in the immediate vicinity of the roots in light) and the CO_2-enhanced zone (covering a larger zone around roots in which CO_2 accumulates) in rhizospheres of *Lobelia dortmanna*.

Oxygen	**Radius (mm)**	**Max (% atm. sat.)**	**Min (% atm. sat.)**
Oxic root zone light	3.1 ± 0.3	29.8 ± 2.3	0
Oxic root zone dark	1.0 ± 0.4	6.6 ± 1.2	0

Carbon dioxide	**Radius (mm)**	**Max (%)**	**Min (%)**
CO_2 uptake zone	2.0 ± 0.7	5.1 ± 0.3	2.5 ± 0.3
CO_2-enhanced zone	9.8 ± 3.6	5.3 ± 0.2	2.0 ± 0.3

The extent of zones was measured from cross-sectional profiles across the root at the widest position. Radius was measured from the root surface to the point in bulk sediment at which the measured effect (O_2 release, CO_2 uptake or CO_2 accumulation) becomes undetectable. In the oxic zone, concentration maxima were measured on the root surface and minima in the bulk anoxic sediment. In the CO_2 uptake zone (detectable in light only), concentration minima were measured at the root surface and maxima were measured in the bulk sediment in the vicinity of the root. In the CO_2-enhanced zone, maxima were measured in darkness at the root surface and the minima in the bulk sediment away from the root. Five roots of individual plants were investigated. In one of the five investigated plants, the CO_2 uptake zone (light) and oxic root zone (dark) were not detectable in the optode images. Thus, the data provided here refer to mean values and standard deviations of four replicates (n = 4). O_2 is expressed as the percentage of O_2 saturation in freshwater at atmospheric equilibrium (% atm. sat.). CO_2 is measured as pCO_2 and is expressed as percentage CO_2 at atmospheric pressure.

3.2 O_2 spatial distribution

Under both light and dark conditions, O_2 was released along the entire root of *Lobelia* into the sediment, resulting in a zone of oxidized sediment around the root, which is clearly shown in the optode images and cross-sectional profiles (Fig. 4.2a-d). O_2 concentrations declined from the root surface into the anoxic bulk sediment. The maximum O_2 concentration was measured at the root surface at the end of the light period, where it reached an average maximum concentration of 29.8 ± 2.3% O_2 atm. sat. (Table 4.1). At the end of the first dark period, O_2 was still present in the oxic root zone, but the maximum concentration was significantly lower in darkness than in light, reaching an average of 6.6 ± 1.2% O_2 atm. sat. ($P < 0.001$; Table 4.1). The oxic root zone extended further into the bulk anoxic sediment in the light than in the dark, with average radii of 3.1 ± 0.3 mm and 1.0 ± 0.4 mm under light and dark conditions, respectively ($P < 0.01$; Table 4.1). In one of the five plants investigated, no oxic root zone was detected in the dark (Fig. 4.S1; LOB#1). This replicate was omitted from the measurements in Table 4.1.

3.3 CO_2 spatial distribution

In the CO_2-enhanced zone, CO_2 accumulation occurred in light and partly also during the dark period. This resulted in CO_2 concentrations markedly higher than in the bulk sediment unaffected by root presence, which is clearly shown in the optode images and cross-sectional profiles (Figs 4.2e-h, 4.S1).

The CO_2-enhanced zone had a maximum radius of 9.8 ± 3.6 mm (Table 4.1; observed in the second dark period). The maximum pCO_2 was measured to be 5.3 ± 0.2% CO_2 on the root surface, whereas the bulk sediment unaffected by root presence had an average pCO_2 of 2.0 ± 0.3% CO_2 (Table 4.1).

As the root initiated its CO_2 uptake in light, a CO_2-depleted zone appeared around the roots inside of the CO_2-enhanced zone, which is clearly shown in the optode image and cross-sectional profile (Fig. 4.2e,g). This resulted in a local CO_2 minimum with an average pCO_2 of 2.5 ± 0.3% CO_2 located on the root surface, which is comparable with the concentration in the bulk sediment, which was 2.0 ± 0.3% CO_2. The CO_2 maximum during light had an average pCO_2 of 5.1 ± 0.3% CO_2 and was located at an average distance of 2.0 ± 0.7 mm from the root surface (Table 4.1). In one of the five plants investigated, no CO_2 uptake zone was detected in light (Fig. 4.S1; LOB#1). This replicate was omitted from the measurements in Table 4.1. In darkness, the CO_2 uptake zone is not present and the CO_2 maximum is located at the root surface (Fig. 4.2f,h).

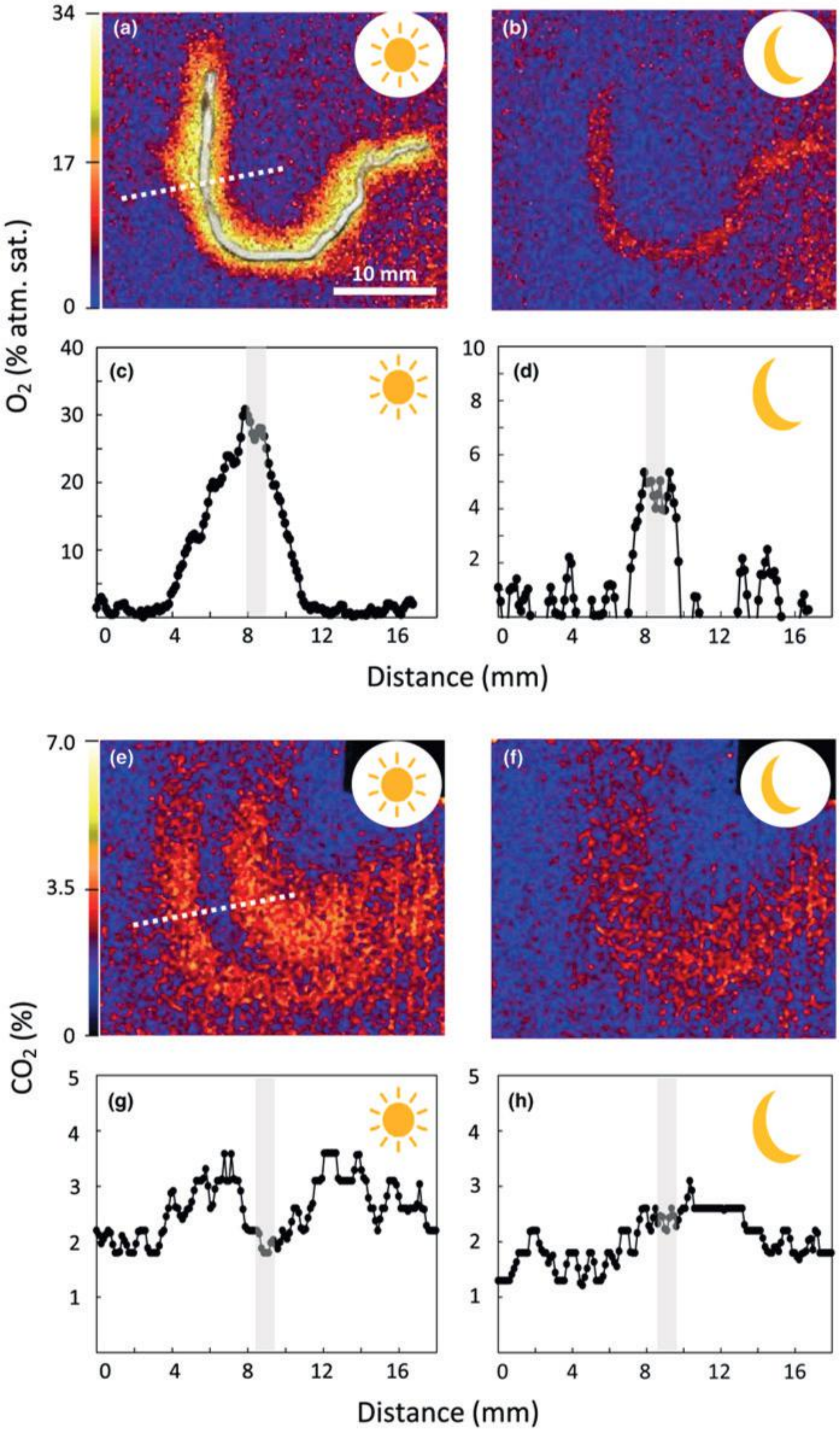

Fig. 4.2 Spatial variation in O_2 and CO_2 concentrations around a single root of *Lobelia dortmanna* (additional replicates are shown as Supporting Information Fig. 4.S1). (a, b, e, f) Optode images of the spatial distribution of O_2 and CO_2 concentrations during light (left) and dark (right) conditions. The exact location of the root is shown in (a). (c, d, g, h) Cross-sectional concentration profiles of O_2 and CO_2 during light and dark conditions; gray bars indicate root position and width. The profile locations are shown as a dashed line in (a, e). O_2 is expressed as the percentage of O_2 saturation in freshwater at atmospheric equilibrium (% atm. sat.). CO_2 is measured as pCO_2 and is expressed as the percentage CO_2 at atmospheric pressure.

3.4 Temporal rhizosphere O_2 and CO_2 dynamics

O_2 dynamics: Over consecutive dark (8 h)-light (8 h)-dark (8 h) periods, the development of the O_2 concentration was followed within a predetermined area covering most of the oxic root zone (Fig. 4.3). At the entry of the first dark period (8-16 h), the O_2 concentration of the oxic root zone had reached a stable level, where the O_2 concentration was in the range of 2-7% atm. sat., which was low and yet distinguishable from the anoxic background (Figs 4.3, 4.S1). One sample (LOB#1) responded differently during both dark phases by completely eliminating the oxic root zone within 1 h, leaving the root in anoxic conditions. However, in general, the oxic root zone persisted throughout the first dark period (8-16 h). During light exposure (16-24 h), O_2 release was immediately enhanced, and the oxic root zone expanded (Fig. 4.3; time-series images). The O_2 concentration of the oxic root zone increased continuously throughout the light period, before leveling off and approaching a steady state towards the end of the 8 h of light exposure (Fig. 4.3). During the subsequent dark period (24-32 h), the O_2 concentration declined continuously, leveling off and approaching a steady state with constant average O_2 concentration of *c.* 5-7% atm. sat. after 8 h of darkness. This level is similar to the level at the entry point to the first dark period (8-16 h), where the sample had been in darkness for 8 h.

CO_2 dynamics: Over consecutive dark (8 h)-light (8 h)-dark (8 h) periods, the development of the CO_2 concentration was followed around five roots of individual plants within two predetermined areas covering the CO_2-enhanced zone (Fig. 4.4a) and the CO_2 uptake zone (Fig. 4.4b). In the latter, one of the five plants showed no CO_2 uptake zone in light (Fig. 4.S1; LOB#1); for clarity, this replicate was omitted from Fig. 4.4b.

At the entry to the first dark period (8-16 h), the pCO_2 of the CO_2-enhanced zone had reached a stable level of 3.3-5.0% CO_2. Throughout the first dark period (8-16 h), the CO_2 concentration remained at this level or showed a tendency to decrease slightly (Fig. 4.4a). The concentration of the CO_2-enhanced zone varied strongly among samples, yet all replicates showed higher CO_2 concentrations around the roots than in the bulk sediment, and the CO_2-enhanced zone was clearly distinguishable in the optode images (Fig. 4.4; time-series images 1 + 2).

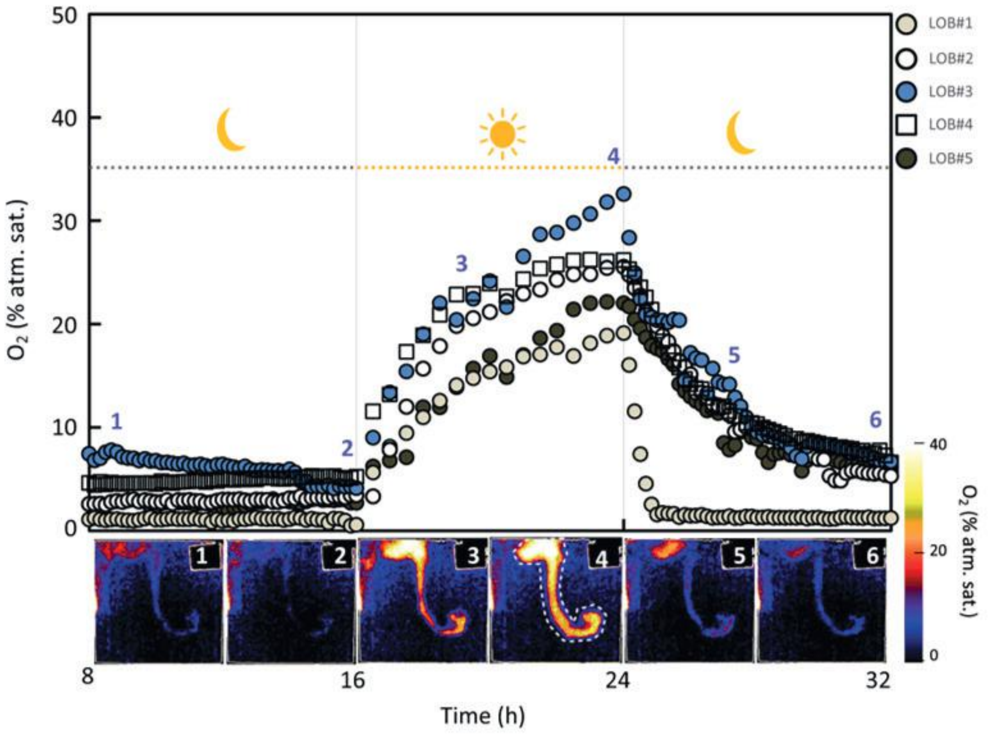

Fig. 4.3 Temporal variation in O_2 around single roots of *Lobelia dortmanna* shown for five individual plants during consecutive dark-light periods. Graph shows mean O_2 concentration (as percentage O_2 saturation at atmospheric equilibrium) of the oxic root zone over time (top). O_2 optode images show the spatial distribution of O_2 and development of the oxic root zone at selected time points 1-6 (bottom; example shown for replicate LOB#3). The O_2 concentration was measured in a designated area covering the largest extent of the oxic root zone, which was manually selected for each root in the optode image captured at the end of the light period (shown as a dashed line in optode image 4).

In light (16-24 h), the CO_2 concentration was immediately depleted in the CO_2 uptake zone, where it remained stable at a lower level throughout the light period (Fig. 4.4b). The CO_2 concentration in the CO_2 uptake zone was markedly lower than in the surrounding sediment, and the CO_2 uptake zone is clearly distinguishable in the optode images (Fig. 4.4; time-series images 3 + 4). Despite CO_2 uptake in the immediate vicinity of the roots throughout the light period (16-24 h), the CO_2 concentration continuously increased in the CO_2-enhanced zone in a larger zone around the roots (Fig. 4.4a). In the subsequent dark period (24-32 h), the CO_2 uptake zone immediately began to diminish and, within 2 h (Fig. 4.4b), it was no longer distinguishable inside the CO_2-enhanced zone (Fig. 4.4; time-series images 5 + 6). The CO_2 concentration in the enhanced zone continued to increase for 1-4 h in the dark, reaching a level of 3.6-6.3% CO_2. Subsequently, the CO_2 concentration remained at this level or showed a tendency to decrease slightly throughout the rest of the dark period (Fig. 4.4a).

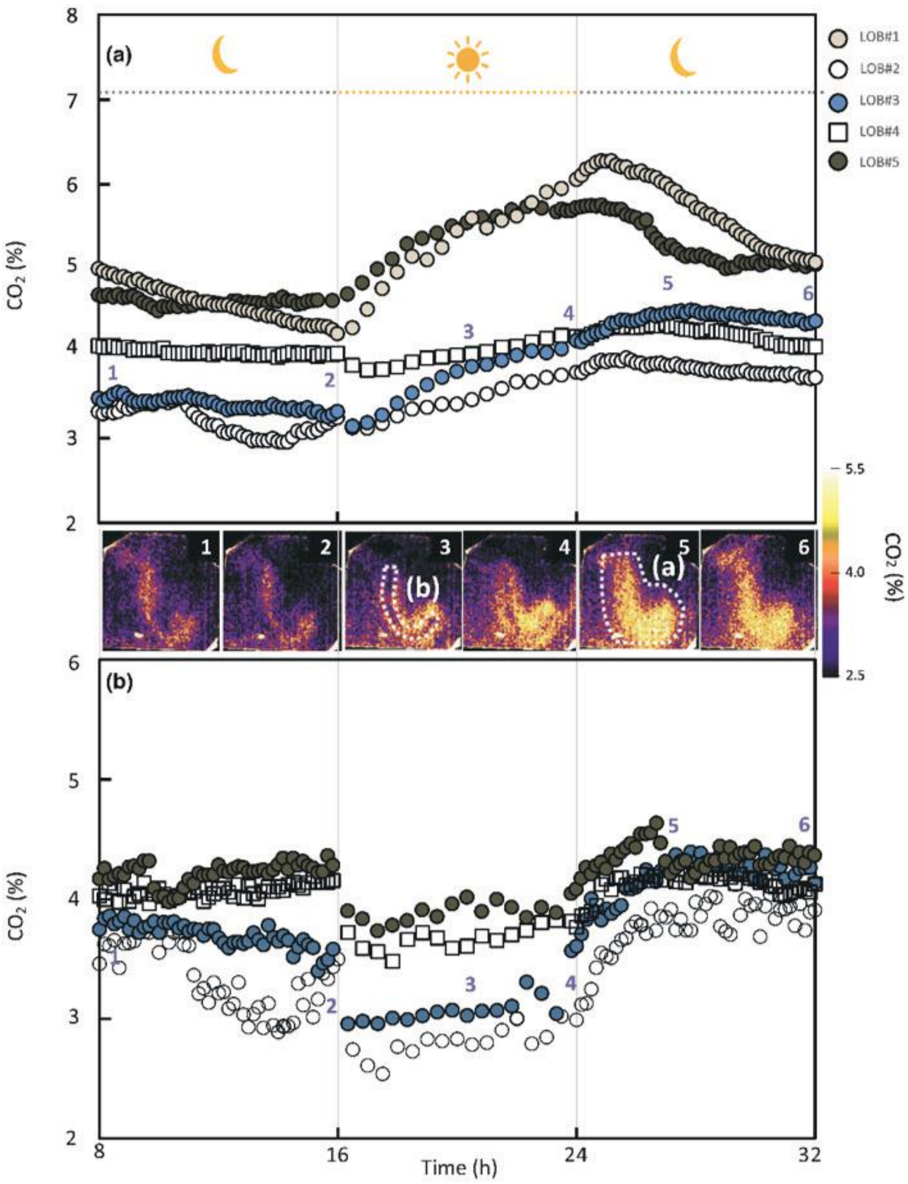

Fig. 4.4 Temporal variation of CO_2 around single roots of *Lobelia dortmanna* during consecutive dark-light periods. The series of CO_2 optode images shows the spatial distribution of CO_2 at selected time points (1-6; shown for replicate LOB#3). The top graph shows the average CO_2 concentration measured in the larger vicinity of the root (radius *c.* 1-2 cm), where CO_2 is enhanced as a result of increased respiration. The bottom graph shows the average CO_2 concentration measured in the immediate vicinity of the root (radius *c.* 0-0.5 cm), covering the area in which CO_2 is depleted as a result of root uptake (replicate LOB#1 was omitted as no CO_2 uptake was detected; Supporting Information Fig. 4.S1). The designated areas were manually selected for each root in the optode image capturing the largest effect. The designated areas for measurement in (a) the CO_2-enhanced zone and (b) the CO_2 uptake zone are shown as dashed lines in optode images 5 and 3, respectively. CO_2 is measured as pCO_2 and is expressed as the percentage CO_2 at atmospheric pressure.

4. Discussion

This study is the first to combine planar optode measurements of O_2 and CO_2 in rhizospheres. It demonstrates a tight coupling between photosynthetic processes in *Lobelia dortmanna* during light exposure of the leaves and the spatiotemporal dynamics of O_2, CO_2 and their interaction in the rhizosphere pore-water.

4.1 O_2 dynamics

In accordance with our first hypothesis, we demonstrate large fluctuations in plant-mediated sediment oxygenation between light and dark periods in the rhizosphere of *Lobelia*. O_2 release across the root surface was pronounced along the entire root in light, and O_2 contents in the resulting oxygenated root zone increased throughout the light phase. In darkness, the O_2 supply was significantly reduced, resulting in a drastic decline in the sediment O_2 content around the roots (Fig. 4.3). These findings support previous studies showing strong diurnal changes in O_2 release from the roots of *Lobelia* and other isoetids (Sand-Jensen et al., 1982, Pedersen et al., 1995; Sand-Jensen et al., 2005a,b; Møller & Sand-Jensen, 2011; Ribaudo et al., 2017).

Furthermore, we demonstrate that *Lobelia* is capable of maintaining oxic root zones around its roots even during prolonged dark periods without input from photosynthetic O_2 production. This O_2 release to the sediment in darkness has been observed previously in *Lobelia* (Sand-Jensen et al., 1982; Risgaard-Petersen & Jensen, 1997). However, as roots and the microbial community will continue to respire O_2, the oxic root zone would be completely depleted of O_2 unless there was continuous supply of O_2 from aboveground sources. In the dark, photosynthetic O_2 production is excluded. Hence, the O_2 release either originates from exchange with the overlying water or from O_2 stored as a reservoir in the plant. Both the land and water forms of *Lobelia* have short stiff leaves, which lack stomata and are covered by a thick cuticle providing high resistance to gas exchange between the aboveground biomass and the water column (Pedersen & Sand-Jensen, 1992). Consequently, O_2 leaking out of the roots during dark periods most probably originates from stored O_2 resources. *Lobelia* possesses large air-filled lacunae between the leaf and root tips (Pedersen & Sand-Jensen, 1992), which may buffer the O_2 depletion in darkness. In support of this concept, Pedersen et al. (1995) found that *Lobelia* was capable of maintaining oxic root zones over an 8-h dark period, but not during extended dark periods of 24 h.

4.2 CO_2 dynamics and O_2-CO_2 interaction

In accordance with our second hypothesis, we demonstrate high spatial and temporal variability in the sediment CO_2 content of *Lobelia* rhizospheres as a result of enhanced CO_2 production facilitated by O_2

release, combined with root uptake of CO_2 for photosynthesis (Figs 4.3, 4.4). These two counterbalancing processes gave rise to a distinct pattern in the CO_2 profile in light, with a CO_2 minimum at the root surface and a CO_2 maximum on both sides of the roots (Table 4.1). In the dark, the profile was reversed, and the CO_2 maximum was located at the root surface. Overall, root-acilitated CO_2 production affected a larger zone than CO_2 uptake.

Following the CO_2 concentration in the CO_2 uptake zone during consecutive light and dark periods (Fig. 4.4b) clearly showed that CO_2 uptake is dependent on the light exposure of the leaves. CO_2 uptake was investigated on five roots of five individual plants (Fig. 4.S1). Three of these roots clearly demonstrated that CO_2 uptake can occur along the entire length of the root. In one of the five replicates, however, CO_2 uptake was not visible. This may be the cause of the natural variation in morphology-determined gas-exchange ability of the root, or lower photosynthesis. In this regard, it is noteworthy that this root also showed the lowest O_2 concentration in the oxic root zone. Furthermore, a lack of a CO_2 uptake zone could be caused by damage to the root exerted during handling. However, as the root generated both an oxic zone and a CO_2-enhanced zone around the root, we find this to be the least likely explanation.

The CO_2 concentration in the CO_2-enhanced zone continued to increase beyond the light period and continued into the subsequent dark period, where the CO_2 concentration peaked after 1-4 h. We demonstrate a strong positive correlation between the O_2 concentration of the oxic root zone at the end of the light period and the time it takes for the CO_2 concentration to peak in the subsequent dark period (Fig. 4.5). This shows that the sustained CO_2 production beyond the light period relied on the reservoir of O_2 built up in the sediment and lacunae tissue during the light phase. As the stored O_2 supply was depleted, CO_2 production decreased, and the CO_2 concentration in the CO_2-enhanced zone reached its maximum (Fig. 4.4a).

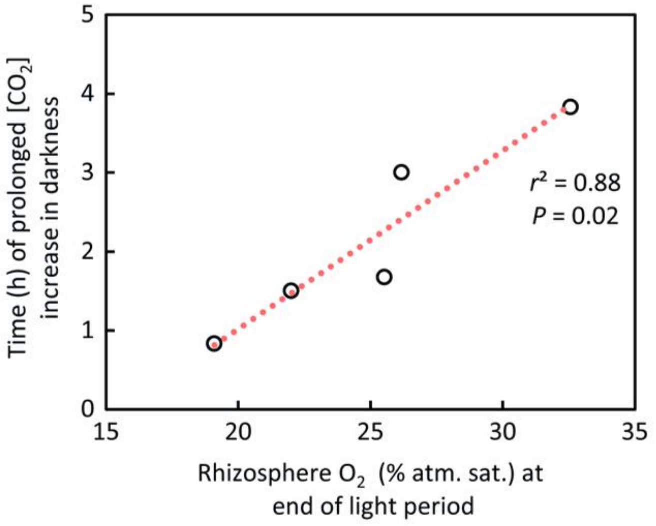

Fig. 4.5 Relationship between O_2 concentration in the oxic root zone at the end of the light period (at 24 h) and the duration (h) of prolonged CO_2 concentration increase in darkness around single roots of *Lobelia dortmanna* (compare Fig. 4.4a; n = 5).

4.3 Roots stimulate microbial activity in the sediment

Although CO_2 was taken up by the roots in light, the impact was restricted to a small area in the immediate vicinity of the roots and, in general, there was a net increase in the CO_2 concentration around the root throughout the light period. As CO_2 was taken up by the roots during the light period, but there was still a net increase in CO_2 observed around the roots, the CO_2 production resulting in this increase must be exclusively generated by the microbial community. Hence, we can hereby demonstrate that roots in *Lobelia* rhizospheres stimulate microbial respiratory processes. The high degree of sediment oxygenation was the primary cause of the stimulated microbial activity. As shown in Fig. 4.5, there is a close correlation between sediment oxygenation and CO_2 production. However, in addition to an O_2-induced stimulation of microbial activity, the release of root exudates as labile organic substrates could have contributed to the observed effect (Mueller et al., 2016). Our observations of increased microbial activity are supported by Karjalainen et al. (2001), who demonstrated that *Lobelia* enhances microbial activity and biomass in the sediment through sediment oxygenation and excretion of dissolved organic carbon.

4.4 Cumulative effects

In this study, we focused primarily on single roots and their impact on the surrounding sediment through sediment oxygenation and CO_2 uptake. However, inside a natural *Lobelia* rhizosphere, with multiple closely located roots simultaneously exerting their impact on the sediment, the cumulative effect may be more pronounced than the effects of single roots. In this study, we recorded an optode image showing O_2 release from multiple roots (Fig. 4.1). In this image, the cumulative effect was clearly shown in the top part of the sediment, resulting in a higher and more uniform O_2 distribution compared with the bottom part of the sediment, where the roots were separated with less overlap between oxic root zones. It is possible that the higher O_2 concentration obtained by this cumulative effect can increase the O_2 concentration to a level at which it can importantly contribute to sustained night-time respiration of the belowground biomass, as suggested by Sand-Jensen et al. (2005b).

Moreover, the average CO_2 concentration in the rhizosphere can be affected in this way, as the roots are closely located and the CO_2 uptake zones overlap. Pedersen et al. (1995) measured CO_2 concentrations inside *Lobelia* rhizospheres and found that the concentration in pore-water decreased in light and increased in darkness. Our study reveals that the effect of root CO_2 uptake is restricted to the immediate vicinity of roots, and that, overall, CO_2 production is stimulated around the root. However, when multiple roots from each plant are located closely together and simultaneously exert their impacts on the sediment, it could result in a net uptake of CO_2 from the rhizosphere. Indeed, the study by Pedersen et al. (1995) reported that CO_2 uptake during light exposure was most pronounced in the top 3 cm of the sediment, corresponding to the depths with the highest root density.

4.5 Planar optodes - methodological considerations

Planar optode technology was used to visualize O_2 and CO_2 dynamics around individual roots. In the samples investigated, the O_2 concentrations were within a range of *c.* 0-35% atm. sat., and *p*CO_2 was within a range of 1-7% CO_2. The analytical performance of the optode foils was sufficient to capture the distinct concentration patterns around the individual roots for both analytes. However, in the anoxic parts of the sediment, the pixel values for O_2 range between *c.* +2 and -2 (% atm. sat.; Fig. 4.2). In the image processing of O_2 optode images, this range occasionally leads to a misleading color-coding of the bulk sediment, as the high values are colored as being different from zero, although the sediment is completely anoxic. The optode images were recorded with a spatial resolution of eight to nine pixels per millimeter, which proved to be sufficient to capture processes going on in the immediate vicinity of the roots on a submillimeter scale. At the same time, the foil size (4 x 4 cm^2) was large enough to capture the entire zones of O_2 and CO_2 accumulation around the roots.

For technical reasons, planar optode measurements in rhizospheres usually need to be conducted *ex situ* and involve the transplantation of plant samples into rhizoboxes for investigation. This may alter the rhizosphere conditions and processes relative to natural conditions in the field. For instance, the root-associated microbial community would temporarily be disturbed, as would the interaction of roots and mycorrhizal fungi (Moora et al., 2016). This may affect the magnitude of rhizosphere oxygenation and CO_2 accumulation, causing a divergence between the experimental and natural conditions. However, our observation of the dynamics of CO_2 uptake, CO_2 accumulation and rhizosphere oxygenation corresponds well with findings of field studies or studies on undisturbed rhizospheres of *Lobelia* (Pedersen et al., 1995; Sand-Jensen et al., 2005a,b; Ribaudo et al., 2017).

The planar optode system has individual foils for O_2 and CO_2, and, consequently, the foils must be exchanged between measurements, which requires the rhizobox to be drained and opened. This procedure must be performed with great care to ensure that the root remains in the same position. In this study, all measurements were conducted serially and the switching of optode foils between measurements occasionally resulted in slight changes to the root position (Fig. 4.S1; LOB#4).

Planar optode measurements have a systematic drawback causing the extent of zones with increased levels of O_2 and CO_2 around the roots to be overestimated. That is, the side of the rhizobox against which the roots are placed (here the front plate) is an impermeable barrier, which restricts the dispersion of dissolved gases. This causes an enlargement of the zone of the gaseous analyte compared with normal conditions, as the gas builds up against the side of the rhizobox (Polerecky et al., 2006). Despite this systematic drawback, the planar optode technique still provides a unique opportunity to visualize the spatial heterogeneity of the O_2 and CO_2 distribution inside natural sediments, capturing the net impact of the interaction between plant processes and microbial and chemical processes in the sediment.

Conclusion

Belowground sediment oxygenation is a mechanism by which aquatic and amphibious plants can improve nutrient uptake (Bradley & Morris, 1990; Lai et al., 2012) and reduce exposure to phytotoxins, such as H_2S and reduced Fe(II) and Mn(II) species (Rozema et al., 1985; Pezeshki, 2001; Lee, 2003). In this study, we have demonstrated a tight coupling between root presence and its O_2 release and the availability and uptake of CO_2 in the rhizosphere of *Lobelia dortmanna*. O_2-induced stimulation of microbial activity resulted in the accumulation of CO_2 around the roots, and root uptake of this inorganic carbon resource was demonstrated during light exposure of the leaves. Hence, for small freshwater plants, such as isoetids, which retrieve their inorganic carbon from the sediment, belowground oxygenation is also a mechanism that can increase the supply of sediment CO_2 to sustain the plant's photosynthetic requirements.

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Supporting Information

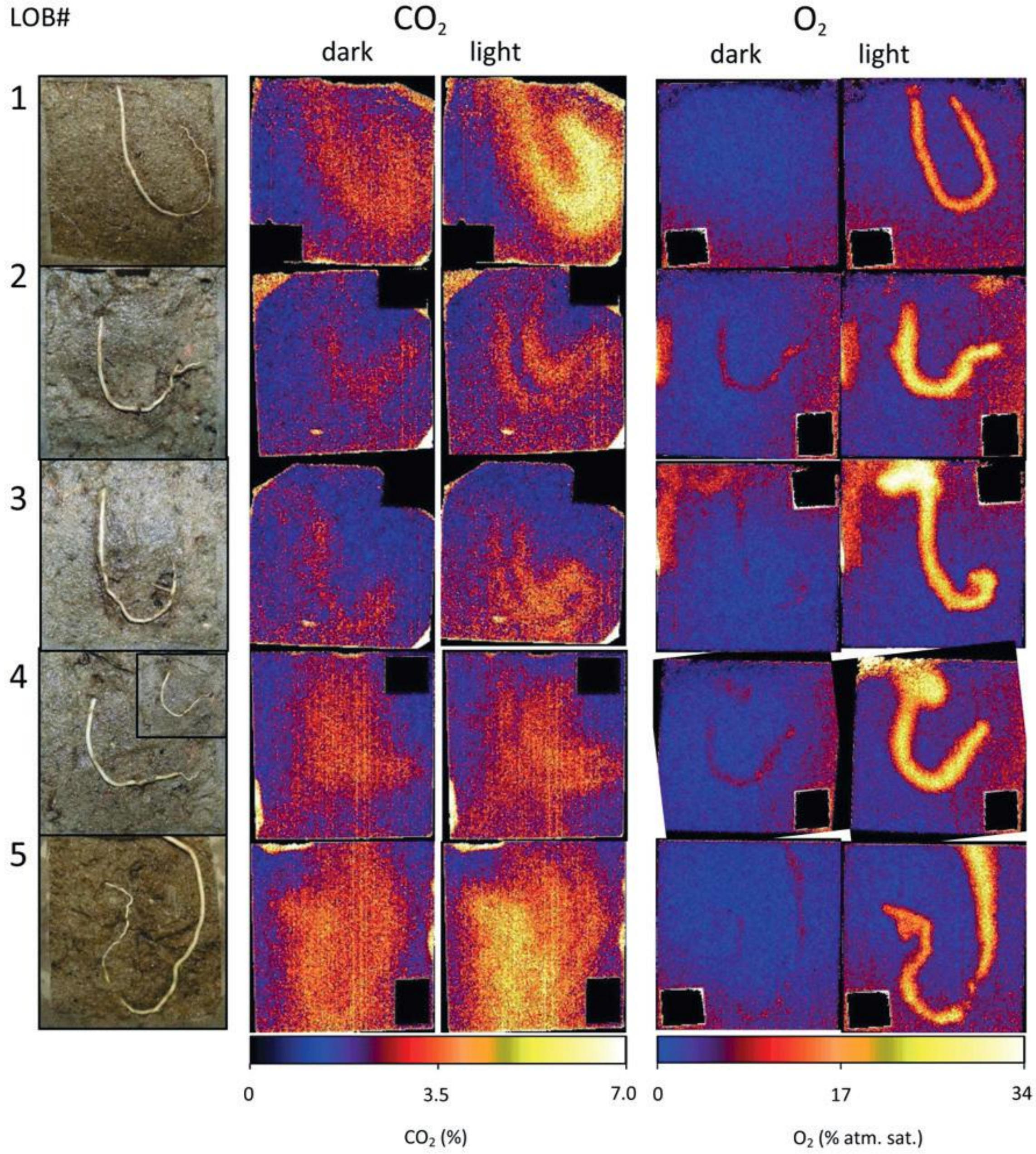
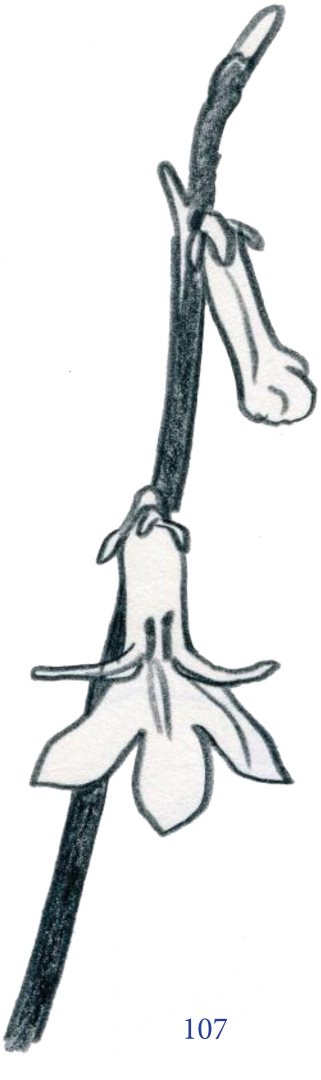
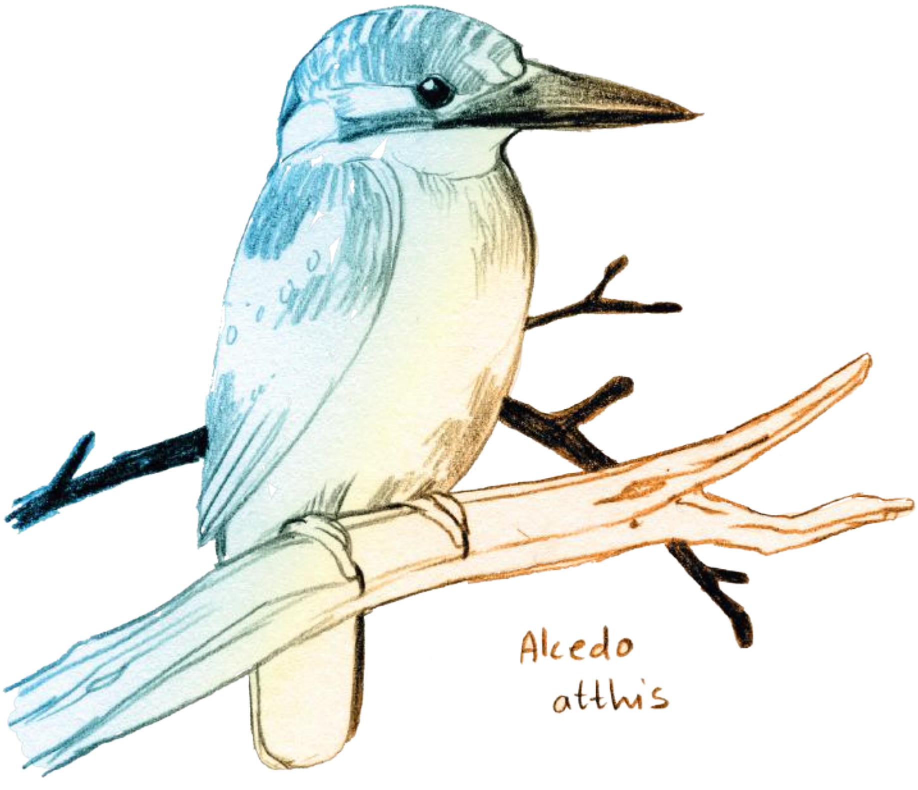


Fig. 4.S1 Optode images of CO_2 and O_2 distribution in a 4 x 4 cm area around single roots of five individual plants of *Lobelia dortmanna* after 8-h dark (dark) and 8-h light (light) periods. Photos in the left column show location of the root relative to the optode images. Inlet in photo #4 refers to the changed root position for the O_2 measurement relative to the CO_2 measurement. O_2 is expressed as % of the O_2 saturation in freshwater at atmospheric equilibrium (% atm. sat.). CO_2 is measured as pCO_2 and is expressed as % CO_2 at atmospheric pressure.

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CHAPTER 5

General discussion

5.1 Plant Biodiversity of urban wetlands

What vegetation patterns are characteristic for urban wetlands in Hamburg?

In this section the number of species and proportion of threatened species recorded in the four surveys are discussed with regard to their lifeforms after Raunkiær and their Ellenberg indicator values (EIV) for moisture, reaction and nutrient (Ellenberg et al., 1991). Further, examples of plant species are named and some species are discussed more in detail with regard to their inhabiting ecosystems and their situation in Germany and more specific in Hamburg.

The studied wetlands in this thesis were highly diverse in relation to vascular plant species richness with a total number of 515 species (including species aggregates such as *Oenothera biennis* agg.) identified in four surveys including 58 non-native plant species of Germany and 30 additional species not reported as established species for Germany (Metzing et al., 2018). In relation to the total number of species recorded for Hamburg (1546 species; Poppendieck et al., 2010), 31 % (483 species) of the plant species of Hamburg were found during the surveys in this thesis. Further, 11 % (70 species) of the threatened plant species and 44 % (20 species) of the near threatened plant species of Hamburg were identified in the studied wetlands (in total, 624 threatened species and 45 near threatened species; Poppendieck et al., 2010). A higher number of species was classified as threatened (70 species) and a lower number of species was classified as least concern (348 species) in the red list of Hamburg (Poppendieck et al., 2010) in comparison to the red list of Germany (14 and 387 species, respectively; Metzing et al., 2018; Fig. 5.1).

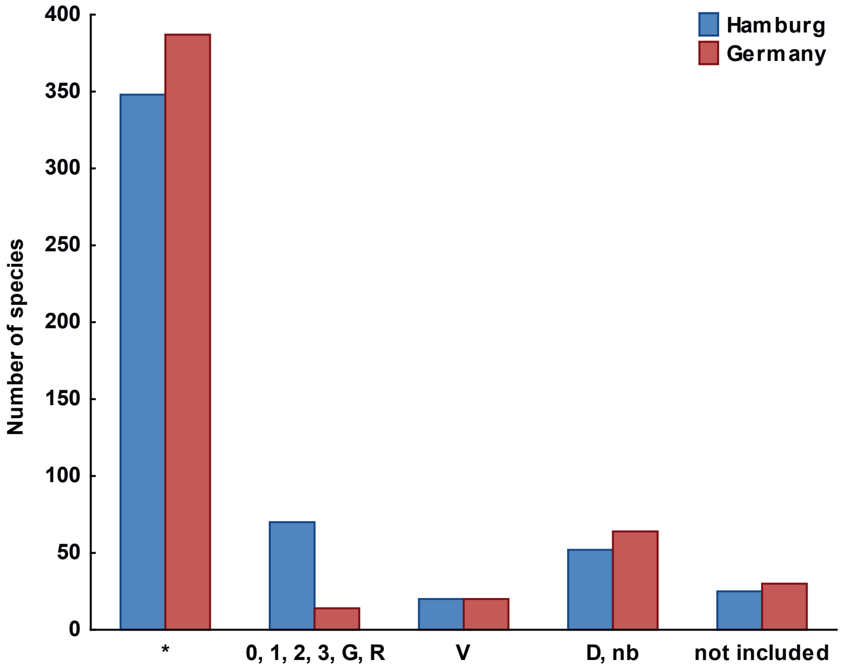
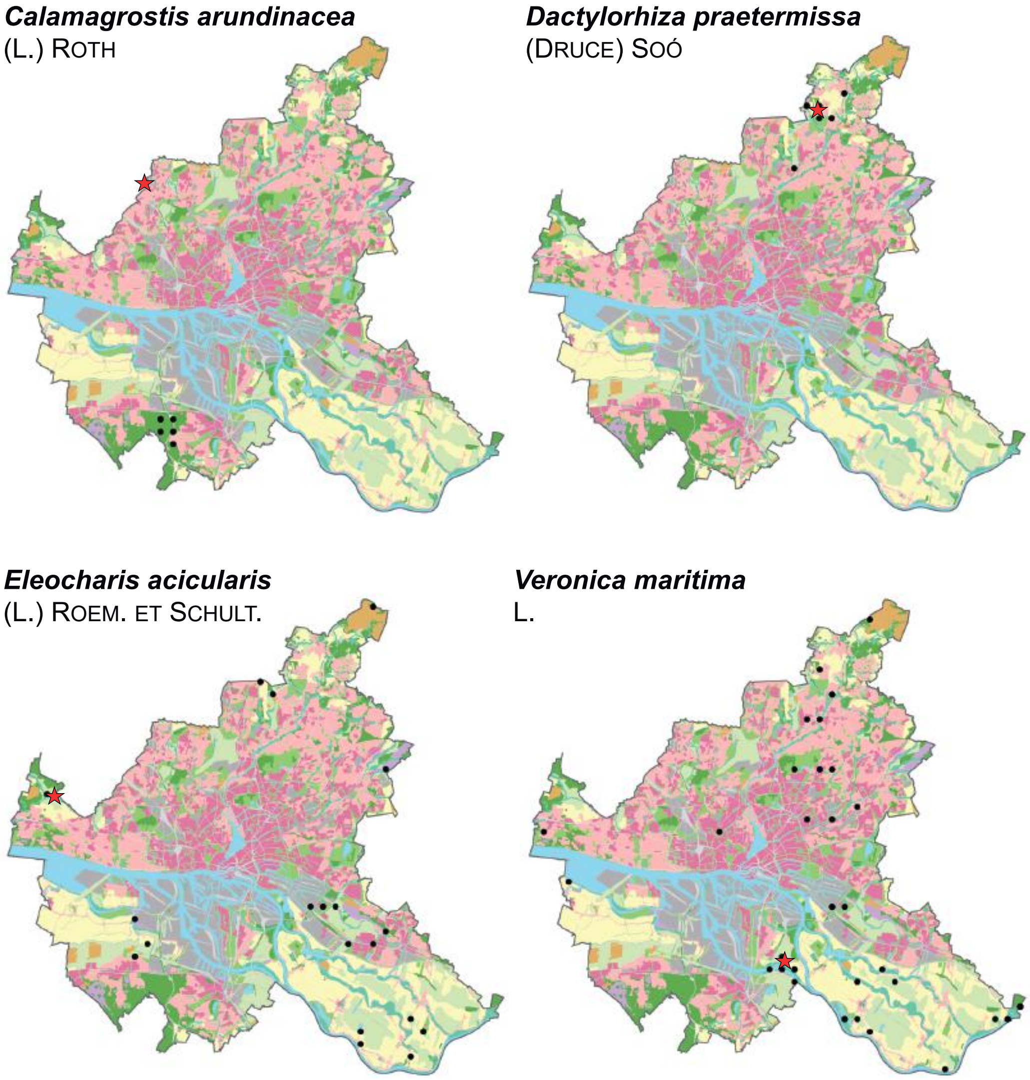


Fig. 5.1 Number of vascular plant species recorded in the surveys of this thesis grouped according to the red list status of Hamburg and Germany. Red list status of Hamburg follows Poppendieck et al. (2010) and red list status of Germany follows Metzing et al. (2018). Abbreviations and symbols used are based on the German notations for red list categories: * = least concern, 0 = extinct in the wild, 1 = critically endangered, 2 = endangered, 3 = vulnerable, G = lower risk, R = rare, V = near threatened, D = data deficient, nb = not evaluated. Not included = species, which were not included on the red lists. Total number of species is 515.

The plant species recorded in this thesis inhabit a broad spectrum of aquatic, semi-aquatic and terrestrial habitats characterised by different environmental conditions. This includes species of oligotrophic to eutrophic water bodies such as *Eleocharis acicularis* (L.) Roem. et Schult., species inhabiting muddy soils such as *Isolepis setacea* (L.) R. Br. and river corridor plants such as *Veronica maritima* L. (Burkart, 2001) recorded along the Elbe River. Further, species of dry to wet meadows and pastures such as *Dactylorhiza praetermissa* (Druce) Soó, dry grassland species such as *Dianthus deltoides* L. and species of different types of forests such as *Calamagrostis arundinacea* (L.) Roth. were identified in the studied wetlands. Ruderal species, which were commonly distributed in Hamburg such as *Urtica dioica* L. (Poppendieck et al., 2010) were found as well as ornamental trees and herbs such as *Aster amellus* L.. Some threatened species, such as *Calamagrostis arundinacea*, were identified outside of their known distribution range in Hamburg inhabiting new locations (Fig. 5.2).



Calamagrostis arundinacea
(L.) Roth

Dactylorhiza praetermissa
(Druce) Soó

Eleocharis acicularis
(L.) Roem. et Schult.

Veronica maritima
L.

Fig. 5.2 Raster based distribution of selected critically endangered vascular plant species, *Calamagrostis arundinacea* (L.) Roth, *Dactylorhiza praetermissa* (Druce) Soó, *Eleocharis acicularis* (L.) Roem. et Schult. and *Veronica maritima* L., in Hamburg identified in the surveys of this thesis. Stars show locations of species from the four surveys. Nomenclature of species follows Jäger (2017). Data from the floristic mapping of Hamburg from the botanical society of Hamburg (Botanischer Verein zu Hamburg e.V.). Reproduction with kind permission of Hans-Helmut Poppendieck (Poppendieck et al., 2010).

Most of the plant species recorded in the surveys are classified as hemicryptophytes (247 species) followed by therophytes (82 species; Fig. 5.3a). This is in accordance with other studies focusing on the occurrence and distribution of life forms of plants in wetlands, which found hemicryptophytes and therophytes as characteristic life forms in wetlands (Rundel & Sturmer, 1998; Deil, 2005). 21% of the Hemicryptophytes are listed as threatened plant species of Hamburg.

Therophytes are annual species with high seed production, which often are able to survive periods with unfavourable conditions as seeds in the soil seed bank. It is known that the urban environment favours therophytes with their short reproduction cycles (Wittig, 2002; Albrecht & Haider, 2013) as they are able to colonize densely built-up areas with less open soils and high frequencies of disturbance events (McIntyre et al., 1995; Godefroid & Koedam, 2007). This strategy is also favourable in highly dynamic wetlands where the hydrological conditions can be less predictable and can range from dried to flooded soils. In these habitats, a fast re-colonization of therophytes out of the soil seed bank can be an important part of vegetation resilience (Abernethy & Willby, 1999; Brock et al., 2003; Chapter 2). 11% of the species classified as therophytes are listed as threatened plant species of Hamburg, which can be classified into two main groups. Characteristic species of arable fields such as *Anchusa arvensis* (L.) M. Bieb. and *Cyanus segetum* Hill as well as species of pioneer communities on muddy soils such as *Bidens tripartitus* L. and *Peplis portula* L. were identified as threatened therophyte species. Periodically dry ecosystems of running and standing water bodies as well as non-extensively used arable fields with species-rich weed communities are listed as threatened ecosystems for Germany (Finck et al., 2017). Intensification of agriculture (Stoate et al., 2001) and usage of arable fields as building sites had led to decline of agricultural weeds in urban areas (Ewing, 2008) and further, has led to a general decline of arable fields with species-rich weed communities in urban areas. All threatened therophytes were found in stormwater ponds, which highlight the importance of stormwater ponds with periodically wet soils in combination with dryer shorelines as habitat for therophyte species in urban areas.

77 woody species, phanerophytes, nanophanerophytes and woody chamaephytes, were documented in the four surveys (Fig. 5.3a) with the threatened species of Hamburg *Populus nigra* L., *Ulmus leavis* Pall. and *Ulmus minor* Mill.. These species are typical for softwood (*Populus nigra*) and hardwood (*Ulmus* species) forests, which were listed as threatened ecosystems of Germany (Finck et al., 2017). The threatened woody species were found in the softwood forest of the nature reserve 'Heuckenlock' at the Elbe River, in the floodplain of the Dove Elbe River and in some stormwater ponds. Further, 17 woody species not reported as established species for Hamburg were identified in the four surveys, which can be classified into two main groups. Ornamental woody plants, such as *Eleutherococcus sieboldianus* (Mak.) Koidz. and *Physocarpus opulifolius* (L.) Maxim., as well as less considered *Salix* species in the past and recently identified *Salix* hybrids, such as *Salix* x *rubra* Huds. and *Salix eriocephala* Michx., were additionally found, most of them in stormwater ponds. Species used as street trees or ornamental plants in garden and parks can have built subspontaneous populations on the drier shorelines of stormwater ponds. In total, 27 *Salix* and *Populus* species were identified in the studied stormwater ponds. Stormwater ponds are suitable habitats for these species as the hydrological conditions can be similar to the conditions in softwood forest. Frequent flooding or periodically to permanent wet soils are favourable for these genera and further, they are characterised by a high vegetative regeneration capacity (Karrenberg et al., 2002). Both genera can regenerate in stormwater ponds under high management pressure as a consequence of desludging, cutting and mowing. This highlights the importance of stormwater ponds as secondary habitats for *Salix* and *Populus* species and further, for the genetic diversity of *Salix* species. *Salix*

species are known to have a pronounced ability for formation of hybrids (Karrenberg et al., 2002; Barker et al., 2003) and up to seven *Salix* species were identified in a single stormwater pond in the surveys of this thesis.

55 hydrophytes, 28 herbaceous chamaephytes and 48 geophytes were further documented in the four surveys (Fig. 5.3a). Hydrophytes were identified mostly in the stormwater ponds with 40 % of them being listed as threatened species for Hamburg. In urban areas, wetlands are often heavily altered by human actions resulting in habitats characterised by altered hydrology, water and soil chemistry, geomorphology and trophic levels in comparison to wetlands in non-urban areas (Ehrenfeld, 2000; Paul & Meyer, 2001). As a consequence, the distribution area of these wetland species decreased and finally, some species became extinct in urban areas (Korsch, 1999; Chen et al., 2014; He et al., 2014) resulting in the classification as threatened species in red lists (see the red lists of Berlin (Seitz et al., 2018) and Hamburg (Poppendieck et al., 2010). With *Pontedaria cordata* L., one hydrophyte species not reported as established species of Germany (Metzing et al., 2018) was found in one stormwater pond. The species has its origin in North, Middle and South America, but was introduced to Europe, where it is used as ornamental plant in park and garden ponds (Casper & Krausch, 1980; Jäger et al., 2016). *Pontedaria cordata* was identified in a stormwater pond located in an area with single detached houses and terraced houses with a high proportion of private gardens. It can be assumed that the individuals have their origin in one of these gardens.

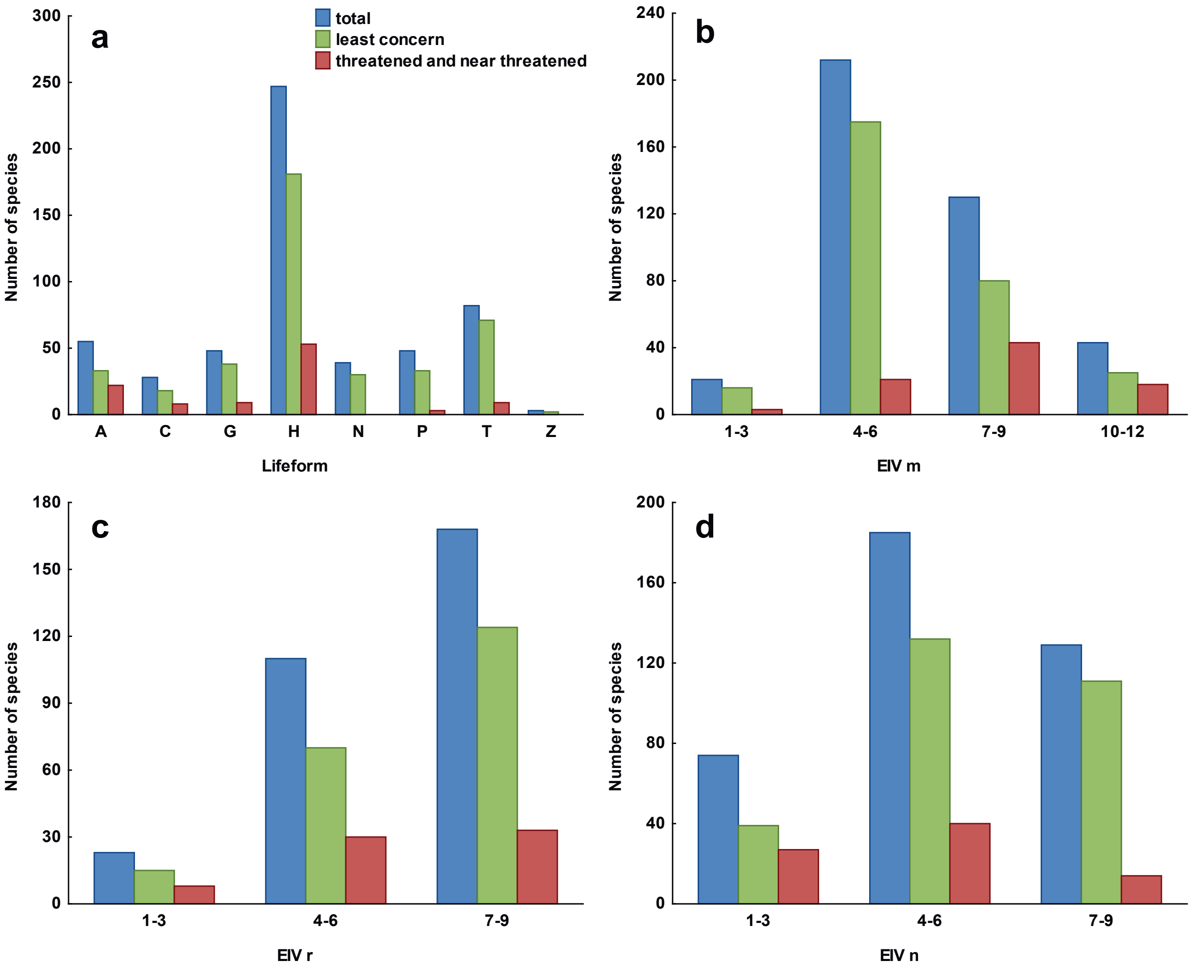


Fig. 5.3 Number of species of (a) lifeform categories, (b) Ellenberg indicator values for moisture (EIV m), (c) Ellenberg indicator values for reaction (EIV r) and (d) Ellenberg indicator values for nutrients (EIV n) grouped after the total number of species (blue), number of least concern species (green) and number of threatened and near threatened species documented in the surveys of this thesis. Lifeforms after Raunkiær: A = Hydrophyte, C = Herbaceous chamaephyte, G = Geophyte, H = Hemicryptophytes, N = Nanophanerophytes, P = Phanerophytes, T = Therophytes, Z = Woody chamaephyte. EIVs were categorised into groups of three classes (1-3, 4-6, 7-9 and 10-12). Lifeforms and EIVs were taken from Ellenberg et al. (1991).

The analysis of EIVs is a simple, reasonable method for gaining information about habitats plant species may inhabit with regard to light, temperature and climate conditions as well as hydrological, pH and nutrient conditions in the soil (Ellenberg et al., 1991). Even if EIVs do not give absolute information on required environmental conditions, EIVs allow conclusion to be drawn concerning environmental conditions of ecosystems and their plant species composition. In the following sections, the EIVs of the species documented in the four surveys were categorised into groups of three classes (1-3, 4-6, 7-9 and 10-12) for simplifying of the data.

Most of the plant species identified in the four surveys are characterised by EIVs for moisture between 4 and 6 (212 species) followed by species characterised by EIVs for moisture between 7 and 9 (130 species; Fig. 5.3b). Thus, the majority of plant species found inhabit habitats characterised by fresh to wet soil conditions. Considerably less species adapted to dry (EIV for moisture between 1 and 3; 21 species) and flooded (EIV for moisture between 10 and 12; 43 species) soil conditions were identified in the surveys. However, the proportion of threatened species of Hamburg is highest among species with EIVs for moisture between 10 and 12 (42%). In the studied stormwater ponds, species adapted to broad hydrological soil conditions were documented indicated by EIVs for moisture between 2 and 12. Stormwater ponds can be characterised by a mosaic of different habitats at a small scale, which is known to support a high number of different plant species (Holtmann et al., 2019). Stormwater ponds are designed for a high efficiency of water retention, which is mainly done by forming depressions into the landscapes. This results in hydrological gradients in stormwater ponds ranging from periodically wet or permanently flooded conditions at the bottom to dry soil conditions at the top of the shoreline (Box 1) resulting in the occurrence of dry grassland species such as *Sedum acre* L., as well as submerged and emerged macrophyte species such as *Ceratophyllum submersum* L. and *Lemna gibba* L.. The studied floodplain of the Dove Elbe River and the forests at the Elbe River and Dove Elbe River were characterised mainly by plant species adapted to fresh to wet soil conditions (see also Jensen et al., 2013). Species adapted to dry and flooded soils were mainly missing in these habitats. In more natural floodplains, a mosaic of different types of permanent and periodical water bodies such as cut-off channels, flood channels or ponds with their characteristic plant species compositions can be found (Scholz et al., 2005). In the floodplain of the Dove Elbe River, only few permanent and periodical water bodies still remain today, such as a cut-off channel of the Dove Elbe River in the area 'Kleiner Brook' in the nature reserve 'Die Reit'. Further, only terrestrial areas of the Dove Elbe River were investigated to compare vegetation changes due to tidal influence loss (Chapter 4). Areas, which are permanently flooded nowadays due to river training, were excluded from the study as vegetation changes in these areas cannot be explained by loss of tidal influence. As a consequence, only few species with high EIVs for moisture were identified in the floodplain of the Dove Elbe River. The same applies for the softwood forests along the Elbe River as permanent and periodical water bodies were not included in the study design. A high proportion of species is threatened and characterised by high EIVs for moisture (42 %, EIV for moisture between 10 and 12) and further, 14 % of species are threatened and characterised by low EIVs for moisture (EIV for moisture between 1 and 3). This pattern was already reported for the Flora of Germany, where the highest proportions of threatened species were found at the lowest and highest EIVs for moisture (Korneck et al., 1998). Reasons are degradation and pollution as well as drainage of wetlands leading to extinction of aquatic species and loss of wetlands in urban areas (Holland et al., 1995; Kozlowski & Bondallaz, 2013; McCauley et al., 2013; Mao et al., 2018). Threatened plant species with low EIVs for moisture were dry grassland species such as *Dianthus deltoids* L.

or *Hylotelephium maximum* (L.) Holub, which are known to be threatened due to habitat degradation and habitat fragmentation (Lauterbach et al., 2013), which can be an influencing factors also in urban areas.

168 of the plant species identified in the four surveys have EIVs for reaction between 4 and 6, while species characterised by lower (23 species) and higher reaction values (110 species) were identified in considerably lower numbers (Fig. 5.3c). The highest proportion of threatened species was found for species with EIVs for reaction between 1 and 3 (35%) such as *Polypodium vulgare* L. or *Galium saxatile* L.. Species adapted to acid soil conditions are known to be often threatened in Germany due to rare occurrences in urban areas (e.g. in Hamburg and Berlin (Germany); Korsch, 1999). Reasons for this are degradation and destruction of acid ecosystems, such as bogs, dry grasslands, heathlands and forests on acid, nutrient-poor soils (Korneck et al., 1998). For example, in Hamburg, intact bogs decreased in their extent from 48 km² in 1780 to 3 km² in 2008 as a consequence of land-use change. Further, 88 % of the species in Hamburg occurring in dry grasslands are threatened nowadays, while already 40 characteristic species of dry grasslands became extinct in Hamburg (Poppendieck et al., 2010).

Most of the plant species recorded in the four surveys are classified by EIVs for nutrients between 4 and 6 (185 species) and are thus adapted to moderate nutrient conditions in the soil (Fig. 5.3d). Further, 129 species with EIVs for nutrients between 7 and 9 were identified and even 74 species adapted to nutrient poor soils conditions (EIVs for nutrients between 1 and 3) were identified in the surveys. The latter were recorded in some study plots in the floodplain of the Dove Elbe River and in some stormwater ponds and were terrestrial, such as *Trifolium arvense* L. as well as aquatic, such as *Comarum palustre* L.. The high number of species of nutrient poor habitats is surprisingly as soils in urban areas are often characterised by high nutrient contents (Wittig, 1996), especially in floodplains used for agriculture and in stormwater ponds influenced by nutrient enriched runoff. Species adapted to nutrient poor soil conditions were also recorded in stormwater ponds in the city of Münster (Germany) with the speciality of the occurrence of orchids and carnivorous plants (*Dactylorhiza* species and *Utricularia australis* R. Br.; Holtmann et al., 2019). In the studied stormwater ponds in this thesis (Box 1), species adapted to a broad spectrum of soil nutrient conditions ranging from nutrient-poor to nutrient-rich conditions can occur. 70 % of the species characterised by EIVs for nutrients between 1 and 3 are listed as threatened species of Hamburg and the proportion of threatened species decreased further from EIVs for nutrients between 4 and 6 (30 %) to EIVs for nutrients between 7 and 9 (13 %). This pattern was already reported for the Flora of Germany (Korneck et al., 1998). The high proportion of threatened species characterised by high EIVs for nutrient identified in the surveys is not surprising. Human-induced nitrogen depositions are a main factor for habitat degradation of nutrient-poor ecosystems, which can lead to shifts in competitive relations and, as a consequence, to changes in species compositions of ecosystems (Vitousek et al., 1997; Carpenter et al., 1998). For Germany, nutrient depositions are one of the main factors for species decline, which were still a major threat in the last 10 years (Korneck et al., 1998).

Which environmental factors determine vegetation patterns in urban wetlands?

Local and landscape factors responsible for vegetation patterns in natural wetlands also influence vegetation communities in urban wetlands (Fig. 5.4). This includes the isolation of wetlands which can be measured by the distance of a wetland to other wetlands and further, the vegetation composition and land-use in the surrounding of a wetland. These landscape factors influence the input of water, nutrient and sediments into wetlands and additional, the local species pool and biotic interactions of a wetland. The vegetation of a wetland is further influenced by hydrology and further, physical settings of a wetland such as soil type. In this section, hydrology and the local species pool as well as land-use are discussed as factors determining vegetation patters of urban wetlands.

The main local factor for the development and functioning of wetlands is hydrology (Junk, 2002; Baldwin, 2011) leading to specific vegetation compositions resulting in macrophyte dominated, herbaceous or woody vegetation in wetlands. Duration and frequency of inundation as well as water depth and their fluctuations have been shown to be important factors determining plant species richness and composition in natural and man-made wetlands (Casanova & Brock, 2000; Koning, 2005; Alvarez-Cobelas et al., 2008; Tousignant et al., 2010; Svitok et al., 2011; Tsai et al., 2012). Hydrology was identified to be a major factor differentiating the total number of species and proportion of threatened species in urban stormwater ponds (Box 1). In detail, total number of species in the bottom of urban stormwater ponds was significantly higher in dry stormwater ponds, which were mainly characterized by herbaceous (meadow) vegetation in comparison to wet stormwater ponds dominated by aquatic conditions with occurrence of macrophyte species. The woody vegetation was documented only in the bottom of few urban stormwater ponds. Reason for this is the frequent mowing of vegetation, which is performed in dry stormwater ponds and prevents the establishment of woody vegetation. From a management perspective, woody vegetation is not desirable in stormwater ponds as it reduces the retention capacity. This is exemplified by the studied stormwater pond 'Farnhornstieg', which was reconstructed because of low retention capacity due to a high woody vegetation cover (see Chapter 2). Macrophyte species richness was found to be higher in shallow-water wetlands in comparison to deep-water wetlands (Tsai, et al., 2012; Svitok et al., 2016). This patterns was also identified in the studied wet stormwater ponds in this thesis (Box 1 and Chapter 2), even if water depth was not analysed as parameter in the surveys. Vegetation compositions of the forests along the Elbe River and Dove Elbe River were influenced by hydrological conditions with duration of flooding being an important factor (Box 2). This result was expected as flooding and its characteristics are the main environmental factors for the development and zonation of (tidal) floodplain vegetation (Blom & Voesenek, 1996; Gurnell, 1997).

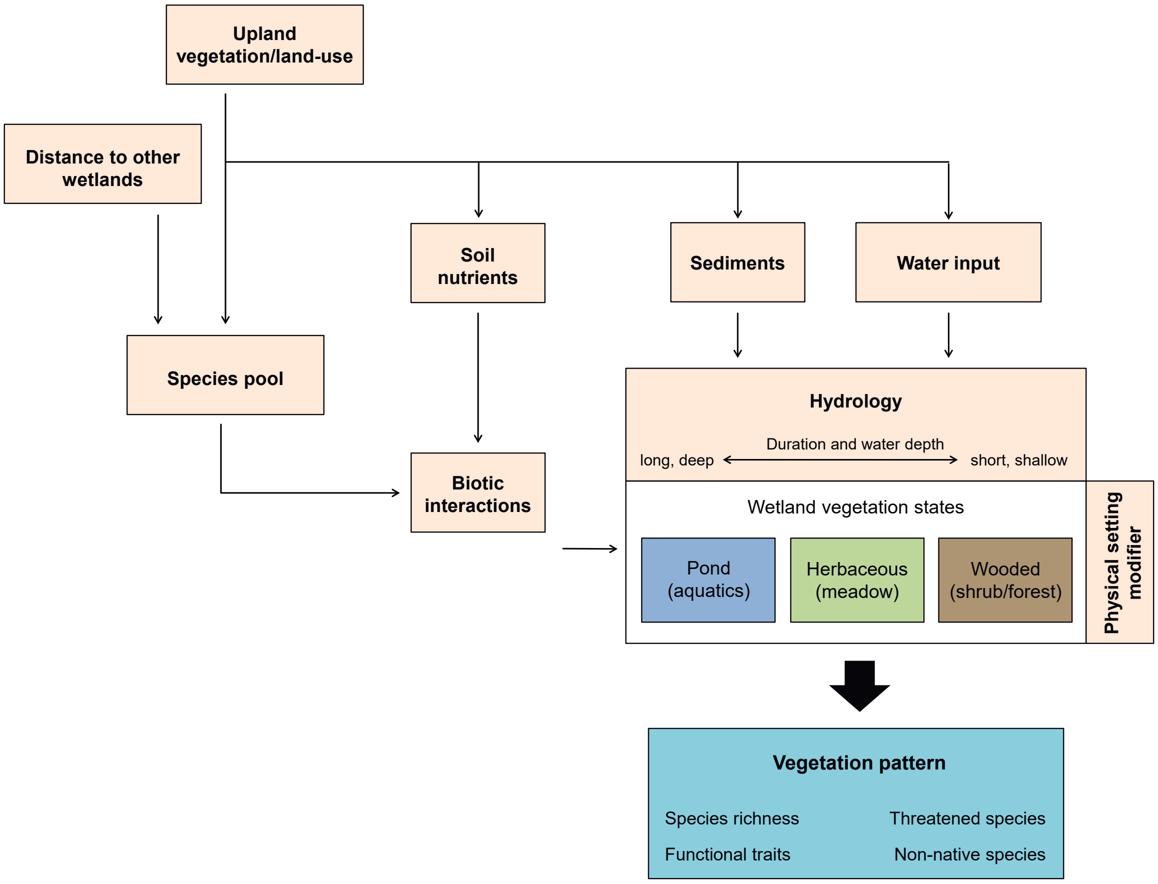


Fig. 5.4 Environmental factors influencing vegetation patterns in natural wetlands. Modified after United States Department of Agriculture (USDA, 2015).

Landscape factors such as land-use and vegetation composition in the surrounding of a wetland as well as the distance to other wetlands additionally influence the vegetation of wetlands (Lopez et al., 2002) by influencing the local species pool of a wetland (Cutway & Ehrenfeld, 2010) and the input of nutrients, sediments and water into a wetland (Allan et al., 1997; Lougheed et al., 2001; Houlahan & Findlay, 2004; Fig. 5.4). Surface runoff was shown to be different between functional zones in urban areas such as high-density residential zone or green space zone, which can be distinguished by the proportion of sealed surface (Li et al., 2018). The amount of water input into wetlands is therefore directly influenced by land-use in urban areas. Further, cover of impervious surface in the watershed of wetlands was found to be negatively correlated with species richness (Reinelt et al., 1998). This patterns was also found for some urban stormwater ponds (Box 1) which were associated with low impervious surface cover (<~5%) in the surrounding and a higher species richness in the bottom and shoreline in comparison to stormwater ponds with a higher impervious surface cover in the surrounding.

The vegetation composition of wetlands is highly influenced by the local species pool. Plant propagule input via hydrochory and to a lesser extent anemochory are the main dispersal process in wetlands (Vogt et al., 2004; Neff & Baldwin, 2005; Vogt et al., 2007; Moggridge et al., 2009), but other dispersal pathways can also be important. The large amounts of migrating birds in spring and fall are known to be effective dispersal agents in wetlands, although each individual is carrying only few propagules in its coat (Mueller & van der Valk, 2002). The local soil seed bank of a wetland is additionally build by seed input of the current vegetation as well as the former vegetation of a wetland. As a consequence, species not present in the current vegetation can be part of the soil seed bank (Jensen, 1998), which needs to be considered when evaluating endangering of species (Poschlod, 1993). Differences in the species composition of the current vegetation and the soil seed bank were recorded for the stormwater pond 'Farnhornstieg' (Chapter 2) as well. Further, plant species not identified in the analysis of the seed bank in 2015 were identified in the current vegetation in the year 2016 in parts of the stormwater pond, which were not sampled. For example, numerous plants of *Isolepis setacea* (L.) R. Br. were identified in the stormwater pond after reconstruction, which promoted the germination of the species. *Isolepis setacea* is classified as endangered species of Hamburg and it is known that the species can survive unfavourable conditions as seeds in the soil seed bank of ponds. When the conditions in the pond change such as drying of the pond, mass appearance of the species can occur (Poppendieck et al., 2010). For *Isolepis setacea*, the mass appearance of the species in the soil seed bank of ponds in Hamburg should be considered in the evaluation of the species as threatened species.

What processes drive vegetation change in stormwater ponds and urban floodplains?

In this section, the effects of an increasing urbanisation on vegetation changes in stormwater ponds and urban floodplains as well as the effects of specific management actions in stormwater ponds and urban floodplains are discussed. Furthermore, vegetation changes induced by management actions for achieving specific targets in wetlands protected by law are discussed.

Wetland vegetation communities are highly dynamic and can change between years and within one year due to altered environmental conditions (see Fig. 5.4). Therefore, the relative abundance of species can change and the total number of species can increase or decrease (Casanova & Brock, 2000; Baldwin, 2011). An increasing urbanisation can alter the vegetation composition of urban wetlands (Magee et al., 1999; White & Greer, 2006). Increasing urbanisation and increasing soil sealing directly lead to stronger destruction of (micro-)habitats potentially available for plant colonization. Higher nutrient, pollutant and sediment inputs into urban wetlands, because of an increased run-off and land-use change in the watershed of wetlands, may occur. Land-use change in the watershed of wetlands can lead to a further lowering of groundwater table (Qi & Luo, 2006; Klimkowska et al., 2010). Increased introduction of non-native species caused by an increasing urbanisation can alter vegetation composition of urban wetlands (Klotz & Kühn, 2010). In the four surveys, 58 non-native plant species of Germany and 30 additional species not reported as established species for Germany were found (Metzing et al., 2018). This high proportion of species not native to Germany (17,1 %) can be explained by an increasing introduction of species in Hamburg due to usage as ornamental plants in ponds, gardens and parks or unintentionally introduction as a consequence of transportation of goods (e.g. *Fagopyrum esculentum* Moench by birdseeds (Hanson & Mason, 1985) and *Senecio inaquidens* Dc. by wool imports (Ernst, 1998)). Urbanisation is further known to lead to a homogenization of species compositions in cities (McKinney, 2006; Trentanovi et al., 2013). Most of the plant species documented in the four surveys are commonly distributed in Hamburg and further, the 20 most frequently species of Hamburg (Poppendieck et al., 2010) were also documented in the surveys with high occurrences. These 20 species are additionally very frequent in Central Europe (Seregin, 2010).

Stormwater ponds are highly dynamic ecosystems with strongly fluctuating environmental conditions (Mayer et al., 1996; Woodcock et al., 2010; van Meter et al., 2011; Herrmann, 2012; Al-Rubaei et al., 2016). In addition, stormwater ponds are directly influenced by human actions: The vegetation of stormwater ponds is frequently mown to prevent the establishment of woody plants. Furthermore, large woody plants are cut and permanently flooded areas of stormwater ponds are desludged, both in irregular intervals. These management actions are performed for preserving the retention function so that high amounts of runoff can be temporarily stored in stormwater ponds after heavy rainfall or snowmelt. Frequent mowing of the bottom and desludging of permanently flooded areas of stormwater ponds prevent the natural vegetation succession in these areas by reduction of the soil nutrient conditions as well as disturbance and destruction of the established vegetation. As a consequence, competitive relations are altered. Consequently, the establishment of dominant stands of few species, such as reed species, can be prevented (Fogli et al., 2014), while species with vegetative reproduction and fast growing species with short reproduction cycles can be favoured, such as species from the Bidentetea tripartitae class (Stępień et al., 2015). This applies for macrophyte species with a pronounced ability of vegetative regeneration and for therophyte species of pioneer communities on muddy soils found in the studied stormwater ponds (Box 1). Further, mowing and desludging can lead to bare soils, which will be again available for plant colonization (Holtmann et al., 2019; Strickman & Mitchell, 2018). In stormwater ponds, germination out of the soil seed bank (Chapter 2) and input of propagules via dispersal processes can lead to changes in the species composition and abundance of single species. As mentioned earlier, because of these management actions, woody plants are rarely identified in the bottom of dry stormwater ponds characterised by grass-dominated vegetation. In contrast, woody species adapted to wet or permanently flooded soil conditions, such as *Alnus glutinosa* or different *Salix* species, can be found in the bottom of wet stormwater ponds. In some cities (as e.g. Hamburg), sowing and planting of species are applied in case of reconstruction of existing as well as construction of new stormwater ponds. By doing this, soil erosion during filling of the stormwater pond should be prevented in unvegetated stormwater ponds in Hamburg (Schneider, personal communication). In stormwater ponds with an existing seed bank, revegetation can take place rapidly when the conditions are suitable, making sowing an unnecessary management action (Chapter 2).

The pastures and meadows analysed in the floodplain of the Dove Elbe River in 2016 were (except for the former reed plots) characterised by a lower number of species and more homogenous vegetation composition in comparison to the situation in the 1950s (Chapter 4). As discussed, changes in the hydrological conditions as a consequence of embanking of the Dove Elbe River and loss of tidal influence as well as agricultural usage of the floodplain are probably the reasons for these changes. Pastures and meadows in 2016 were partly dominated by high productive grass species, such as *Festuca rubra* L. or *Lolium perenne* L., which are commonly used in seed mixtures (Prach et al., 2014; Gentili et al., 2015). Seeding of some of the studied pastures and meadows along the Dove Elbe River in the past can therefore be assumed.

Due to large wetland losses in the past and degradation of the remaining wetlands (Junk et al., 2013), nowadays, wetlands are often protected by law, such as in the United States of America, where the Clean Water Act has the goal to 'restore and maintain the chemical, physical, and biological integrity of the Nation's waters' (33 U.S.C §§ 1251 *et seq.*). In Hamburg, all 34 nature reserves include different types of wetlands (FHH, 2017) and are therefore specially protected. Wetlands protected by law as part of nature reserves or other categories of protected areas may underlie a regular management for gaining specific protection targets. Both tidal softwood forests analysed in this thesis (Box 2) are part of nature reserves: the softwood forest Heuckenlock is part of the nature reserve 'Heuckenlock' and the softwood forest Spadenland is part of the nature reserve 'Auenlandschaft Obere Tideelbe'. Management actions in both nature reserves include hydraulic management actions for development and conservation of tidally influenced habitats as well as monitoring of non-native species such as *Fallopia japonica* (Houtt.) Ronse Decr. and *Impatiens glandulifera* Royle, and if necessary, removal of their stands (FHH, 1999; Gerversmann & Winter, 2018). Hydraulic management actions were especially implemented in the nature reserve 'Auenlandschaft Obere Tideelbe' as in this area the softwood forest developed from an intensively used agricultural field after dike relocation in the year 2001. Creeks and higher terrains for initialising the development of softwood forest were created during restoration (Brandt, 2005). Evidence for an applied removal of non-native species in the recent past in both softwood forests were not found. However, *Impatiens glandulifera* was documented in all study plots of the Heuckenlock with high coverages.

In Germany, wet grasslands in large cities are often to a large proportion protected by law (Fischer et al., 2013). This also applies for some study plots in the floodplain of the Dove Elbe River (Chapter 3). Four plots are located in the nature reserve 'Die Reit' and for this area, sowing of seeds as a management action for development of a species-rich wet grassland is documented (Jaschke, 2006). Seed addition by sowing or hay transfer are often conducted as restoration actions in grass-dominated ecosystems and can be successful when the basic conditions are suitable (Hölzel & Otte, 2003; Rasran et al., 2007). However, the vegetation of the four study plots was especially species-poor with up to 13 species on 20 m² in comparison to the known high number of species of wet meadows with a mean of up to 51 species on 25 m² (*Molinia caerulea* meadows; Tischew & Hölzel, 2019). It therefore can be assumed that in this part of the nature conservation site, seed addition was not performed yet, or was not successful as indicated by a low number of species. Seed banks and their characteristics are an important factor for vegetation development in wetlands. Natural vegetation succession and vegetation resilience are highly dependent on the local seed bank of wetlands (Brock et al., 2003; Capon & Brock, 2006). Further, ecosystem services of wetlands are highly dependent on physiological belowground processes, which are additionally influenced by the wetland vegetation composition. The relationship of physiological belowground processes and vegetation composition are poorly understood.

5.2 Planar optodes as an analysing tool for rhizosphere processes

How can processes responsible for the delivery potential of ecosystem services be studied in rhizospheres of urban wetlands?

The transition area between plant roots and soil is of great importance for biogeochemical cycling (Hinsinger et al., 2009) and biotic interactions in ecosystems (Moore et al., 2003) and therefore, rhizospheres are important components of ecosystems. As hotspots of plant-soil-microbe interactions (Pathan et al. 2020) and microbial activity and diversity (Kuzyakov & Razavi, 2019), rhizosphere processes have to be considered when studying soil-plant related ecosystem services. In comparison to visible aboveground interactions of plants and animals or plants and soil, little is known about the hidden rhizosphere and its processes and interactions (Hinsinger et al., 2009). Knowledge of rhizosphere processes can help to understand mechanisms of plant invasions in wetlands facilitated by oxygen release into the rhizosphere (Roley et al., 2018). Further, trees are highly dependent on rhizosphere processes, which is of great importance in urban areas, where the soil for root colonization is limited but where trees are an important component of climate regulation (Day et al. 2010).

Planar optode technology has been successfully applied in analysing oxygen and pH dynamics in the rhizosphere of marine and freshwater plants in the past, such as *Spartina anglica* C. E. Hubb. (Koop-Jakobsen & Wenzhöfer, 2015; Koop-Jakobsen et al., 2017), *Vallisneria spiralis* L. (Han et al., 2016; Marzocchi et al.,

2019) and *Zostera marina* L. (Frederiksen & Glud, 2006; Jovanovic et al., 2015). Oxygen dynamics in the rhizosphere of one of the most important food plants (Seck et al., 2012), *Oryza sativa* L., was also analysed with planar optodes (Larsen et al., 2015). Further, pH dynamics in the food plants *Cicer arietinum* L. and *Triticum durum* Desf. were analysed with planar optodes (Blossfeld et al., 2013). In wetland rhizospheres, various biogeochemical processes are affected by the release of oxygen from roots of macrophytes and hydrophytes (Brix, 1997; Gutknecht et al., 2006). The study on O_2 and CO_2 dynamics in the rhizosphere of *Lobelia dortmanna* L. (Chapter 4) showed, that planar optodes are also suitable for analysing sensitive macrophyte species as *Lobelia dortmanna* is highly sensitive to changes in organic sediment contents (Møller & Sand-Jensen, 2011) or chemical conditions in the water column (Pulido et al., 2012).

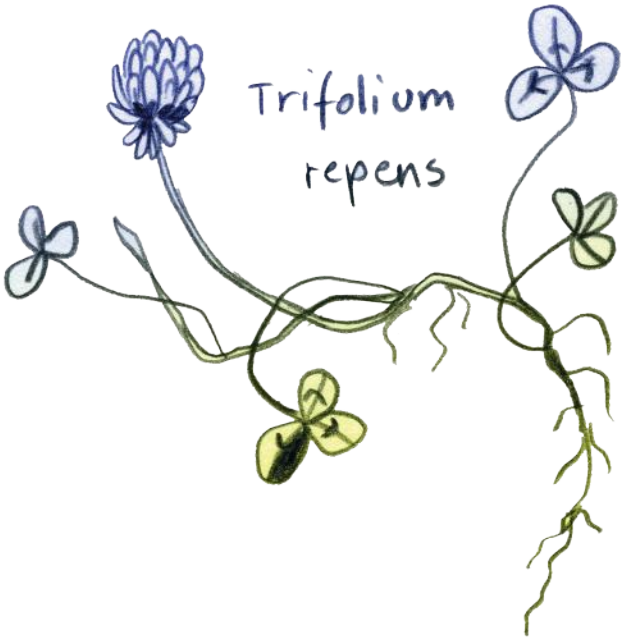
Rhizosphere related ecosystem services are dependent on the release of root exudates by plants, which includes the release of oxygen and rhizodeposits (release of carbon compounds) into the rhizosphere (Jones et al., 2004; Bais et al., 2006). In Wetlands, rhizosphere processes and interactions influence dynamics of nutrient and pollutants by altering the geochemical cycles for example of carbon, nitrogen, phosphate or iron (Le Mer & Roger, 2001; Smolders et al., 2002; Weiss et al., 2004; Racchetti et al., 2017). For example, rhizosphere oxygenation by isoetides is a key mechanism for preservation the oligotrophic conditions in their habitats. Oxygen in the rhizosphere promotes decomposition of organic compounds, the formation of insoluble iron-3-phosphates and nitrification of ammonia to nitrate (Pedersen et al., 1995; Christensen, 1997; Risgaard-Petersen & Jensen, 1997; Smolders et al. 2002; Vila-Costa et al., 2016). Remediation of polluted soils and sediments is an important ecosystem services influenced by rhizosphere processes, which is important especially in urban wetlands as they can contain high levels of pollutants in the sediment and water (Adams et al., 2000; Waltham et al., 2014). For example, high levels of pollutants were found in the sediment of stormwater ponds in Hamburg and after potentially desludging, additional handling of these sediments might be necessary before utilisation of the sediments (Kalinski, unpublished data). Vegetated retention ponds, which were often planted with reed species, were constructed in urban areas for nutrient and heavy metal retention from input of roads and highways (Tromp et al., 2012; Ladislas et al., 2015).

5.3 Future research perspectives

Urban stormwater ponds can be highly diverse ecosystems with regard to plant species composition and especially threatened species (Box 1). It can be questioned, how plant biodiversity of urban stormwater ponds can be arranged with their function for flood protection as both ecosystem services usually exclude each other. Future research should identify biotic and abiotic factors of the studied stormwater ponds, which can be associated with a high proportion of threatened species and the occurrence of specific threatened species. Therefore, additional data for each stormwater pond should be collected including information on the soil hydrology, flooding duration and frequency, nutrient and pollutant conditions in the soil as well as management actions such as mowing or desludging. Knowledge on the occurrence of threatened species in the stormwater ponds in relation to the abiotic and biotic characteristics of the stormwater pond can help to develop stormwater ponds with a high function for flood protection by simultaneously promoting biodiversity of threatened plant species. The importance of the soil seed bank for natural recolonization of urban stormwater ponds (Chapter 2) can be reinforced by additional surveys on vegetation development after conducted management actions, such as desludging or mowing with heavy machines.

The proceeding of the 9th deepening of the tidal Elbe River may have large effects on tidal-influenced ecosystems with their flora and fauna along the Elbe River. It can be assumed that the hydrological conditions in the softwood floodplain forest along the Elbe River will changed dramatically, so that a long-term monitoring of the vegetation in the study areas Heuckenlock and Spadenland should be established (Box 2). Especially, the locations of the rare and threatened species *Oenanthe conioides* LANGE and *Deschampsia wibeliana* (SOND.) PARL. should be assessed precisely. Restoration of the tidal influence at the Dove Elbe River is discussed nowadays for reduction of sediment depositions in the tidal Elbe River (Donner & Brandt, 2019). In the case of a reconnection and reintroduction of tidal-influence at the Dove Elbe River, the study plots assessed in 2016 should be surveyed again (Chapter 3). A long-term monitoring of the study plots can show the vegetation development under more natural environmental conditions. Additional study plots in vegetation types not represented in the reassessed study should be established and analysed for vegetation development. This would include the two not-tidal-influenced forests at the Dove Elbe River (Box 2).

Planar optodes are a suitable ex-situ method for analysing dynamics of O_2 and CO_2 in the rhizosphere of plants (Chapter 4). Future research should focus on the implementation of planar optodes in (more) natural environments. This would include the analysis of whole plant communities and the integrated analysis of the composition of the microorganism community. So far, urban stormwater ponds were not studied concerning their overall contribution of ecosystem services. Interdisciplinary projects should analyse ecosystem services of urban stormwater ponds from a geomorphological, socioecological, ecological and economical perspective.


Trifolium
repens


Ökologie

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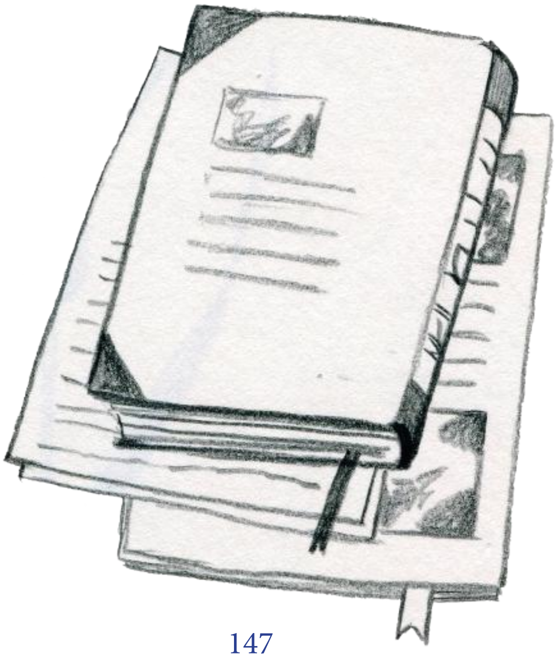
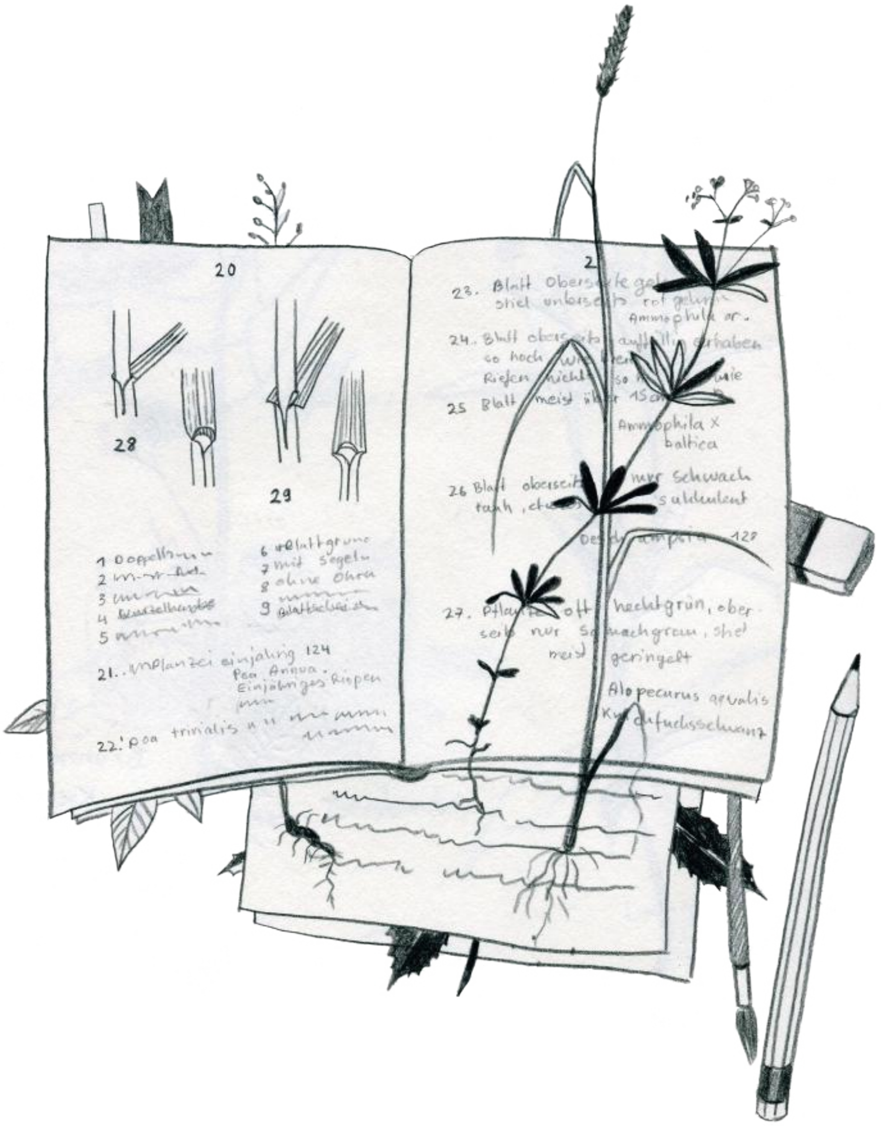



20
28
29
1 Doppelh
4 Wurzelhaube
6 Blattgrüne
7 mit Segeln
8 ohne Ohren
9 Blattscheide
21. Pflanze einjährig 124
Poa Annua.
Einjähriges Rispen
22. Poa trivialis
2
23. Blatt Oberseite gel
stiel unterseits rot gelb
Ammophila ar.
24. Blatt oberseits auffällig erhaben
so hoch wie
Riefen nicht so wie
25 Blatt meist über 15
Ammophila x
baltica
26 Blatt oberseits nur schwach
sukkulent
128
27. Pflanze oft hechtgrün, ober-
seits nur schwachgrün, stiel
meist geringelt
Alopecurus aqualis
Kurzfuchsschwanz

SUMMARY

Wetlands are known to be hotspots of biodiversity and provide various ecosystems services. Further, plant biodiversity may have large effects on ecosystem services related to rhizosphere processes. Wetlands have been destroyed worldwide and further, the remaining wetlands are often heavily altered in case of their geomorphological and chemical conditions. For urban areas, wetlands have been valued as multifunctional ecosystems as they are used for recreational purposes, are important components for flood protection and in the drainage system, provide habitats for plants and animals and act as climate regulating systems. The objective of this thesis was to analyse vegetation patterns and process of vascular plants of stormwater ponds, floodplains and different types of forests in the city of Hamburg (Germany). Further, a method for studying rhizosphere processes in wetlands using planar optodes was evaluated. This thesis is structured in five chapters and two boxes including a general introduction to the topic of urban wetlands (Chapter 1), five manuscripts presenting detailed results of studies on vegetation patterns and processes of urban wetlands (Chapter 2 to 4 and Box 1 and 2) and a general discussion linking the results of the single manuscripts and giving future research perspectives (Chapter 5).

Chapter 2 focuses on the vegetation development of an urban stormwater pond in Hamburg as a consequence of reconstruction to improve the retention capacity. The aim of the study was to test if the soil seed bank of the stormwater pond has the potential for a natural recolonization of the bare soil after reconstruction and to analyse which plant species profit from colonization from the seed bank and from sowing. High numbers of seeds of *Juncus* and *Epilobium* species were found in the soil seed bank in the year before the reconstruction and further, only few plant species used in seed mixtures during the reconstruction were found in the current vegetation in the years after reconstruction. The results indicate that a natural re-colonization of bare soils can take place and thus, sowing and planting of species as a management action to prevent soil erosion is not necessary.

Box 1 gives preliminary results of a large study on plant biodiversity of urban stormwater ponds in Hamburg. The aim of the study was to analyse differences in plant biodiversity between wet and dry stormwater ponds, which are characterised by different hydrological conditions. In 80 stormwater ponds, a total of 503 species and a high proportion of threatened species of Hamburg were documented and further, these species inhabiting a wide range of dry to wet and flooded habitats. Number of species and proportion of threatened species differed between the bottom of wet stormwater ponds and the bottom and shoreline of dry stormwater ponds

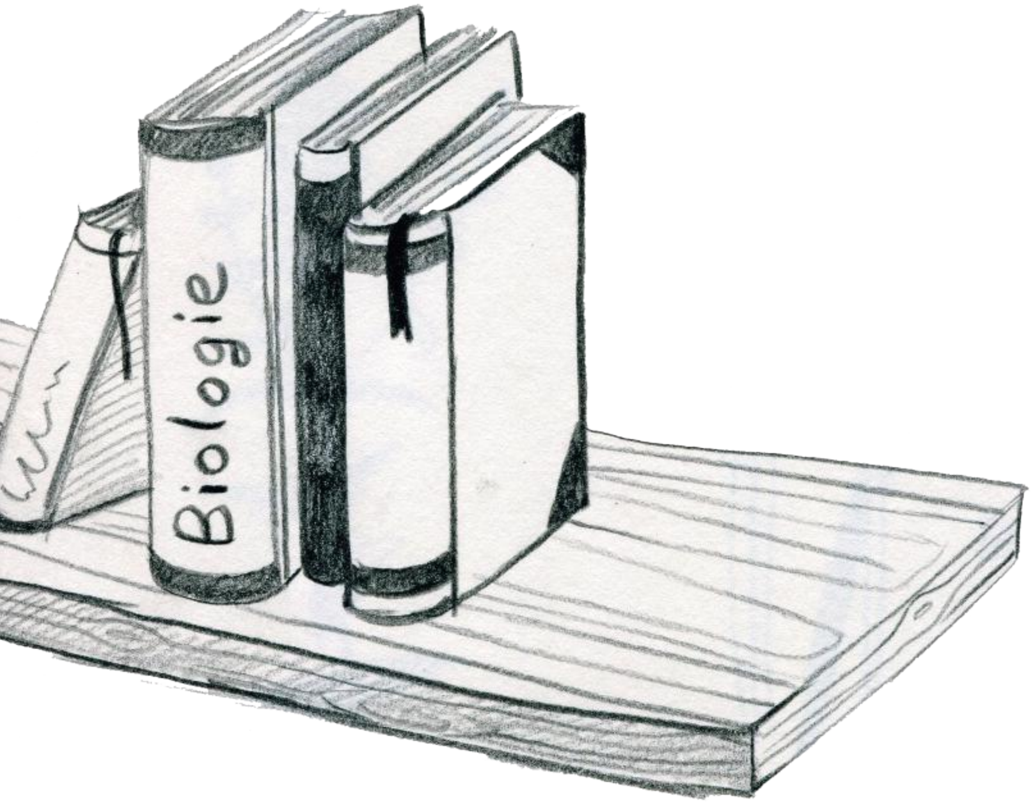
as well as the shoreline of wet stormwater ponds. The result indicate the importance of stormwater ponds in urban areas as habitat for plants by containing 32.5% of the species of the local flora of Hamburg.

Chapter 3 presents results of a study on vegetation changes in the floodplain of the Dove Elbe River in Hamburg 65 years after the tidal influence was lost due to the installation of a sluice. The aim of the study was to determine to which extent the vegetation types, plant biodiversity, species composition and environmental conditions changed in the floodplain between 1951 and 2016. As a consequence of loss of tidal influence, wet pioneer vegetation types and some threatened plant species were not identified in 2016 anymore. Additional, species richness and weighted mean Ellenberg indicator values for moisture per plot decreased. The results reinforce the restoration of the tidal dynamics at the Dove Elbe River, which can restore characteristic tidal-influenced habitats with their characteristic species composition.

Box 2 gives results of a study on the effect of tidal influence loss on the vegetation of softwood forests along the tidal Elbe River and Dove Elbe River in Hamburg. The aim of the study was to analyse differences in the number of species and species composition of tidal-influenced softwood forests and non-tidal forests and further, to identify environmental parameters determining these differences. Tidal-influenced softwood forests had a higher number of species and a higher number of herbaceous species per plot in comparison to non-tidal forest and further, nearly all threatened plant species and river corridor plants were found only in the studied tidal-influenced softwood forests. It can be assumed that these differences in the vegetation may be due to different hydrological conditions of the tidal-influenced softwood forests at the tidal Elbe River and non-tidal forests at the Dove Elbe River.

Chapter 4 shows findings of a study on the effects of light on the dynamics of O_2 and CO_2 in the rhizosphere of the freshwater isoetid plant *Lobelia dortmanna* L. by using recently developed planar optode technology in combination with O_2 and newly developed CO_2 foils. The aim of the study was to analyse the spatial and temporal variation of O_2 and CO_2 in the rhizosphere and the impact of light exposure of the leaves. A tight coupling between O_2 and CO_2 dynamics in the rhizosphere of the species was found by identification of an oxic root zone (in lightness and darkness) and a CO_2 enhanced zone (in lightness and darkness) as well as a CO_2 uptake zone (in lightness) in the rhizosphere of the plant. The study reveals that planar optodes are a suitable method for studying rhizosphere dynamics of O_2 and CO_2 also for sensitive plants such as *Lobelia dortmanna*.

In conclusion, this thesis highlights the importance of different types of wetlands in urban areas for vascular plants. Even though urban wetlands are highly altered in case of their geomorphological and chemical conditions, they can contain a wide range of different types of plant species including highly threatened plant species. Planar optodes are a suitable method for analysing rhizosphere processes and as biodiversity may have large effects on rhizosphere processes, the method should be applied when analysing ecosystem services related to rhizosphere processes.


Biologie

ZUSAMMENFASSUNG

Feuchtegebiete sind als 'hotspots' der biologischen Vielfalt bekannt und stellen darüber hinaus vielfältige Ökosystemleistungen bereit, wobei die Biodiversität einen großen Einfluss auf rhizosphärenabhängige Ökosystemleistungen haben kann. Feuchtgebiete wurden weltweit zerstört und des Weiteren sind die verbliebenen Feuchtgebiete stark in ihrer Geomorphologie und ihrem chemischen Zustand verändert. In urbanen Gebieten sind Feuchtgebiete multifunktionale Ökosysteme, welche zur Naherholung genutzt werden, die ein wichtiger Bestandteil des Hochwasserschutzes und des Entwässerungssystems sind, die als Habitat für Pflanzen und Tiere dienen und das Stadtklima regulieren. Das Ziel der vorliegenden Arbeit war die Analyse von Vegetationsmustern und Vegetationsprozessen von Gefäßpflanzen von Rückhaltebecken, Auen und verschiedenen Typen von Wäldern in Hamburg (Deutschland). Weiterhin wurde eine Methode zur Untersuchung von Rhizosphärenprozessen in Feuchtgebieten mit Hilfe von planaren Optoden bewertet. Die vorliegende Arbeit ist in fünf Kapitel und zwei Boxen gegliedert: eine allgemeine Einleitung zur Thematik von urbanen Feuchtgebieten (Kapitel 1), fünf Manuskripte über die detaillierten Ergebnisse der Untersuchungen zu Vegetationsmustern und Vegetationsprozessen in urbanen Feuchtgebieten (Kapitel 2 bis 4 und Box 1 und 2) und eine allgemeine Diskussion der Ergebnisse sowie daraus folgenden Forschungsthemen für die Zukunft (Kapitel 5).

In Kapitel 2 werden die Vegetationsänderungen eines Rückhaltebeckens in Hamburg als Folge einer Baumaßnahme zur Verbesserung der Retentionsfunktion dargestellt. Das Ziel der Studie war es zu untersuchen, ob die Samenbank des Rückhaltebeckens das Potential für eine natürliche Wiederbesiedelung der vegetationsfreien Böden nach der Baumaßnahme hat. Weiterhin wurde untersucht, welche Pflanzenarten aus der Samenbank und als Bestandteil von Ansaaten, welche im Rahmen der Baumaßnahme durchgeführt wurden, von der Baumaßnahme profitieren. Hohe Anzahlen von Samen von *Juncus*- und *Epilobium*-Arten wurden in der Samenbank im Jahr vor der Umgestaltung des Rückhaltebeckens gefunden und weiterhin wurden nur wenige Arte, die in Samenmischungen verwendet wurden, in der stehenden Vegetation in den Jahren nach der Baumaßnahme gefunden. Die Ergebnisse deuten darauf hin, dass eine natürliche Wiederbesiedlung von vegetationsfreien Böden stattfinden kann und dass Ansaaten und Anpflanzungen nicht notwendig sind, um Bodenerosion zu verhindern.

Box 1 zeigt vorläufige Ergebnisse einer großen Untersuchung zur Biodiversität von Gefäßpflanzen von urbanen Rückhaltebecken in Hamburg. Das Ziel der Studie war es zu untersuchen, ob sich die pflanzliche Biodiversität

zwischen Dauerstaubecken und Trockenbecken unterscheidet. Beide Typen von Rückhaltebecken sind durch unterschiedliche hydrologische Bedingungen charakterisiert, wodurch sich die Biodiversität zwischen beiden Typen unterscheiden könnte. Insgesamt wurden in 80 Rückhaltebecken 503 Pflanzenarten und ein hoher Anteil von gefährdeten Arten für Hamburg dokumentiert. Die dokumentierten Arten besiedeln ein breites Spektrum von trockenen zu nassen und überstauten Ökosystemen. Die Anzahl Arten und der Anteil gefährdeter Arten unterschied sich zwischen der Sohle von Dauerstaubecken und der Sohle und Böschung von Trockenbecken sowie der Böschung von Dauerstaubecken. Die Ergebnisse verdeutlichen die Bedeutung von Rückhaltebecken als Habitat in urbanen Gebieten, da in den untersuchten Becken 32,5 % der Pflanzenarten der lokalen Flora Hamburgs gefunden wurden.

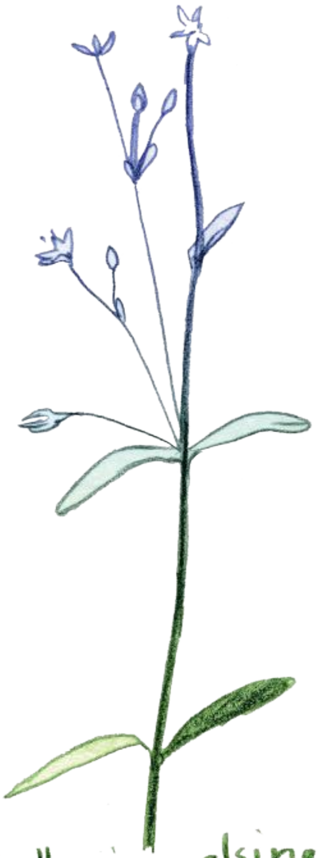
Kapitel 3 zeigt Ergebnisse einer Untersuchung zu Vegetationsänderungen in der Aue der Dove Elbe in Hamburg 65 Jahre nach der Inbetriebnahme einer Schleuse und daraus folgend dem Verlust des Tideeinflusses. Das Ziel der Studie war es zu untersuchen, inwiefern sich die Vegetationstypen, pflanzliche Biodiversität, Artenzusammensetzung und Umweltbedingungen in der Aue zwischen 1951 und 2016 verändert haben. Pioniervegetation von feuchten Habitaten und einige gefährdete Pflanzenarten wurden im Jahr 2016 nicht mehr identifiziert. Zusätzlich nahm der Artenreichtum und der gewichtete, mittlere Ellenberg Zeigerwert für Feuchte je Untersuchungsfläche ab. Die Ergebnisse bekräftigen Bemühungen zur Wiederherstellung der Tidedynamik in der Dove Elbe, wodurch sich charakteristische Tidehabitate und deren Artenzusammensetzung wiedereinstellen können.

Box 2 zeigt Ergebnisse einer Untersuchung zum Effekt des Tideverlustes auf die Vegetation von Weichholzauenwäldern an der Tideelbe und Dove Elbe in Hamburg. Das Ziel der Studie war es zu untersuchen, inwiefern sich die Artenanzahl und Artenzusammensetzung zwischen tidebeeinflussten Weichholzauenwäldern und nicht tidebeeinflussten Wäldern unterscheidet und welche Umweltbedingungen für diese Unterschiede verantwortlich sein können. Tidebeeinflusste Weichholzauenwälder zeichneten sich durch eine höhere Anzahl Arten und höhere Anzahl krautiger Arten je Untersuchungsfläche im Vergleich zu nicht tidebeeinflussten Wäldern aus. Weiterhin wurden nahezu alle gefährdeten Arten und Stromtalarten in den untersuchten tidebeeinflussten Weichholzauenwäldern gefunden. Es kann davon ausgegangen werden, dass die Unterschiede in der Vegetation auf unterschiedliche hydrologische Bedingungen der tidebeeinflussten Weichholzauenwälder an der Tideelbe und nicht tidebeeinflussten Wälder an der Dove Elbe beruhen.

Kapitel 4 stellt Ergebnisse einer Studie zu Effekten von Licht auf O_2 und CO_2 Dynamiken in der Rhizosphäre der Süßwasserart *Lobelia dortmanna* L. unter Verwendung von planaren Optoden in Kombination mit O_2-Folien und neu entwickelten CO_2-Folien dar. Das Ziel der Studie war es die räumlichen und zeitlichen Dynamiken von O_2 und CO_2 in der Rhizosphäre zu untersuchen und weiterhin den Effekt von Lichtexposition der Blätter zu untersuchen. Eine starke Verknüpfung von O_2 und CO_2 Dynamiken wurden in der Rhizosphäre der Pflanzenart festgestellt, wobei eine Sauerstoffanreicherung in der Rhizosphäre unter Lichtexposition und in

Dunkelheit nachgewiesen wurde (‚oxic root zone'), während eine CO_2 Anreicherung unter Lichtexposition und Dunkelheit (‚CO_2 enhanced zone') und eine CO_2 Abnahme unter Lichtexposition (‚CO_2 uptake zone') in der Rhizosphäre festgestellt wurde. Die Studie zeigt, das planare Optoden eine geeignete Methode zur Analyse von O_2 und CO_2 Dynamiken in der Rhizosphäre sind und auch für empfindliche Pflanzenarten, wie *Lobelia dortmanna*, geeignet sind.

Die vorliegende Arbeit hebt die Bedeutung von verschiedenen Feuchtgebieten für Gefäßpflanzen in urbanen Gebieten hervor. Auch wenn urbane Feuchtgebiete stark verändert in Bezug auf ihre Geomorphologie und chemischen Zustand sind, können sie ein breites Spektrum an Arten inklusive stark gefährdeten Arten aufweisen. Planare Optoden sind eine geeignete Methode, um Rhizosphärenprozesse zu untersuchen und da Biodiversität einen großen Einfluss auf Rhizosphärenprozesse haben könnte, sollten planare Optoden angewandt werden, wenn rhizosphärenabhängige Ökosystemleistungen untersucht werden.



stellaria alsine

AUTHOR CONTRIBUTIONS

Chapter 1	N. Lenzewski wrote this chapter. Fig. 1.4 shows work in progress of a planar optode study on O_2 and CO_2 dynamics in the rhizosphere of *Littorella uniflora* by K. Koop-Jakobsen and N. Lenzewski
Chapter 2	N. Lenzewski designed and conducted the study, prepared and analysed the data (including statistics) and wrote the initial manuscript.
Box 1	N. Lenzewski designed the study, conducted the field work, prepared and analysed the data (including statistics) and wrote the initial manuscript. P. Drews, J. A. Klann and N. Lissowsky provided assistance during field work in the framework of their bachelor theses.
Chapter 3	N. Lenzewski designed the study, prepared and analysed the data (including statistics) equally with M. Asdonk. Further, N. Lenzewski commented and edited the manuscript together with K. Ludewig and K. Jensen.
Box 2	N. Lenzewski designed the study, prepared and analysed the data (including statistics) and wrote the initial manuscript.
Chapter 4	N. Lenzewski designed and conducted the study, prepared and analysed the data (including statistics) and wrote the manuscript equally together with P. Mueller and K. Koop-Jakobsen. Further, N. Lenzewski provided plant, water and sediment material.
Chapter 5	N. Lenzewski wrote this chapter. Fig. 5.1 and Fig. 5.3 show summarised vegetation data of the four surveys conducted during this thesis.

Information on published chapters

Chapter 3

Diversity decrease due to loss of tidal influence at the Dove Elbe River between 1951 and 2016

Published in:	Flora, 258, 151438
Publisher:	Elsevier
Year:	2019
DOI:	10.1016/j.flora.2019.151438
Authors:	Mareike Asdonk*, Nikola Lenzewski*, Kai Jensen, Kristin Ludewig

*These authors contributed equally to this work

N. Lenzewski designed the study, prepared and analysed the data (including statistics) equally with M. Asdonk. Further, N. Lenzewski commented and edited the manuscript together with K. Ludewig and K. Jensen.

Signature
Prof. Dr. Kai Jensen (first advisor)

Information on published chapters

Chapter 4

Dynamics of oxygen and carbon dioxide in rhizospheres of *Lobelia dortmanna* – a planar optode study of belowground gas exchange between plants and sediment

Published in: New Phytologist, 218, 131-141

Publisher: WILEY

Year: 2018

DOI: 10.1111/nph.14973

Authors: Nikola Lenzewski*, Peter Mueller*, Robert Johannes Meier, Gregor Liebsch, Kai Jensen, Ketil Koop-Jakobsen

*These authors contributed equally to this work

N. Lenzewski designed and conducted the study, prepared and analysed the data (including statistics) and wrote the manuscript equally together with P. Mueller and K. Koop-Jakobsen. Further, N. Lenzewski provided plant, water and sediment material.

Signature
Prof. Dr. Kai Jensen (first advisor)

Information on published chapters

Box 2

Effects of loss of tidal influence on the herbaceous vegetation of tidal-influenced softwood forests in Hamburg

Original article:
Auswirkungen des Tide-Verlustes auf die Krautschichtvegetation von tidebeeinflussten Weichholz-Auenwäldern in Hamburg

Published in: Berichte des Botanischen Vereins zu Hamburg, 31, 27-42

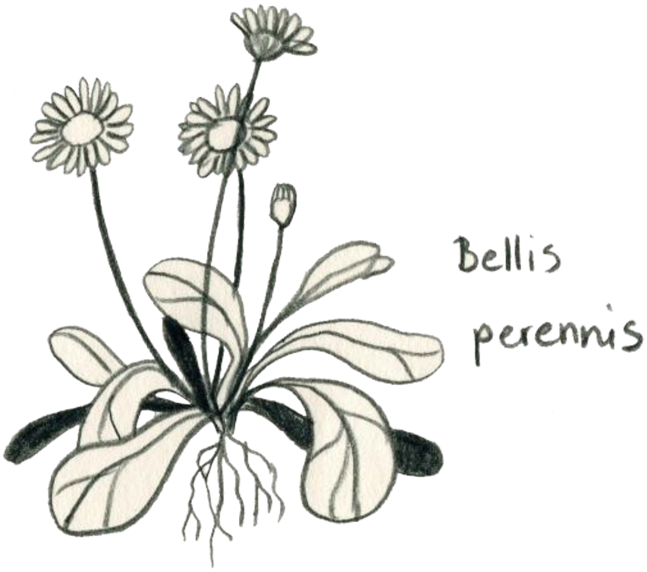
Publisher: Botanischer Verein zu Hamburg e.V.

Year: 2019

Authors: Nikola Lenzewski, Luca A. Schebesch, Kai Jensen, Kristin Ludewig

N. Lenzewski designed the study, prepared and analysed the data (including statistics) and wrote the initial manuscript.

Signature
Prof. Dr. Kai Jensen (first advisor)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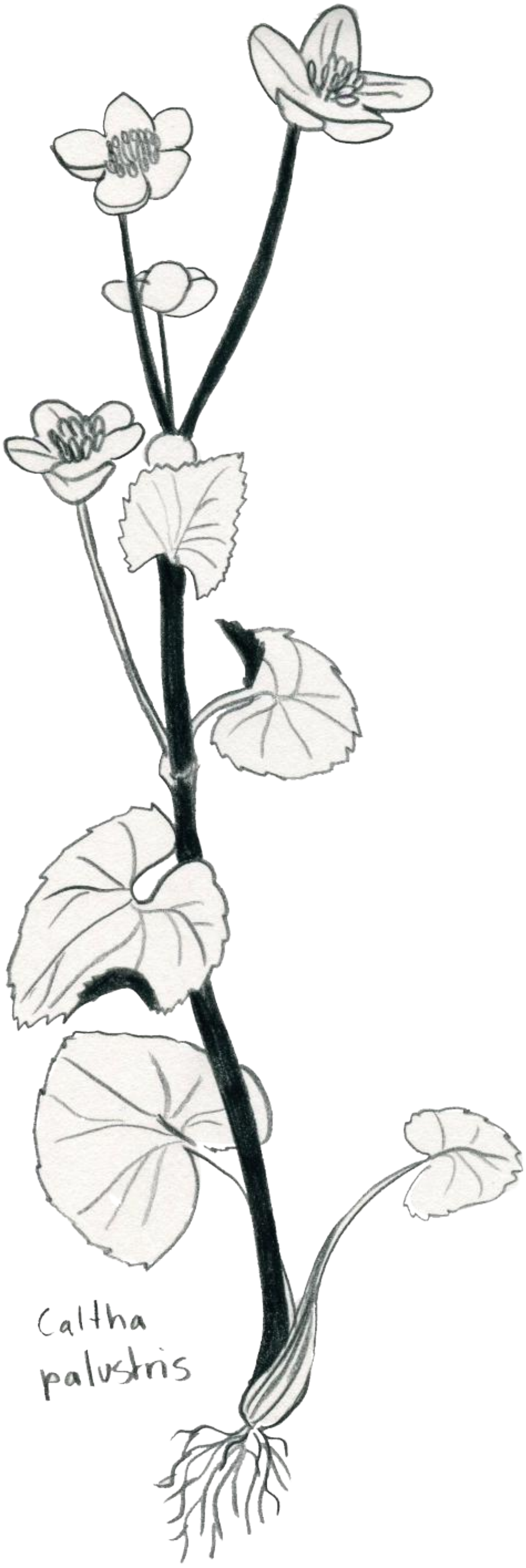

Caltha palustris

CO-AUTHOR AFFILIATIONS

Mareike Asdonk
Applied Plant Ecology, Institute of Plant Science and Microbiology, Universität Hamburg, Ohnhorststraße 18, 22609 Hamburg, Germany

Kai Jensen
Applied Plant Ecology, Institute of Plant Science and Microbiology, Universität Hamburg, Ohnhorststraße 18, 22609 Hamburg, Germany

Ketil Koop-Jakobsen
MARUM – Center for Marine Environmental Sciences, University of Bremen, Loebener Straße 8, 28359 Bremen, Germany

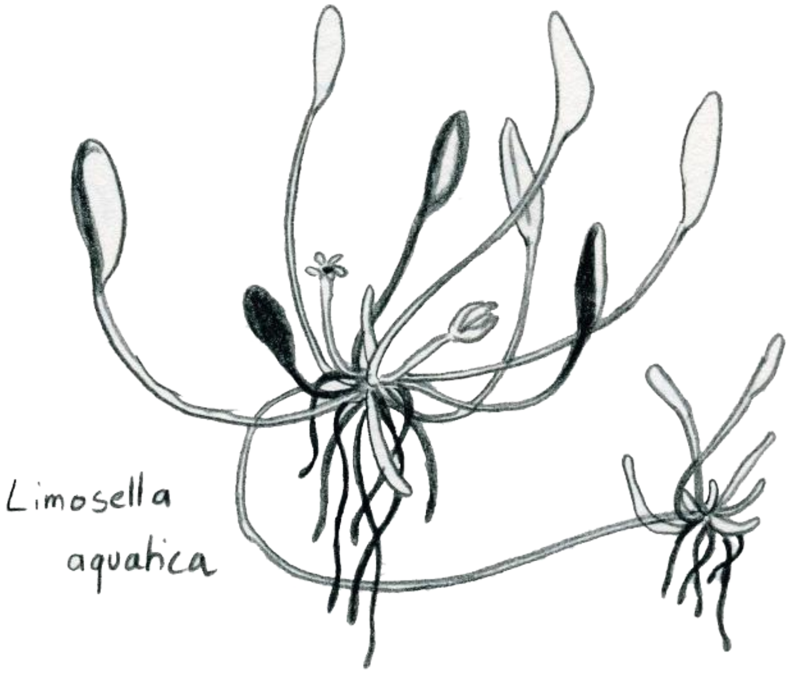
Gregor Liebsch
PreSens, Precision Sensing GmbH, Am BioPark 11, 93053 Regensburg, Germany

Kristin Ludewig
Applied Plant Ecology, Institute of Plant Science and Microbiology, Universität Hamburg, Ohnhorststraße 18, 22609 Hamburg, Germany

Robert Johannes Meier
PreSens, Precision Sensing GmbH, Am BioPark 11, 93053 Regensburg, Germany

Peter Mueller
Biogeochemistry Lab, Smithsonian Environmental Research Center, 647 Contees Wharf Road, Edgwater MD 21037, United States

Luca A. Schebesch
Applied Plant Ecology, Institute of Plant Science and Microbiology, Universität Hamburg, Ohnhorststraße 18, 22609 Hamburg, Germany


Limosella
aquatica

DANKSAGUNG

Freunde der Sonne,

nach fast 5 Jahren, 2 Drittmittelprojekten, 14 betreuten Abschlussarbeiten und zahlreichen kleineren Projekten ist es nun geschafft: meine Dissertation ist fertig! An dieser Stelle möchte ich allen danken, die zum Gelingen meiner Promotion auf verschiedenste Weisen beigetragen haben (Achtung! Der Text ist etwas länger!).

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nemorosa

Eidesstattliche Versicherung

Hiermit erkläre ich an Eides statt, dass ich die vorliegende Dissertationsschrift selbst verfasst und keine anderen als die angegebenen Quellen und Hilfsmittel benutzt habe.

Ort, Datum

Nikola Lenzewski


Crepis
paludosa
Ballota nigra
veron
Beccab
Limosella
aquatica
A
ton
Caltha
palustris
Vicia parviflora
Draba ve


ica
ounga
Bellis
perennis
Trifolium
repens
Persicaria
amphibia
rctium
nentosum
Stellaria
alsine
rna
Lathyrus
pratensis