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von

Kai Frederik Behn

aus

Zeven, Deutschland

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Referent: Prof. Dr. Mathias Becker

Korreferentin: Prof. Dr. Anja Linstädter

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“Typology”-team in October 2013 in Ewaso Narok swamp, Kenya. This was my first trip to East Africa.

II Abstract

Wetlands in East Africa provide various ecosystem services. They are important habitats for biodiversity, regulate and purify water, store carbon, and provide wild plants for food and medicinal use. At the same time, they are suitable sites for agricultural production, with usually fertile soils and secure water availability for most parts of the year. As demand for cropland and food increases, driven for instance by demographic growth, economic development, climate risks, and upland field degradation, wetlands in East Africa are increasingly in the center of land use conflicts. The BMBF funded GlobE-project "**Wetlands in East Africa: Reconciling future food production with environmental protection"** aimed at researching the status quo of East African wetlands, evaluating management options for their agricultural uses, formulating policy recommendations, and building capacity among scientists in the region and beyond. The presented work was conducted within this framework, focusing on three key aspects of wetland vegetation, with specific methods and addressing the following overarching research questions.

(1) Integrity: What is the ecological state of representative East African wetlands and how can it be assessed? For this chapter, the WET-Health approach was applied with a multidisciplinary team at wetland sites in Kenya, Rwanda, Tanzania, and Uganda. In this assessment scheme, the ecological state of wetlands was estimated on scales from 0 (natural conditions) to 10 (complete loss of wetland properties) in four modules ("Vegetation", "Hydrology", "Geomorphology", and "Water quality"). Additionally, at each study site, structural attributes of wetland vegetation and dominant vascular plant species were recorded. A "vegetation-based index of biotic integrity" (VIBI) was calibrated via multiple linear models to predict the WET-Health scores with vegetation attributes. In all wetlands, the WET-Health vegetation module showed the strongest effect with intensive agricultural use. While the prediction of WET-Health scores with vegetation attributes yielded satisfactory results for the vegetation module, the approach did not provide acceptable results for the remaining WET-Health modules. Nevertheless, the VIBI appears to be a useful strategy to rapidly assess ecological states of East African wetlands.

(2) Diversity: How diverse is East African wetland vegetation? Here, we conducted detailed, plot-based vegetation surveys (relevés), comprising a record of all vascular plant species and their abundances. The survey was conducted along a hydrological gradient in the Namulonge inland valley wetland in Uganda, and in the Kilombero floodplain around the town of Ifakara in Tanzania. It included agricultural fields, fallow plots, and areas of undisturbed vegetation. Based on these relevés, vegetation units were identified with the Cocktail Classification approach. For each unit, an unequivocal definition was created and compiled in an expert system. In a second step, the expert

system was applied to a database, comprising relevés from other East African wetlands (SWEAdataveg) and revised. Thirteen vegetation units were matched either with existing syntaxa or were newly described.

(3) Regeneration dynamics: How does East African wetland vegetation recover after disturbance? Lastly, the recovery of vegetation after an induced disturbance was monitored over a period of two years at the Namulonge inland valley and the Ifakara floodplain study sites, with regular samplings of aboveground biomass and species composition at different hydrological positions in each of the wetlands. While uninterrupted favorable growing conditions led to a fast recovery with gradual changes in species dominances in the inland valley wetland, a natural reference state was not reached within two years. Yet, fast changes in species composition and occurrences of useful plants highlight the importance of early succession stages for biodiversity and ecosystem services. In the floodplain, both dry season drought and wet season submergence events restricted the recovery potential of vegetation.

Overall, this work provides adapted tools to assess the integrity and diversity of East African wetland vegetation. Results support land use management recommendations to reconcile biodiversity conservation with agricultural wetland uses.

III Zusammenfassung

Feuchtgebiete in Ostafrika liefern zahlreiche Ökosystemdienstleistungen. Sie sind wichtige Habitate für Biodiversität, regulieren und reinigen Wasser, speichern Kohlenstoff, und in ihnen werden Wildpflanzen für Ernährung und medizinische Zwecke gesammelt. Gleichzeitig eignen sie sich aufgrund fruchtbarer Böden und sicherer Wasserverfügbarkeit besonders für landwirtschaftliche Nutzung. Mit steigendem Bedarf an Ackerflächen zur Erzeugung von Nahrungsmitteln, unter anderem aufgrund von Bevölkerungswachstum, wirtschaftlicher Entwicklung, des Klimawandels und der Degradierung traditioneller Ackerflächen, stehen ostafrikanische Feuchtgebiete zunehmend im Zentrum von Landnutzungskonflikten. Das vom Bundesministerium für Bildung und Forschung (BMBF) geförderte GlobE-Projekt „Feuchtgebiete in Ostafrika: Vereinbarkeit von Naturschutz und künftiger Nahrungsmittelproduktion“ hatte die Ziele, den Status quo ostafrikanischer Feuchtgebiete zu erforschen, Managementoptionen für landwirtschaftliche Nutzungen zu evaluieren, Empfehlungen für die Politik zu formulieren sowie Kapazitäten in der regionalen Wissenschaft aufzubauen. Die vorliegende Arbeit wurde im Rahmen dieses Projektes mit Schwerpunkt auf Feuchtgebietsvegetation durchgeführt und behandelt folgende Aspekte und übergreifende Forschungsfragen:

(1) **Integrität: In welchem ökologischen Zustand sind repräsentative ostafrikanische Feuchtgebiete und wie kann das bewertet werden?** Für dieses Kapitel wurde das WET-Health Bewertungsverfahren mit einem multidisziplinären Team in Feuchtgebieten in Kenia, Ruanda, Tansania und Uganda angewendet. Bei diesem Verfahren wird der ökologische Zustand eines Feuchtgebiets im Vergleich zu einer natürlichen Referenzfläche auf einer Skala von 0 (natürliche Bedingungen) bis 10 (kompletter Verlust von Feuchtgebietseigenschaften) in vier Teilbereichen, sogenannten Modulen (Vegetation, Hydrologie, Geomorphologie und Wasserqualität), abgeschätzt. Zusätzlich wurden in jedem Feuchtgebiet strukturelle Eigenschaften der Vegetation sowie dominierende Pflanzenarten aufgenommen. Ein „Vegetationsbasierter Index der Biotischen Integrität (VIBI)“ wurde mit multiplen linearen Modellen kalibriert, um die mit WET-Health geschätzten Zustandswerte mit den Vegetationseigenschaften zu ermitteln. In allen Feuchtgebieten zeigte das Vegetationsmodul von WET-Health die höchsten Werte als Folge intensiver landwirtschaftlicher Nutzung. Die Ermittlung von WET-Health Werten mit dem VIBI lieferte reproduzierbare Ergebnisse für das Vegetationsmodul, während dieser Ansatz sich als nicht zufriedenstellend für die anderen Module erwies. Grundsätzlich ist die Ermittlung des VIBI ein vielversprechender Ansatz zur schnellen Bewertung des ökologischen Zustands ostafrikanischer Feuchtgebiete.

(2) **Diversität: Wie unterschiedlich ist ostafrikanische Feuchtgebietsvegetation?** Für dieses Kapitel wurden detaillierte Vegetationsaufnahmen (relevés) in Untersuchungsquadraten mit Aufnahme aller

Gefäßpflanzen und deren Deckungsgraden durchgeführt. Die Untersuchungen wurden entlang eines hydrologischen Gradienten im Namulonge Tal, Uganda, und im Überschwemmungsgebiet des Kilombero-Flusses bei Ifakara, Tanzania, durchgeführt. Sie enthielten landwirtschaftlich genutzte Flächen, Brachen und naturnahe Vegetation. Basierend auf diesen Vegetationsaufnahmen wurden mit dem Ansatz der „Cocktail Classification" Vegetationseinheiten identifiziert. Für jede Einheit wurde eine eindeutige Definition (Vorkommen bestimmter Arten bzw. Artenkombinationen) erstellt und diese wurden in einem „expert system" zur automatischen Klassifizierung von Plots zusammengeführt. In einem folgenden Schritt wurde dieses „expert system" auf eine Datenbank mit weiteren Vegetationsaufnahmen aus Ostafrika angewendet und mit den zusätzlichen Daten verbessert. Dreizehn Vegetationseinheiten wurden entweder mit bereits beschriebenen Pflanzengesellschaften (Assoziationen) zusammengeführt oder als neue Assoziation beschrieben.

(3) **Regenerationsdynamiken: Wie erholt sich ostafrikanische Feuchtgebietsvegetation nach einer Störung?** Für den letzten Teil der Arbeit wurde die Vegetationsentwicklung nach einer herbeigeführten Störung über einen Zeitraum von zwei Jahren im Namulonge Tal, Uganda, und dem Kilombero Überschwemmungsgebiet bei Ifakara, Tanzania, mit regelmäßigen Erfassungen von oberirdischer Biomasse und Artenzusammensetzung entlang von hydrologischen Gradienten beobachtet. Während dauerhaft günstige Bedingungen im Namulonge Tal zu einer schnellen Erholung mit graduellen Veränderungen dominierender Arten führten, wurde der Zustand ungestörter Vergleichsflächen innerhalb von zwei Jahren nicht erreicht. Dennoch unterstreichen schnelle Änderungen der Artenzusammensetzung und des Vorkommens nutzbarer Pflanzenarten die Bedeutung früher Sukzessionsstadien für Biodiversität und die Bereitstellung von Ökosystemdienstleistungen. Im Kilombero-Überschwemmungsgebiet wurde die Regenerationsfähigkeit der Vegetation sowohl durch die strenge Trockenzeit als auch durch Überschwemmungen in der Regenzeit eingeschränkt.

Insgesamt stellt die vorliegende Arbeit Werkzeuge für die Bewertung der Integrität und Diversität für ostafrikanische Feuchtgebietsvegetation bereit, die an die entsprechenden Bedingungen angepasst sind. Die gesammelten Daten und Forschungsergebnisse können Empfehlungen für Landnutzungsplanung unterstützen, um so zu einer Vereinbarkeit von Naturschutz und Nahrungsmittelproduktion in ostafrikanischen Feuchtgebieten beizutragen.

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VII List of Abbreviations

DCA	Detrended Correspondence Analysis
DRC	Democratic Republic of the Congo
ESS	Ecosystem services
IBI	Index of Biotic Integrity
MRPP	Multiple Response Permutation Procedure.
RMSPE	Root mean square prediction error
VIBI	Vegetation-based Index of Biotic Integrity

VIII Nomenclature

CJBG & SANBI (2012) for vascular plant species, unless stated otherwise. For plant associations, see table 15, page 67 in chapter 6.2.

1 General introduction

View on Kilobero floodplain, Tanzania (top left), natural papyrus marsh in Uganda (top right), grazed fringe of the Ewaso Narok swamp with *Acacia xanthophloea* (Fever tree) in Kenya (bottom left), and the fringe of a papyrus marsh in Rwanda (bottom right).

1.1 Problem statement

"**Vegetation** is an assemblage of plant species and the ground cover they provide" (Burrows, 1990). As autotrophic organisms, plants (and some microorganisms such as algae and cyanobacteria) can convert inorganic carbon into organic matter (primary production), which is the base of the food web in almost all ecosystems (Pace et al., 2021). Consequently, plants and vegetation (including cultivated crops) are crucial for human life. Vegetation is extremely versatile, and can be described and classified using various easily recognizable properties: composition, structure, physiognomy, spatial patterns, and temporal patterns (Burrows, 1990). Vegetation and its properties are determined by various biotic and abiotic factors, whose individual importance largely depends on the scale of interest. On a global scale, the type of vegetation is determined by climatic zones on the earth (**zonal vegetation;** e.g., tropical rainforest, savannas, temperate forests, or tundra), provided that the vegetation has not been completely transformed by human activity. On a smaller (regional and sub-reional) scale, the determinants for vegetation types include meso- and microclimate, geomorphology, soil chemistry, hydrological regimes, and natural or anthropogenic disturbance regimes (Frey & Lösch, 2014). With knowledge on the determinants and drivers of vegetation changes, the actual vegetation at a site can therefore comprise a valuable indicator on e.g., the habitat, the state of the ecosystem, the degree of hemeroby, its ability to provide ecosystem services, as well as the potential of the site for agricultural land uses. Studying and understanding vegetation is thus crucial for basic science of the environment, but also for applied sciences, implementing and regulating land management, land use planning, and conservation (Dengler et al., 2008).

Wetlands are ecosystems, in which the temporary or permanent availablility of water is the defining factor. They 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" (Ramsar Convention Secretariat, 2016). Besides this rather broad definition, numerous others exist (Amler et al., 2015), referring more specifically to spatial or temporal scales, or to potential and actual uses (Becker et al., 2018). While the total extent of wetlands varies according to the wetland definition used, Lehner & Döll (2004) estimate the global wetland area to around 9.2 million km², which corresponds almost the size of the United States of America. Wetlands are highly productive ecosystems and they are important sites for biodiversity; yet they have been degraded and destroyed in many parts of the world, particularly during the 20th century (Munishi & Jewitt, 2019). In 1971, in the Iranian city of Ramsar, a multilateral treaty was signed, drawing attention to wetlands of global importance and promoting their conservation (Ramsar Convention Secretariat, 2016). Initially focusing on water birds, the Ramsar Convention addresses today all the various functions that wetlands have or services that they provide.

These include (1) the supply of water and land for the production of products such as food, feed, medicinal plants, or building materials (provisioning services); (2) the regulation of water flows and flood mitigation, wastewater treatment, air quality, carbon sequestration, and pollination (regulating services); (3) the provision of shelter and habitat for plant and animal biodiversity (supporting services); and (4) the provision of non-material goods, green spaces for recreation and tourism, or social/spiritual uses (cultural services).

Vegetation may best inform on wetland attributes and the potential to support a wide range of these ecosystem functions and services (indicator value). This includes the role of wetlands for carbon sequestration that has recently received increasing attention (e.g., Mitsch et al., 2013). The vegetation in wetlands is generally considered **azonal**, meaning that extreme conditions created by the prevailing water regime overlay effects of the macroclimate (Mueller-Dombois & Ellenberg, 1974). However, Sieben (2019) argues that only few types of wetland vegetation (e. g., reedbeds dominated by *Phragmites australis*) are truly azonal, meaning that they have a distribution across continental borders. As for vegetation in general, besides climate and water, numerous other factors, including land use, determine wetland vegetation.

As in many parts of the world, wetlands are widespread in East Africa. Thus, in Kenya, Tanzania, Uganda, and Rwanda, they cover an area of 0.17 million km², which is about half the size of Germany. The most important types of East African wetlands are inland valleys and floodplains, representing around 80% of the total wetland area (Leemhuis et al., 2016). Inland valley wetlands commonly occur in the headwaters of rivers on volcanic base rock or gneiss. They are typically concave valleys with a central stream, and upland slopes limit them. The water sources in inland valleys comprise, besides the *in-situ* rainfall, the runoff from the adjacent slopes, springs, subsurface interflow, and the overflow of the river in the riparian zone around the stream. Soils in inland valleys are seasonally or permanently waterlogged or submerged. Typical soil types include Histosols and Gleysols (Sakané et al., 2011). Floodplains on the other hand are flat wetlands in plains or broad valleys on alluvial sediments. Typical soil types comprise Fluvisols and Vertisols. Floodplains occur both as lowland and highland wetland ecosystems, but they are always located downstream of inland valleys. Apart from on-site rainfall and runoff (in the fringe parts of the floodplain), water originates mainly from the river as seasonal overbank flooding (Leemhuis et al., 2016; Sakané et al., 2011). Flooding depths and duration depend on the landscape physionomy and on rainfall in the catchment area. Hence, the seasonality of rainfall in the catchment results in the seasonality in the discharge of the river. In addition, the biophysical attributes of the catchment, particularly land cover and land use, shape the hydrological regime of the floodplain (Näschen et al., 2018). Within the floodplain, flooding and soil moisture are also determined by the position, i.e., the distance from the river (Gabiri, et al., 2018a).

Table 1: Conceptual scheme of a typical intensification pathway in East African wetlands in the past decades (simplified and modified after Sakane et al., 2014).

	Before 1970	1970s	1982	1994	Since 2007
Wetland accessibility	limited	limited	limited	improved	Full
Main Uses	gathering; water collection	grazing	rainfed crops	rainfed crops and grazing	irrigated rice, vegetables
Drainage	no	no	partial	partial	complete
Irrigation	no	no	no	no	Yes
Crops per year	0	0-1	1	1-2	2-3
Input use	none	none	none	organic amendments	agro-chemicals

Wetlands have been used for gathering of wild plants, water collection, grazing, and crop cultivation. However, limited access to the wetter zones (Sakane et al., 2014) and health risks associated with wetlands (Anthonj et al., 2017) have restricted wetland uses. Since the 1970s, agricultural use has been expanding rapidly in East Africa (Näschen et al., 2019) as wetlands are general suitable for agriculture. These changes have been driven by - among others - population growth, upland field degradation, climate change and variability, the desire to improve food security, and international trade opportunities (e.g., Beuel et al., 2016; Dixon & Wood, 2003; Sakane et al., 2014). Besides an expansion of the cultivated land area, the intensity of land use may increase, and is associated with the introduction of agrochemical inputs, hydrological modifications by drainage and irrigation, and reduction of fallow periods (Table 1; Sakane et al., 2014). While agricultural expansion and intensification have altered or even degraded many wetlands in East Africa, other wetlands in the region remain at least in parts unused and are in a close to natural state (Behn et al., 2018; Beuel et al., 2016).

Wetland protection policies differ between East African countries, and even within countries, depending on wetland type. They further often conflict with and are modified by changing political priorities. For instance, Tanzania is lacking a comprehensive wetland legislation, and policies are often weakly enforced. The Kilombero valley in Tanzania is declared a Ramsar-site, yet agricultural expansion – including in form of the nationally and internationally supported SAGCOT-Initiative – are conflicting with the aims of the Ramsar Convention (Materu et al., 2018; Mombo et al., 2011). Uganda is generally committed to conserve the country´s wetlands, but there are several obstacles for effective wetland protection and management, such as conflicting political interests between ministries, insufficient funding of protection agencies, and lack of involvement of local communities (Barakagira & De Wit, 2019).

These political aspects cannot be addressed by vegetation ecology, and neither policy frameworks nor agricultural practices are the scope of this work. However, the understanding of wetland vegetation in East Africa is of paramount importance for conservation and for sustainable management and use of wetlands, and, it consequently contributes to guiding decisions on use or protection, or generally for wetland policy formulation (Langensiepen et al., 2023). With many research gaps remaining, this work aims at contributing to our understanding of wetland vegetation, with a focus on vegetation integrity, vegetation diversity and vegetation dynamics in natural and agriculturally used wetlands of East Africa.

1.2 Research objectives and questions

Considering (1) the importance of wetlands, (2) the rapid transitions occurring in their uses, and (3) vegetation being a key feature of wetland attributes and indicator of their changes, the main objective of this thesis is to study "**integrity", "diversity", and "recovery dynamics"** of East African wetlands from a vegetation ecology´s point of view. The changes in wetlands, the need for political decision-making on whether wetlands should be protected or used, and the need for conserving ecosystem functions and services, including the maintenance of biodiversity, require quantitative data and a sound understanding of wetland vegetation, its composition, and its dynamics.

I hypothesize that wetland vegetation in East Africa differs both regarding floristic composition and vegetation structure depending on combination of environmental factors and the land use intensity. Further, I hypothesize that differences exist in recurrent patters, that can be used in ecological assessments of integrity, diversity and recovery dynamics.

1.2.1 Integrity

Integrity refers to the ecological state or health of the wetland. It is an abstract and qualitative construct and can be understood as a condition without human impact close to a (hypothetical) natural reference state (Anderson, 1991; Kotze et al., 2012) in terms of species composition, diversity, and functionality (Karr & Dudley, 1981). Integrity is in line with the concept of *potential natural vegetation* of the site (Beuel et al., 2016; Mueller-Dombois & Ellenberg, 1974). Its quantification is challenging, but it can be approached by using expert assessments and proxy indicators (Chapter 4). This thesis focuses on the WET-Health framework (Kotze et al., 2012), a criteria-based in-field expert evaluation system of wetland health. It attempts to predict the state of a wetland based on a set of vegetation attributes, estimated simultaneously in the sense of vegetation-based indicators of biotic integrity VIBI (e.g., Karr, 1991; U.S. EPA, 2002). The overarching research question of this section is thus: **What is the ecological state of representative East African wetlands and how can it be assessed?**

1.2.2 Diversity

Vegetation can differ regarding floristic composition, physiognomy or functional traits, and these criteria have been used to classify vegetation (de Cáceres et al., 2018). Different vegetation units, regardless of their method of classification, can inform on the natural state, on the provision of ecosystem services, on land use (history), and on hydro-edaphic site conditions, and such insights contribute to understanding vegetation diversity within and between wetlands. Such vegetation units are commonly used for assessing and guiding land use management and conservation, for instance in the Natura 2000 program of the European Union (Dengler et al., 2008). One popular framework to classify vegetation is the Braun-Blanquet approach. It uses species composition to classify vegetation in a hierarchical order of specific vegetation units, called syntaxa (Dengler et al., 2008). The association level describes particular species composition. This section of the thesis therefore addresses the overarching question: **How diverse is East African wetland vegetation?**

1.2.3 Recovery dynamics

Disturbance in ecology describes an event that is temporarily and spatially restricted (as opposed to stress) and "disrupts the structure of an ecosystem, community, or population, and changes resource availability or the physical environment" (White & Pickett, 1985). Disturbances can have various causes of natural or anthropogenic origin. In wetlands, common natural disturbances include flooding, fire during the dry season, or trampling and grazing by wild animals. In agriculturally used wetlands, common disturbances are livestock grazing, clearing of vegetation, tillage for crop cultivation, and the application of agrochemicals. These disturbance events normally initiate "secondary successions" (Burrows, 1990), a process of regrowth and recolonization starting from surviving and newly introduced diaspores. Typically, these processes are directed and follow reoccurring patters, in which short-lived plants establish first, and are later replaced by plants with longer life spans (Burrows, 1990). In the context of this work, disturbance was induced via tillage with the objective to observe recovery dynamics of biomass production and species composition in a tropical wetland with year-round vegetation period. Further, as a side aspect, a comparison is made with a tropical floodplain wetland in a savanna climate, leading to the key question of this chapter: **How does East African wetland vegetation recover after disturbance?**

1.3. Research framework

The research was conducted within the framework of the BMBF-funded GlobE-wetlands project (FKZ: 031A250 A-H). The project was conducted from 2013-2018 with an overall aim of "Reconciling future food production with environmental protection".

Table 2: Overview on participating entities in the GlobE-wetlands project.

	Country	Institution
Project partners	Germany	University of Bonn University of Cologne University of Mainz Research Center Jülich
	Kenya	Kenyatta University National Museums of Kenya University of Nairobi
	Rwanda	University of Rwanda Rwanda Environmental Management Authority
	Tanzania	Africa Rice Center University of Daressalaam
Collaborating ministries	Kenya	Ministry of Environment and Natural Resources Ministry of Education, Science and Technology
	Rwanda	Ministry of Natural Resources Ministry of Education
	Tanzania	Ministry of Education and Vocational Training Vice President´s office, Division of Environment
	Uganda	Ministry of Water and Environment Ministry of Agriculture, Animal Industry and Fisheries
Funding	Germany	German Federal Ministry of Education and Research (BMBF)
Co-funding	Germany	German Federal Ministry for Economic Cooperation and Development (BMZ)
Implementation	Germany	Projektträger Jülich (PTJ)

Project partners were universities and institutions in Germany, Kenya, Rwanda, Tanzania and Uganda in collaboration with ministries from the focal countries. Table 2 provides an overview of project partners involved.

The GlobE-wetland project consisted of five multi-disciplinary research clusters: (1) Status quo, (2) Technology options, (3) Integration, (4) Extrapolation, and (5) Capacity building. The work presented in this thesis was embedded in the "Status quo" cluster, even though activities and results also contributed to the other clusters. In the "Status quo"-cluster, the work was part of the work packages A1: "Wetland characterization and typology" and the work package A4: "Ecosystem services". In general, the project aimed at performing multi- and transdisciplinary research. Of particular importance for this work were two multidisciplinary activities: the "typology" and the "central field trials".

The "typology" comprised a field campaign performed in the beginning of the GlobE-wetlands project from September to December 2013 by a multidisciplinary team of hydrologists, agronomists, soil scientists, remote sensors, economists, and ecologists. The team, of which I was part, assessed wetlands in the project´s study areas in Kenya, Tanzania, Rwanda, and Uganda (more on the studied wetlands or wetland complexes in chapter 3). Within the wetlands, squares of 250 by 250 m (in the following called “tiles”) were randomly pre-selected and then a subset was selected for assessment together with local experts (for details, see Beuel et al., 2016). Each tile was mapped and subdivided into assessment units of similar land use and physiognomy. In each assessment units and in plots within these units, each discipline collected rapidly assessable data typical for the respective discipline. A subset of these data was used for the “integrity”-section of this work (Chapter 5; Behn et al., 2018; Beuel et al., 2016).

The second multidisciplinary activity concerned the central field experiments in Namulonge, Uganda, and Ifakara, Tanzania. In these trails, rice (Ifakara and Namulonge) and maize (only Namulonge) were grown in a random-block design with different management and fertilization treatments at different positions in the wetland (the fringes of the wetland, the riparian zone close to the river/stream and a middle position between these two). Details for the central field trials can be found in Kwesiga et al. (2019) and Grotelüschen et al. (2021). Relevant for this work were the three different control treatments, in which sampling for the diversity and the recovery dynamics chapters were conducted. “T0” stands for a long-term fallow control, vegetation that was not cleared before the establishment of the central field trail. It was located in strips between the blocks of the different positions (only in Namulonge). “T1” was the non-cultivated control treatment, which was cleared and tilled in the beginning of the trials, but neither weeded nor cultivated. The plots were sampled regularly for diversity and regeneration dynamics. Lastly, “T2” consisted of a treatment simulating “farmers practice”, which was cropped with lowland ice, but without bunding or fertilization, and with one single hand weeding. In this treatment, weed communities associated with lowland rice were used in the diversity study (chapter 6).

2 Structure of the thesis

Sampling in Ewaso Narok swamp, Kenya (top left), view on the Namolonge valley, Uganda, with experimental rice plots (top right), sampling in a papyrus marsh in Rwanda (bottom left), black-headed weaver (*Ploceus melanocephalus*) in a wetland in Rwanda (bottom right).

The core of this thesis is structured in three main chapters referring to the topics of "Integrity", "Diversity" and "Recovery Dynamics". The "Integrity" chapter is divided into two research articles (one as co-author and one as first author) both published in *Ecological Indicators*. The diversity chapter consists of a first-author research article published in *Phytocoenologia* and a floristic guidebook for East African wetlands that I co-authored. The "Recovery dynamics" chapter consists of a manuscript published in *Wetland Ecology and Management*. The "Application" chapter brings together aspects from the previous chapters and further includes results of a recovery dynamics experiment in Kilombero floodplain (Table 3). Results of all chapters were presented as poster or talk on international scientific conferences. Table 4 proviedes an overview on these scientific contributions.

Table 3: Summary of the key scientific publications and further major results of this thesis.

Chapter	Publication	Key points	Main contribution
5 Integrity	Beuel, S., Alvarez, M., Amler, E., **Behn, K.,** Kotze, D., Kreye, C., Leemhuis, C., Wagner, K., Willy, D. K., Ziegler, S., & Becker, M. (2016). A rapid assessment of anthropogenic disturbances in East African wetlands. *Ecological Indicators*, *67*, 684-692.	WET-Health was adapted in terms of a rapid assessment suitable for large wetlands in East Africa. Wetland disturbance in East Africa is highly associated with agricultural activities.	Application of a modified WET-Health method in East Africa (collaborative paper, contribution mainly in the field assessment of the vegetation module).
	Behn, K., Becker, M., Burghof, S., Möseler, B. M., Willy, D. K., & Alvarez, M., (2018). Using vegetation attributes to rapidly assess degradation of East African wetlands. *Ecological Indicators 89,* 250–259.	Vegetation attributes are suitable indicators for degradation of wetlands. Ex-post application of this method may enable use of historic data.	Assessment method for east African wetlands as an add on to the wet health approach.
6 Diversity	Becker, M., Alvarez, M., **Behn, K.,** Möseler, B. M., Handa, C., Oyieke, H., Misana, S., & Mogha, N. (2014): Small wetlands in East Africa: A field guide to the representative flora. Selbstverlag, Bonn. Germany. 202 pp. ISBN 978-3-00-047349-4.	80 plant species with description of their morphology, ecology and use. All species with pictures taken in East African wetlands. Species are grouped into categories of ecological niches they predominantly occur in.	Pocket-sized field guide particularly for East African wetlands. Scientific, English and Swahili names of plants.
	Behn, K., Alvarez, M., Mutebi, S., & Becker, M. (2022). Vegetation diversity in East	Eight units of marsh and reed vegetation and five units of weed and pioneer	Extension of an existing classification for

	African wetlands: Cocktail algorithms supported by a vegetation-plot database. *Phytocoenologia 51(3)*, 199-219.	vegetation were recognized. The classification approach starting with limited field data followed by a revision with database data seems promising.	east African wetlands. Development of an expert system and a method that allows further extension for classification.
7 Recovery dynamics	**Behn, K.,** Alvarez, M., Mutebi, S., & Becker, M. (2024). Recovery dynamics of wetland vegetation along a hydrological gradient in an agriculturally used inland valley in Uganda. *Wetlands Ecology and Management*, *32*(6), 959–974.	Recovery after disturbance in wetlands is fast, diverse and dynamic. Intermediate succession stages are important for biodiversity and ecosystem service provision, but may favor invasive species.	Short-term succession processes were studied in an inland valley in Uganda.
8 Application	Combination of aspects from the integrity, diversity, and recovery dynamics chapter	The biotic integrity increases during the recovery process. There are changes of phytosociological associations during the recovery process. Recovery differs between inland valley and floodplain wetlands.	Application of the VIBI-tool from chapter 5.2, the vegetation classification of 6.2 to the succession study from chapter 7 Short presentation of the recovery experiment in Kilomber floodplain and comparison with Namulonge (7.)

Table 4: Overview on presentations on scientific conferences. Abbreviation in Topic columns refer the main chapters of this work: Integrity (INT), Diversity (DIV), and Recovery dynamics (RDY).

Conference	Location	Year	Type of presentation	Topic	Title of presentation
13th Meeting on Vegetation Databases	Koblenz, Germany	2014	Poster	INT	Assessment of floristic and structural variables of vegetation: the impact of agricultural use in East African wetland ecosystems
14th Meeting on Vegetation Databases	Oldenburg, Germany	2015	Talk	INT	A vegetation-based index of biotic integrity applied to riparian vegetation in East Africa
Tropentag	Berlin, Germany	2015	Poster	RDY	Monitoring wetland vegetation regeneration in an inland valley in Uganda.
Tropentag	Vienna, Austria	2016	Poster	DIV	Flora and vegetation in East African wetlands in the context of land use changes
European Conference of Tropical Ecology	Brussels, Belgium	2017	Poster	DIV RDY	Regeneration dynamics in floodplains: plant species guilds in the Kilombero Floodplain, Tanzania
16th Meeting on Vegetation Databases	Freiburg, Germany	2017	Talk	DIV	Combining current and historical surveys for classification of wetland vegetation in East Africa
Tropentag	Bonn, Germany	2017	Talk	DIV	Diversity of East African wetland vegetation: A classification based on current and historic Surveys
Summer School	Kampala, Uganda	2018	Poster	DIV	Classification of East African wetland vegetation using recent and historic surveys
GlobE-Wetlands reporting day	Namulonge, Uganda	2018	Talk	DIV RDY	Wetland vegetation around Namulonge: classification and regeneration
GlobE Pan-African Conference	Naivasha, Kenya	2018	Poster	DIV, RDY	Wetlands in East Africa – Biodiversity*
GlobE Wetlands Closing workshop	Dar es salaam, Tanzania	2018	Talk	INT, DIV, RDY	Wetlands in East Africa – Vegetation ecology*

* Poster / Presentation representing the full project group working on biodiversity/vegetation ecology

3 Study area

Rice fields in Kilombero floodplain, Tanzania (top left), Crested crane (*Balearica regulorum*) in Uganda (top right), wetland agriculture near Kigali, Rwanda (bottom left), cattle in Ewaso Narok floodplain, Kenya (bottom right).

The study area of this work are the East African countries Kenya, Rwanda, Tanzania and Uganda. In each of the countries, one specific locality (Table 5) was selected as study site for the whole GlobE-wetlands project based on their suitability for the research aims of the project and not specifically for this work. They were selected by researchers and policy-analysts based on and their designation as national priority areas for research, development, or conservation by the collaborating ministries of the respective countries (Behn et al., 2018; Langensiepen et al., 2023), while at the same time representing the two major wetland types in East Africa: floodplains (highland and lowland) and inland valleys (Leemhuis et al., 2016).

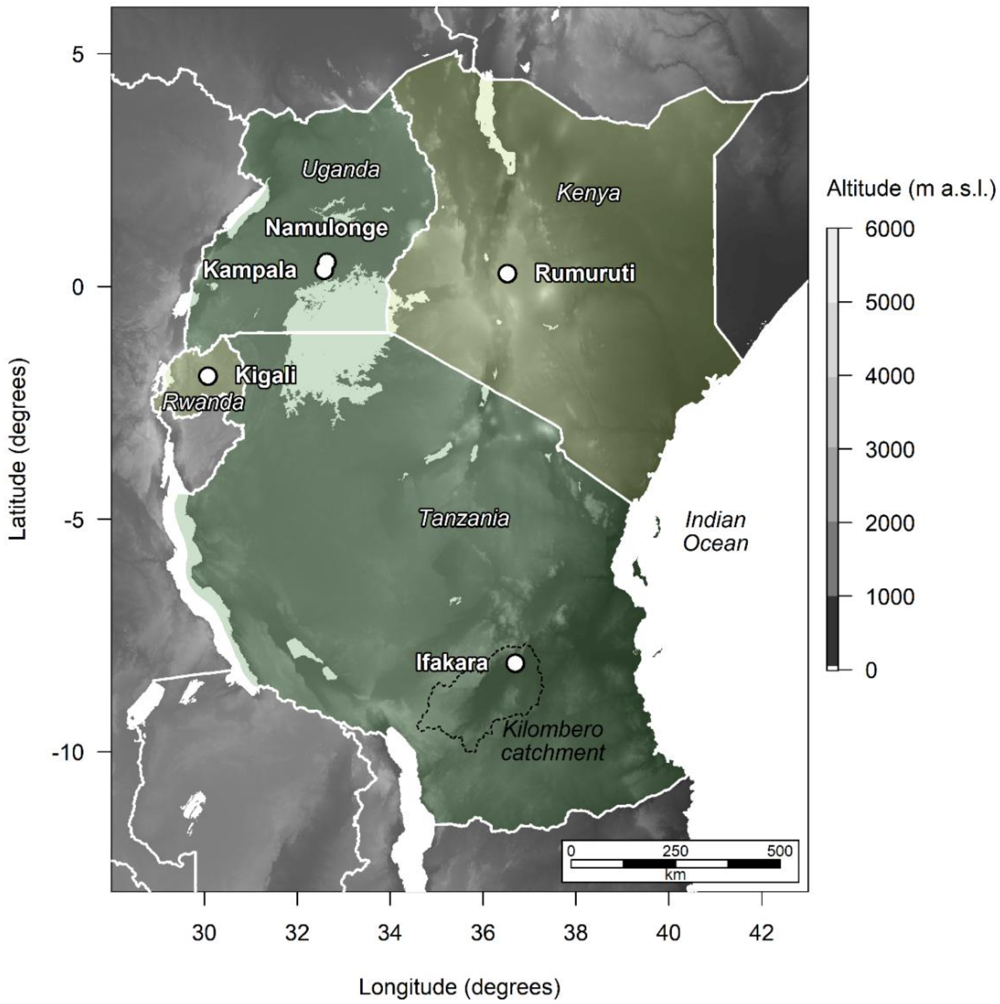

Figure 1: Location of the survey wetlands (white dots) in East Africa. Darkgreen shaded are the countries with major research activities for this work, lightgreen are countries with additional acitivites. The altitude data is accessed from the WorldClim database (Hijmans et al., 2005) which is based on SRTM elevation data (USGS, 2004). International borders are based on Global Administrative Areas Database(GADM, 2015). Lakes are displayed in white and based on Global Lakes and Wetland Database (Lehner & Döll, 2004).

Table 5: Comparion of the study sites regarding biophysical attribures, land use, research activities for this work. Modified after (Behn et al., 2018).

	Ifakara	Kampala	Kigali	Rumuruti
Country	Tanzania	Uganda	Rwanda	Kenya
Wetland type	Lowland floodplain	Inland valleys	Inland valley / floodplain	Highland floodplain
Wetland name/ description	Kilombero floodplain / valley; most work was done around the city of Ifakara	Various inland valleys in Kampala and Wakiso district; Most work was done in the Namulonge valley on and close to the Namulonge Research Station	inland valleys in the Lake Muhazi catchment, Nyabarongo floodplain	Ewaso Narok
Altitude	250 m a.s.l.	1,100 m a.s.l.	1,500 m a.s.l.	1,800 m a.s.l.
Average temperature	25 ° C	22 ° C	20 ° C	17 ° C
Average annual rainfall	1,427 mm	1,291 mm	990 mm	714 mm
Bioclimate	Aw (“Tropical Savanna”)	Af (“Tropical Rainforest”), Am (“Tropical Monsoon”)	Aw (“Tropical Savanna”)	Aw (“Tropical Savanna”), Csb (“Temperate with dry and warm Summer”)
Geology	Fluvial sediments	Gneisses and granitoides	Micaschists and quartzites	Alluvial sediments on crystalline basements
Main wetland soils	Arenosols, Fluvisols, Vertisols	Gleysols, Fluvisols, Histosols	Histosols, Gleysols (floodplain), Ferralsols	Fluvisols, Histosols
Natural vegetation	Edaphic grassland, miombo woodland	Tropical rainforest, swamp forest, papyrus marsh	Papyrus marsh, shrubland, forest	Papyrus marsh, (seasonally flooded) savanna
Main crops	Rice, maize, sweet potato	Rice, maize, taro, cassava, tomato, sweet potato	Maize, beans, taro, tomato, rice, sweet potato, cassava, sugar cane	Maize, tomato, cabbage
Activities conducted	Integrity, Diversity, recovery dynamics	Integrity, Diversity, recovery dynamics	Integrity	Integrity

The Kilombero valley in Tanzania, in which the city of Ifakara is located, has seen massive expension of agricultural lands in the past decades as well as a strong immigration from other parts of Tanzania (Munishi & Jewitt, 2019). Expansion of agriculturally used land is expected to continue (Höllermann, 2024). The main reason for choosing the Kilombero study site were however political ambitions to extend and intensify rice production (Langensiepen et al., 2023) Activities belonging to the "Integrity" chapter were conducted at several sites in the Kilombero floodplain, while further activities were centered around the city of Ifakara. Kampala, Uganda, was selected as an example of wetlands along an urban to rural gradient. The Namulonge research station, where key experiments were conducted, is located along this gradient. The Kigali site in Rwanda, comprises wetlands north and south of Rwanda´s capital city Kigali, was included to study sustainable intensification along an altitudinal gradient (Langensiepen et al., 2023). Last but not least, Ewaso Narok in Kenia, close to the town of Rumuruti, is a site of land users´conflicts and ethnically based violence between farmers and herders occur that include the wetland access and use of wetland resources (Langensiepen et al., 2023). Similar to the Kilombero study site, in-migration hereby plays an important role (Anthonj et al., 2019).

4 Theoretical and methodological background

Acacia xanthophloea (top left), *Ludwigia adscendes* var. *diffusa* (top right), *Leersia hexandra* (bottom left), *Ipomoea aquatica* (bottom right).

Chapter 1 of this thesis introduces the major topics of “Integrity”, “Diversity”, and “Recovery Dynamics” in reference to East African wetlands. The following subchapters provide background information on underlying concepts and related research history. They aim at bridging these concepts with the empirical research and the detailed methodological descriptions in the respective sections of chapters 5, 6, and 7.

4.1 Integrity

Ecological integrity refers to a state of an ecosystem that is close to a natural reference in terms of species composition, diversity, and functionality. It is an abstract concept that cannot be measured directly (Chapter 1.2.1) but can only be approached indirectly by comparing it to a reference. This reference might be an actual reference site with an ecosystem of the same type, but with little anthropogenic disturbance, or – as completely undisturbed sites rarely exists – a hypothetical, natural state of the ecosystem. Any deviation from this reference can be assessed by expert judgement, or by using ecological parameters, which can either be estimated, measured, or both. Two examples that were used in this work are described in the following – the “WET-Health” approach and “Indices of Biotic Integrity”.

4.1.1 WET-Health

Based on the need to halt wetland loss and degradation, a toolbox of several modules to assess, restore and manage wetlands was developed in the Republic of South Africa (Macfarlane et al., 2009). One component of this WET-Management series is the WET-Health tool, aiming to assess a wetlands integrity and possible causes of degradation. It should ultimately guide the identification and prioritization of wetlands for rehabilitation. WET-Health is targeting both the wetland itself (on-site) as well as the wider catchment (off-site). Wetlands are divided into hydrogeomorphic units that are subsequently assessed separately in the modules of hydrology, geomorphology, and vegetation. In a later version, water quality was added as a fourth module. For each module, scores are assigned by experts based on how far the situation differs from the hypothetical reference state, ranging from 0 (no impact) to 10 (total loss of wetland properties). Overall scores are calculated based on the proportion of the wetland affected and the magnitude of the impact. Additionally, estimated trajectories of change are used as correction factors and are based on expected improvements or deteriorations within five years following the assessment (Kotze et al., 2012).

The WET-Health assessment has been successfully applied in different wetlands in Southern Africa (Kotze et al., 2018) and within the GlobE-Project for the first time in East Africa (Beuel et al., 2016). The approach was however simplified and modified to make it applicable in the focal wetlands of the GlobE-Wetlands project that exceeded by far the sizes of the wetlands normally assessed with WET-

Health. For instance, the total size of the Kilombero floodplain in Tanzania exceeds 500 km². Hence, off-site factors and trajectories of change were not considered. Secondly, instead of the whole wetland, randomly selected 250 m by 250 m tiles were sampled. Thirdly, instead of using hydrogeomorphic units, the tiles were divided into units of similar land use. The assessment in the four modules was subsequently applied for each land use unit (Beuel et al., 2016). Scores were assigned in the field, based on standard scores for different land uses that were increased or decreased as required, depending on the actual conditions in the field.

4.1.2 Indices of biotic integrity (IBI)

In the 1980s, scientists from the US Environmental Protection Agency observed a continuous decline of water resources despite massive efforts to counteract such trends (Karr, 1991). As direct measures of water quality are very costly, Karr (1981) proposed the use of Indices of Biotic Integrity (IBI). These indices use certain metrics showing a clear response to human disturbances or declining resource quality, while being relatively easy to assess. Thus, a fish-based index was developed using metrics such as number of fish species, the percentage of fish with different feeding strategies, or their health condition. The values for each metric were scored based on expertise and comparison with “natural” reference sites in the region. Eventually, the sum of individual metric scores leads to a defined integrity class (e.g., “Excellent”, “Fair”, “No Fish”) that can be intuitively understood. This concept has been applied and further developed by several scientists. In their works, they also used other metrics, based on e.g. plants or invertebrates (Table 6). Reference sites have often been used as baseline, in accordance with a definition of integrity as resembling the natural habitat in the region. However, systems that have not been altered by human activities vary, and undisturbed reference sites may be not available or accessible in a respective study area. Further, sites of little disturbance may be restricted to certain environmental conditions such as permanent or seasonally deep flooding (Beuel et al., 2016). Hence, several alternatives have been suggested as reference (Table 6). For instance, Miller et al. (2006), Mack (2007), and Behn et al. (2018) used scores of different rapid assessment approaches that assessed external human impacts or the ecological condition, following different approaches than those of the original IBI. Thus, Reiss (2006) used a “Landscape Development Index” for her work in Florida. This index is based on the use of nonrenewable energy and hence an independent, quantitative, and reproducible measure of a human disturbance gradient. However, these data need to be available, and their usefulness may be limited in regions where agriculture is often not mechanized as in many parts of Africa. Depending on the use of the reference for disturbance or integrity, the metrics are weighted differently. Common approaches are scores given for different value ranges of the metric, or their calibration using of distinct units.

Table 6: Selected published studies using the concept of "indices of biotic integrity" and applied it to various regions and using different metrics.

Publication	Ecosystem	Region	Reference	Metrics based on:
Karr (1981)	Rivers	USA (Indiana, Illinois)	Reference sites	Fish
Miller et al. (2006)	Wetlands	USA (Pennsylvania)	Rapid assessment scores	Plants, Vegetation
Reiss (2006)	Wetlands	USA (Florida)	Quantification of human impacts (index based on non-renewable energy use around the wetland)	Plants, Vegetation
Mack (2007)	Wetlands	USA (Ohio)	Rapid assessment scores	Plants, Vegetation
Raburu et al. (2009)	Rivers	Kenya (Lake Victoria basin)	Reference sites	Macroinvertebrates
Moges et al. (2016)	Wetlands	Ethiopia (Jimma Highlands)	Reference sites	Plants, Vegetation
Aura et al. (2017)	Coastal river basin	Kenya (Tana River)	Reference sites	Macroinvertebrates
Behn et al. (2018)	Wetlands	East Africa (Kenya, Rwanda, Tanzania, Uganda)	Rapid assessment scores (WET-Health, hence indirectly using hypothetical reference states)	Vegetation

4.2 Diversity

Vegetation scientists have debated for a long time whether assemblages of plant species should be viewed as distinct entities / superorganisms (Clements, 1916) or rather as random intersections of different plant species occurring on their individual gradients of site conditions (Gleason, 1926). Consequently, vegetation can be seen either as a mosaic of distinct units or as a continuum (Scott, 1995). Both theories have received empirical support (Liautaud et al., 2019). A recent modeling study (Liautaud et al., 2019) suggests that the type of gradient and the levels of competition between species are the factors distinguishing between continuum and entity, thus both theories should be viewed as complementary rather than contradictory. This theoretical question is relevant for instance for predictive modeling of species distributions. It has also implications for the justification of vegetation classification itself, as the continuum-theory can be seen as contradictory to the concept of vegetation units. However, Dengler et al. (2008) do not see this as a practical problem for vegetation classification, for which they formulate three fundamental goals: (1) "Delimiting and naming parts of the vegetation continuum to enable communication about them"; (2) "Predicting a multitude of ecosystem attributes (e.g., species composition, site conditions, and ecological processes) from the assignment of a particular stand to a vegetation unit" and (3) "making multispecies co-occurrence patterns representable by verbal descriptions, tables, diagrams, and maps." (Dengler et al., 2008). As such, they recommend "floristically defined vegetation types (…) as reference entities for ecological research, bioindication, and nature conservation", even though multiple other criteria such as physiognomy, structure, functional traits, or ecological conditions can be used to classify (de Cáceres & Wiser, 2012).

4.2.1 Vegetation classification with special focus on Braun-Blanquet and Cocktail Classification

Josias Braun-Blanquet laid the foundation for floristic classification of vegetation in the 1920s. His approach for classifying vegetation has three key features (Dengler et al., 2008): (1) It is based predominantly on the floristic composition, while vegetation structure or site conditions may be used additionally; (2) Vegetation units (syntax) are arranged in hierarchical order; (3) These syntaxa are named following specific rules in accordance with the International Code on Phytosociological Nomenclature (ICPN; Theurillat et al., 2021), analogue to similar conventions for individual species.
Base of the classification are individual plot observations called *relevés*. In these plots, all plant species (in practice this is often restricted to vascular plant species) are recorded with abundances estimated on a cover-abundance scale or simply as percent cover. Species lists are complemented with metadata (location, date, etc.) and known ecological properties of the site. Plot size depends on vegetation type and the purpose of the study. Plots can be chosen randomly or preferentially. Both approaches have their advantages and disadvantages. For instance, random samples may select inaccessible plots, heterogeneous plots, or neglect plots of particular ecological interest. On the other hand, preferential samples are biased and at a high risk of over- and underrepresentation of specific vegetation. It therefore depends on the objectives of a study which method to choose (Dengler et al., 2008).

In the Braun-Blanquet approach, relevés are sorted according to the presence (or absence) of diagnostic species into expert-defined vegetation units (syntaxa). Their fidelity, frequency, and constancy in a respective unit, and their absence in other units define diagnostic species. They are divided into those occurring specifically in the respective unit (character species) and those used to differentiate specific syntaxa from other (related) syntaxa (differential species). The expert-defined syntaxa are arranged hierarchically on four major ranks (from broad to specific: Class, Order, Alliance, Association). They are named after characteristic species with a specific ending according to their syntaxonomic rank (Table 7). While subranks may also be used, the association-rank is the most important for most applications.

Table 7: Example of syntaxonomic ranks in the Blaun-Blanquet approach for tropical papyrus marsh.

Rank	Ending	Example	Explanation
Class	-etea	***Phragmito-Magno-Caricetea*** Klika ex Klika & Novák 1941	Herbaceous semi-aquatic vegetation in sweet or brackish water
Order	- alia	***Cyperetalia papyri*** (Lebrun 1947) Alvarez 2017	Herbaceous semi-aquatic vegetation in Africa
Alliance	-ion	***Cyperion papyri*** (Lebrun 1947) Alvarez 2017	Tall reed vegetation on seasonally or permanently inundated soils
Association	-etum	***Cypero papyri-Dryopteridetum gongylodes*** (Germain 1951) Schmitz 1963	Vegetation dominated by *Cyperus papyrus*, conmmonly accompanied by the fern *Cyclosorus interruptus* (= *Dryopteris gangylodes)*

While widely applied, the original Braun-Blanquet approach of classifying vegetation has received substantial criticism for being too subjective and expert-biased. As a response, and with the new opportunities offered by computers and specific programs easing statistical calculations, purely numerical, non-supervised classification methods emerged in the second half of the 20th century as alternatives to traditional approaches. These methods comprise TWINSPAN (two-way indicator species analysis), hierarchical clustering, or k-means clustering. While these methods are non-biased and easily reproducible, they have other disadvantages, such as excluding expert knowledge and lacking transferability to other sites. Thus, addition of new data, even from the same site, may readily alter the outcome of the classification (Behn et al., 2022; Dengler et al., 2008).

As an alternative, the Cocktail Classification (Bruelheide, 1997) was developed to combine both supervised and non-supervised approaches. The phi-coefficient was hereby introduced as a standard measure of fidelity (Chytrý et al., 2002; Tichý & Chytrý, 2006), and used to create sociological species groups and identify diagnostic species (Kočí et al., 2003). While keeping the already described vegetation units, the Cocktail Classification creates unequivocal definitions for each unit. These definitions are a “cocktail” with one or more species groups and, in some cases, dominating species as the ingredients. These ingredients can be combined or excluded with logical operators “AND”, “OR”, and “AND NOT”. For species groups, the occurrence of half of the species included in the group is normally considered as “presence”, while for individual species, an abundance threshold is defined. Such single species may be useful in special cases such as species-poor wetland vegetation (Landucci et al., 2013). A fulfilled definition of a vegetation unit could be: presence of species group A or species group B, absence of species group C, and species Z not exceeding 25% cover.

The Cocktail Classification has been widely applied in Europe, particularly in Czechia, where a complete classification of vegetation units and databases containing thousands of vegetation relevés are available. Hence, Cocktail definitions were developed with sophisticated statistics and based on large numbers of plots in each category (e.g., Kočí et al., 2003). In other regions of the world, the lack of a comprehensive classification and limitations in available or accessible data constitute a major challenge. In East Africa, general vegetation classifications according to Braun-Blanquet do exist but are often limited to specific regions or ecosystems (e.g., Schmitz, 1988). Studies using the Cocktail classification method in East Africa are to the best of my knowledge restricted to Alvarez (2017) and Behn et al. (2022). The latter study (chapter 6) presents an adaption of the Cocktail Classification to data-scarce regions. Consequently, the Cocktail Classification method has great potential for vegetation classification in East Africa.

4.3 Recovery dynamics

An ecological succession is the "directional sequence of populations of different plant species on a site" (Burrows, 1990). The scientific study of successions has been emerging since the late 19th century, mainly by US-American botanists Cowles (1899) and Clements (1916). Concepts of succession have since been studied, theorized, controversially discussed, and even rejected (see e.g., Burrows, 1990; Johnson & Miyanishi, 2021). Despite all controversies of the various theories of succession and different usage of the term "succession" itself (Burrows, 1990), a common understanding and the types of succession will briefly be introduced thereafter.

Primary succession means a colonization of an area that has not been vegetated before. This is examplified be a new island, by debris of an avalanche, by lava flow fields after a volcanic eruption, or also by human-made structures of concrete. The surface is initially bare and does not contain any diaspores. In the early stage, highly specialized species, mainly lichens and mosses, can grow directly on the rocky surface. In the course of time, particularly after soil formation or an accumulation of organic material, also other plants can grow slowly replacing the first colonizers. Secondary successions, on the other hand, refer to areas that has been vegetated before, but where a disturbance event was removing parts or all of the (aboveground) biomass. These events may comprise fire, flood, bioturbation, or tillage. Unlike in the case of primary succession, diaspores of the previous vegetation are often still present and the ecological conditions for their growth may still be favorable. Nevertheless, ecologists have observed that the recovery or regrowth after such disturbance events is happening in different stages over time. Clements' theory of succession (Clements, 1916) postulates that vegetation develops after a disturbance event via different successional stages to an endpoint. This endpoint represents a specific climax vegetation (or an alternative stable state), depending on the sites' ecological conditions, unless it faces new disturbance events. Furthermore, external changes in biotic or abiotic factors can induce vegetation changes, a process referred to as "allogenic succession", e.g., changes in climate or newly introduced grazing animals. On the other hand, "autogenic succession" refers to situations where plant species themselves modify their environment, e.g., by improving soil fertility or by litter accumulation, and are subsequently replaced by other species. Finally, a "direct succession" occurs, when the initial species are not replaced by another one, and when pioneer vegetation does thus not change (Burrows, 1990).

The study of succession is often challenging due to long periods of some ecological processes, particularly in the development of forests. Hence, field observations have often used space-for-time substitutions and compare areas that were subject to disturbances at different points of time, and where the (forest) vegetation had developed after a disturbance event for a certain period of time. However, a key concern with this approach is that ecological conditions such as soils or water supply, may differ between sites that supposedly represent different successional stages. Therefore, different vegetation may not (only) be explained by different recovery times, but in fact by variations in site conditions. Similarly, the type of the disturbance event or its intensity may have induced the observed differences, rather than the time after disturbance (Johnson & Miyanishi, 2021). While forest vegetation often takes decades to grow or to reach a different successional stage, initial successions occurring within few years, can be studied easier. After a natural disturbance event or after an induced disturbance in an experimental set up, successional processes can be monitored at the same site, e.g., after abandonment of cropland, during fallow periods, following shifting cultivation, or after fire events. Burrows (1990) described a theoretical example from the temperate zone in New Zealand. He expected annual grasses and forbs to dominate the growing season after abandoning a garden, followed by perennial forbs in the next season. These will subsequently be replaced by sward-forming perennial grasses and taller, more competitive perennial forbs. Shrubs and eventually trees would emerge in the final stages of succession. This succession pattern and the trajectory from annual grasses to perennial trees is expected to be similar around the world. However, the speed and intensity of successional change may vary and is expected to be highest in the humid tropics (Burrows, 1990).

5 Integrity

Land use categories in Ewaso Narok, Kenya: Cropland (top left), fallow with *Cyperus dives*) (top right), grazing land (bottom left), largely unused, near-natural wetland with *Cyperus papyrus* (bottom right).

5.1 A rapid assessment of anthropogenic disturbances in East African wetlands

For this chapter, I was the main collector of the vegetation data including the estimation of the WET-Health impact scores for vegetation. In addition, I contributed to the data analysis and the manuscript writing. The abstract is displayed in the following. It was published as:

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Abstract

The use of East African freshwater wetlands for agriculture has increased in recent decades, raising concerns about potential impacts on wetlands and the long-term sustainability of such land use trends. WET-Health is an indicator-based rapid wetland assessment approach developed in South Africa. It allows determining the conditions of wetlands in four assessment modules (hydrology, geomorphology, vegetation, and water quality) by observing the degree of deviation of a wetland from its anticipated natural reference state. We tested the transferability of the WET-Health concept for East African inland valley swamps and floodplain wetlands based on 114 assessment units at four study sites. Due to large wetland areas and different environmental settings in East Africa, we modified the original approach using a random selection of assessment units and an assessment scheme based on disturbance types (Appendices A and B). Estimated WET-Health impact scores were matched with biophysical and socioeconomic variables using a generalized linear mixed model. Land use included largely undisturbed wetland units occurring side by side with seasonally cropped or grazed units, and drained, permanently cultivated units. A strong differentiation of impact scores between the four assessment modules was apparent with highest scores for vegetation and lowest scores for geomorphology. Vegetation and water quality responded most sensitively to land use changes. The magnitude of wetland disturbance is predominantly determined by management factors such as land use intensity, soil tillage, drainage intensity, and the application of agrochemicals and influences vegetation attributes and the provision of ecosystem services. The proposed modification of WET-Health enables users to assess large wetland areas during relatively short periods. While further studies will be required, WET-Health appears to be a promising concept to be applied to wetlands in East Africa and possibly beyond.

Keywords: East Africa, flooding regime, land use, wetland health, wetland monitoring

5.2 Using vegetation attributes to rapidly assess degradation of East African wetlands

This chapter is based on:

Behn, K., Becker, M., Burghof, S., Möseler, B.M., Willy, D.K., Alvarez, M. (2018). Using vegetation attributes to rapidly assess degradation of East African wetlands. *Ecological Indicators*, *89*, 250-259. https://doi.org/10.1016/j.ecolind.2018.02.017

Abstract

Wetlands in East Africa harbor a large biodiversity and provide diverse ecosystem services. In addition, wetlands are highly suitable for crop production due to generally fertile soils and water availability. Because of rising demand for cropland that is driven by population growth, degradation of upland areas and changing food demand patterns, wetlands are increasingly used for agricultural production. Such land use changes can negatively affect biodiversity and the provision of ecosystem services, especially when formerly little-disturbed wetlands are converted into croplands. For evaluating wetlands and developing land use or conservation strategies, we require methods to assess disturbance and degradation of wetlands. For instance, many indices of biological integrity for wetlands using vegetation attributes have been developed especially in the USA, but to date, no comparable assessment schemes are available for East Africa. To develop such a scheme, we sampled four different wetland localities, covering both floodplain and inland valley wetlands in Kenya, Rwanda, Tanzania and Uganda. A total of 198 wetland plots were characterized regarding land use and evaluated in terms of geomorphology, hydrology, vegetation and water quality regarding their deviation from a theoretical natural reference state without human disturbances and given respective impact scores using the WET-Health approach. Additionally, nine variables characterizing vegetation attributes were recorded. The impact scores were rescaled from 0 to 1 and used as response variables in multiple linear regression models. The predictor variables were selected for each regression model out of the nine vegetation attributes in a stepwise process. The regression models for the different response variables differed strongly regarding their accuracy. The root mean square prediction error (RMSPE) ranged between 0.14 for the “vegetation disturbance” and 0.27 for the “hydrological modification” regression model. However, we conclude that vegetation attributes such as “absolute cover of perennial species” or “average height of vegetation” are generally useful to estimate anthropogenic impacts on East African wetlands as assessed with the WET-Health approach. The presented approach can hence be a pragmatic addition to the WET-Health approach as a cost-efficient and rapidly applicable method. Furthermore, it may also be useful for ex-post application to historic data and vegetation surveys.

Keywords: Assessment, Index of Biological Integrity (IBI), land use, monitoring, WET-Health

5.2.1 Introduction

Wetlands are widespread ecosystems in East Africa (Denny, 1993) that cover up to 167.000 km² in Kenya, Rwanda, Tanzania and Uganda (Stevenson & Frazier, 1999). They supply diverse ecosystem services such as the provision of food and medicine, water regulation, water purification and carbon sequestration (Millennium Ecosystem Assessment, 2005). They are also important habitats for plant and animal species (Denny, 1994). On the other hand, wetlands have a large potential for agriculture due to generally fertile soils and water availability (Sakané et al., 2011). Over the last decades, this potential has been increasingly exploited (Dixon & Wood, 2003; Sakané et al., 2011) with the rising demand for cropland driven by population growth, lack of arable land and alternative livelihoods (Namaalwa et al., 2013). Degradation of upland fields (Symeonakis & Drake, 2004) and increasing rainfall variability in the context of climate change (Boko et al., 2007) also drive farmers into the wetlands (Sakané et al., 2011). Governmental policies have been promoting wetlands for agricultural use to supply local as well as export markets (Dixon & Wood, 2003). On the other hand, policies protecting wetlands have often been weakly enforced (Mombo et al., 2011; Namaalwa et al., 2013). Resulting land use changes, especially conversions of formerly little-disturbed wetlands to croplands, can entail negative effects on biodiversity and on providing and regulating ecosystem services (Schuyt, 2005; Wood et al., 2013). Information gained about a wetland's condition becomes increasingly important for supporting and evaluating management decisions to mitigate wetland destruction and loss of functions (Miller et al., 2006; U.S. EPA, 2002). Despite major difficulties in assessing quantitatively the current state of a wetland, methods have been developed to assess their biological integrity or to quantify degradation and disturbance in different regions and for different types of wetland ecosystems. Biological integrity is hereby referring to conditions compared with wetlands without anthropogenic impact (Anderson, 1991) or to a condition being comparable to the natural habitat in terms of species composition, diversity and functional organization (Karr & Dudley, 1981). For instance, the WET-Health approach has been developed to assess impacts of human activities on wetlands in South Africa (Kotze et al., 2012; Macfarlane et al., 2009) and was adapted to a finer scale for assessing East African wetlands by Beuel et al. (2016). Another way of assessing wetland conditions is using indices of biological integrity (IBI) which are also known as indices of biotic integrity. Originally proposed by Karr (1981) for the evaluation of aquatic environments using fish community attributes, they became popular, especially in the USA. In East Africa, IBIs were developed for river habitats in Kenya by (Aura et al., 2010, 2017; Masese et al., 2009; Raburu et al., 2009) and for wetlands in the Jimma Highlands of Ethiopia by Moges et al. (2016). Indices of biological integrity use a variety of metrics that are weighted in different ways and subsequently summed up to a total score, indicating the state of the wetland. In different approaches, plants and vegetation, macro-invertebrates or fish are being used as indicators (U.S. EPA, 2002). Vascular plants and vegetation attributes such as proportion of annual species, cover of invasive species or floristic quality indices (DeBerry, 2015) have frequently been regarded as suitable indicators and have been applied to assess wetland ecological states or levels of anthropogenic disturbance (Mack, 2007; Miller et al., 2006; Reiss, 2006). They are sensitive to human disturbances and easy to record and to quantify (Miller et al., 2006). However, unlike for the USA, where they were developed for several states and for different habitat types (e.g. Mack, 2007; Miller et al., 2006; Reiss, 2006), such indices are not yet available for wetlands in East Africa, apart from the study of Moges et al. (2016).

In this study, we combined the WET-Health approach (Kotze et al., 2012) and the concept of IBIs. We developed multiple linear regression models to predict impact scores assessed with the WET-Health approach and used vegetation attributes such as “vertical structure”, “absolute cover of perennial species”, “average height of vegetation” or “relative cover of monocots” as predictors. Our approach is intended to serve as an addition to WET-Health that can be easily, rapidly and efficiently applied in different wetland types along with any vegetation sampling. Additionally, an ex-post application to already recorded data or historical datasets may be possible.

5.2.2 Material and methods

Study sites

Data were collected in four wetland localities distributed across four East African countries, namely Kenya, Uganda, Rwanda, and Tanzania (Figure 1 & Table 5 in Chapter 3). The sites were selected based on them being national priority areas for research, development or conservation (MOWE, 2016; MOE, 2016; NEMC, 2016; REMA, 2016; SAGCOT, 2016). They comprise the two major freshwater wetland types in East Africa, namely inland valleys and floodplains, and differ strongly in their geomorphological and hydrological attributes as well as bioclimatic properties (Beuel et al., 2016). Further, the studied wetlands feature different land uses and use intensities, ranging from intensively cropped plots to little-disturbed patches of natural vegetation.

The Rumuruti wetland site in Kenya represents a highland floodplain (1800 m a.s.l.) formed by the Ewaso Narok river on the Laikipia plateau. It is underlain by thin alluvial sediments on crystalline basements, composed of volcanic phonolites (Heinrichs, 2001). The wetland has been modified by partial large-scale drainage, and these parts are intensively used for crop cultivation and domestic ruminant grazing. Wetland segments unaffected by drainage are largely undisturbed and characterized by *Cyperus papyrus* L. (Thenya, 2001). Stands of fever trees (*Acacia xanthophloea* Benth.) are common along the drier fringes. According to the classification of Köppen-Geiger, the Rumuruti site is included in the transition between the bioclimates “Tropical Savanna” and

“Temperate with Dry and Warm Summer” (Peel et al., 2007). Derived from the interpolated climate surface based on observations from 1950 to 2000, available in the WorldClim database (Hijmans et al., 2005), the average annual temperature is 17 °C and the mean annual rainfall 714 mm.

The Kampala wetlands in Uganda consist of many small inland valleys north of the capital city at an altitude of 1100 m a.s.l. The area is underlain by gneisses and granitoides (GTK Consortium, 2009.) The wetlands are located along a gradient from urban to rural areas and from intensively cultivated to less disturbed inland valley bottom lands. The latter ones are dominated by swamp forests (Lind et al., 1974) and papyrus marshes, as common in the headwaters of the Nile River (Denny, 1993). The site is located within the transition between the bioclimates “Tropical Rainforest” and “Tropical Monsoon” (Peel et al., 2007), with an average annual temperature of 22 °C and an annual rainfall of 1291 mm (Hijmans et al., 2005).

The Kigali site in Rwanda comprises both the Nyabarongo floodplain in the south, and several small inland valleys in the north of Kigali City at around 1500 m a.s.l. The area is underlain by micaschists and quartzites (Institut Geographique National de Belgique, 1981). The area is densely populated, and most wetlands are intensively used for cultivating crops. Unused patches are mostly found in the Nyabarongo floodplain and are characterized by papyrus marshes. The bioclimate according to (Peel et al., 2007) is “Tropical Savanna”. The average annual temperature is 20 °C and the annual rainfall 990 mm (Hijmans et al., 2005).

Finally, the Ifakara site in Tanzania is part of the Kilombero river floodplain at around 250 m a.s.l. It is characterized by thick fluvial sediments (Geological Survey of Tanganyika, 1962) and the floodplain is widely used for cultivating rainfed lowland rice during the wet season. Unlike the other study sites, undisturbed areas of the seasonally flooded center are characterized by edaphic grasslands with *Hyparrhenia* spp., *Panicum fluviicola* Steud. and *Phragmites mauritianus* Kunth. With decreasing duration and depth of flooding towards the fringes of the floodplain, woodlands gradually replace the grasslands (Hood et al., 2002). The Ifakara site belongs to the “Tropical Savanna” bioclimate with 25 °C and 1427 mm of annual rainfall (Hijmans et al., 2005).

Sampling strategy

Sampling was done in randomly selected tiles (Beuel et al., 2016) of 250 m by 250 m within the wetland area, however adjusted to the survey’s period (around two weeks per site) and the accessibility of plots (conditions of roads, requirements for permissions, etc.). Each tile was subdivided into assessment units that were characterized by homogeneous vegetation cover and similar land use (Beuel et al., 2016). Within the assessment units, plots of 10m by 10m were preferentially selected (Dengler et al., 2008) for vegetation sampling. The size of 100 m^2 was chosen to have sampling area suitable for all occurring vegetation types (Dengler et al., 2008) while still being manageable regarding the period. Settlement units were not sampled. In total, 198 plots in 48 tiles were sampled, 30 plots (in 7 tiles) in Rumuruti (Kenya), 73 (13) in Kampala (Uganda), 56 (18) in Kigali (Rwanda), and 39 (10) in Ifakara (Tanzania). The distribution of the plots in the respective study site is available in the attached kml-file.

Assessment of site characteristics and human impacts

Plots were classified according to the predominant land use at the sampling date into “croplands”, “fallows”, “grazing lands” and “unused plots with semi-natural vegetation” (Alvarez et al., 2012). Plots that had been harvested within three months prior to the survey were included in the cropland category. Land use intensity was recorded in four categories, depending on whether plots were used for cropping or grazing: (1) never or rarely, (2) occasionally, meaning less than once per year, (3) one season per year or (4) throughout the year. The plots were also classified regarding their flooding regime into four classes: plots that were seasonally saturated but never flooded were classified as “non-flooded”, while plots with an average yearly inundation period of less than one month were classified as “sporadically flooded”. “Seasonally flooded” plots were under water more than one month but less than twelve months. The last class was defined as “permanently flooded”, meaning that these plots are inundated throughout the year, regardless of the season. Land use, land use intensity and flooding regime were acquired by both field observation and interviews. To quantify the degree of impact of human activities on the wetlands, we assessed the wetlands in terms of geomorphological and hydrological modifications, vegetation disturbance and water quality. We used the WET-Health approach (Kotze et al., 2012a), applying a score ranging from 0 to 10 to each plot. The value 0 was assigned for plots with conditions close to the theoretical natural reference state without human disturbances. The scores are gradually increasing with deviation from the undisturbed reference condition up to a maximum of 10, representing a complete loss of wetland properties (Beuel et al., 2016).

Vegetation attributes

In each observation plot, nine vegetation-related variables (Table 8) were collected (Frey & Lösch, 2014; Mueller-Dombois & Ellenberg, 1974) as potential indicators to assess the wetland’s biological integrity and the intensity of anthropogenic disturbance. We selected the variables among attributes that are reportedly related to disturbances in wetlands, and hence used in other assessment schemes or represent typical features of natural wetland vegetation in East Africa. In addition, the variable should be suitable for a rapid assessment in the field. Variables related to functional groups were “absolute cover of woody species”, “relative cover of annual species” and “absolute cover of perennial species”. “Absolute cover of woody species” was chosen referring to naturally forested swamps in the study site (Lind et al., 1974). Annual species are generally favored by (recent) disturbance over perennials (Galatowitsch et al., 2000; Grime, 1974). Consequently, we expected the relation between annual and perennial species to be a valuable indicator for disturbance. To avoid misrepresentation in sparsely vegetated croplands, we used the relative cover for annuals and the absolute cover for perennials. Variables related to taxonomic groups were "relative cover of monocots", "absolute cover of Cyperaceae" and "absolute cover of Poaceae". These variables were chosen because non-forested wetlands in the region are normally dominated by either grasses or sedges (Denny, 1993; Lind et al., 1974). For both groups of variables, absolute cover refers to the sum of the visually estimated cover values (in percent) of each respective species. Relative values were calculated as the sum of cover values of respective species divided by the sum of the cover values of all species and multiplied with 100. Additional variables refer to the structure of the vegetation. The "absolute vegetation cover" was visually estimated and expressed on a percentage scale, excluding the cover of cultivated plants. The "vertical structure" was quantified as numbers of observed layers (Mueller-Dombois & Ellenberg, 1974), whereas herbal layer (< 0.5 m, including herbs with annual stems > 0.5 m), shrub layer (0.5 m–5 m, including tall herbs with perennial stems such as *Cyperus papyrus* L.) and tree layer (> 5 m) where distinguished. Hence, the value for vertical structure ranged from 0 (no vegetation) to 3 (forest with tree, shrub and herb layer). The "average height" of the vegetation was estimated in meters as the average height of the highest layer. If the highest layer covered the plot only partially, the weighted average of the parts covered by the respective layers was taken. Furthermore, dominant vascular plant species were recorded for each plot. Species were identified mostly in the field. Unknown plants were determined at the East African Herbarium in Nairobi, Kenya, using the key of the Flora of Tropical East Africa (Polhill, 1949-2010).

Table 8: Description of the vegetation attributes assessed in each plot.

Vegetation attribute	Type	Description
Absolute vegetation cover	Continuous	Visual estimation of vegetation cover (%) excluding crops
Vertical structure	Discrete	Number of layers (Herb, shrub, tree layer; 0-3).
Average height	Continuous	Estimated average of vegetation height in m
Absolute cover of woody species	Continuous	Sum of cover values (%) of woody species
Relative cover of annual species	Continuous	Sum of cover values (%) of annual species divided by sum of cover values (%) of all species multiplied with 100
Absolute cover of perennial species	Continuous	Sum of cover values (%) of perennial species
Relative cover of monocots	Continuous	Sum of cover values (%) of monocotyl species divided by sum of cover values (%) of all species multiplied with 100
Absolute cover of Cyperaceae	Continuous	Sum of cover values (%) of Cyperaceae
Absolute cover of Poaceae	Continuous	Sum of cover values (%) of Poaceae

Data analysis

All four impact variables (geomorphological modification, hydrological modification, vegetation disturbance and water quality) were rescaled and inverted to obtain gradients from highly disturbed plots (low values) to less disturbed ones (high values) using the formula:

$$x' = 1 - x/\max(x)$$

where x' are the transformed values of the variable x and max(x) represents the theoretical maximum (highest class) of the variable. Descriptive analysis of the plots was conducted based on flooding regime, land use and vegetation. Mean values of the impact variable for the different land use classes and localities were calculated. A principal component analysis (PCA) (Venables & Ripley, 2002) was used for an ordination of the plots based on the impact variables and to visually present the relation to land use and locality. A linear regression model was applied for each impact variable, using this variable as response indicator and the vegetation attributes as predictors. We regarded the ordinal WET-Health scores as quasi-numerical and hence decided for a linear model approach to have easily applicable models with intuitively interpretable results. In each regression model, the intercept was forced to zero to simulate a complete loss of properties at highest disturbance levels. The predictor variables for each model were selected following a both-direction stepwise procedure using Bayesian information criterion (BIC; Schwarz, 1978) which estimates the "in-sample prediction error" and penalizes the number of parameters. We preferred the BIC over the closely related Akaikés information criterion (AIC; Akaike, 1974) in order to get less complex models, as the BIC includes a higher penalty on the number of parameters than the AIC (Hastie et al., 2009). At each step, one variable was added to or removed from the model until reaching the lowest possible BIC value. Subsequently, the candidate regression models with the lowest BIC values were selected and applied (Hastie et al., 2009). The accuracy of each model was estimated by root mean square error (RMSE) (Janssen & Heuberger, 1995) and the modified coefficient of efficiency (E1) (Legates & McCabe, 1999). A fivefold-cross validation was performed and the root mean square prediction error (RMSPE) was calculated (Hastie et al., 2009). Five folds were chosen according to Hastie et al. (2009) who recommend using either five or ten folds. This process was done in ten repetitions and the mean value for the RMSPE was calculated to reduce the effect of the random selection of the folds in the cross-validation. Mean RMSPEs served to classify the regression models according to their accuracy. All analysis was performed in R (R Core Team, 2017), with the packages cvTools (Alfons, 2012), Metrics (Hamner & Frasco, 2017), stats (R Core Team, 2017) and vegan (Oksanen et al., 2017).

5.2.3 Results

Land uses and their impacts

Most of the 198 study plots were classified as cropland (103), followed by unused plots with semi-natural vegetation (56), grazing lands (25) and fallows (14). In terms of flooding regime, about half of the plots were flooded less than one month per year, of which 49 were never flooded and 51 sporadically flooded. Some 76 plots were flooded longer than one month per year (seasonally flooded) and 22 were classified as permanently flooded. Land use and flooding regime were often depending on each other. All permanently flooded plots were unused, while for all other categories cropland was the dominating land use. Nevertheless, unused plots were also seasonally flooded (13), sporadically flooded (16) and even non-flooded (5). In this matter, the study sites varied. Thus, in the Rwandan study sites around Kigali, 13 out of 17 unused plots were found under permanent flooding, in Kampala out of 25 unused plots 9 were permanently but 16 sporadically or never flooded. In Ifakara and Rumuruti, most unused plots were seasonally flooded. Regarding the land use intensity, more than half of the plots (54%) were permanently used, while 36% were not used. Occasional and seasonal uses represented only 7.5 and 2.5% of the study cases, respectively. Almost all variables covered the complete range of impacts from 0 (high impact) to 1 (no impact). Solely the geomorphological modification did not cover the most severe impact scores (recorded ranges of 0.5–1) as no extreme impacts like large-scale excavations did occur within the assessment units. The vegetation state was generally strongly impacted (mean of 0.34), with especially high impacts for croplands (0.13) but often also in unused patches (0.68). Impact scores regarding hydrological modification were on average moderate (0.60). Table 7 shows the average impact scores for each land use class. Especially for the hydrological modification, there were strong differences between the studied wetlands.

Table 9: Relation between impact levels and land uses. Values are means of the impact variable for all plots with the respective land use. A value of 0 indicates high impact, a value of 1 low impact.

Impact variable	Cropland	Fallow	Grazing land	Unused
Geomorphological modification	0.66	0.82	0.71	0.92
Hydrological modification	0.45	0.71	0.71	0.79
Vegetation disturbance	0.13	0.34	0.44	0.68
Water quality	0.42	0.81	0.52	0.88

Thus, the impact was much higher in the fully drained valley bottomlands of Kigali (0.42) than in the hydrologically untampered floodplain of Ifakara (0.80). Figure 2 shows the result of an ordination (PCA) of the plots using the impact variables and visualizes their relations to both the study sites and the recorded land uses.

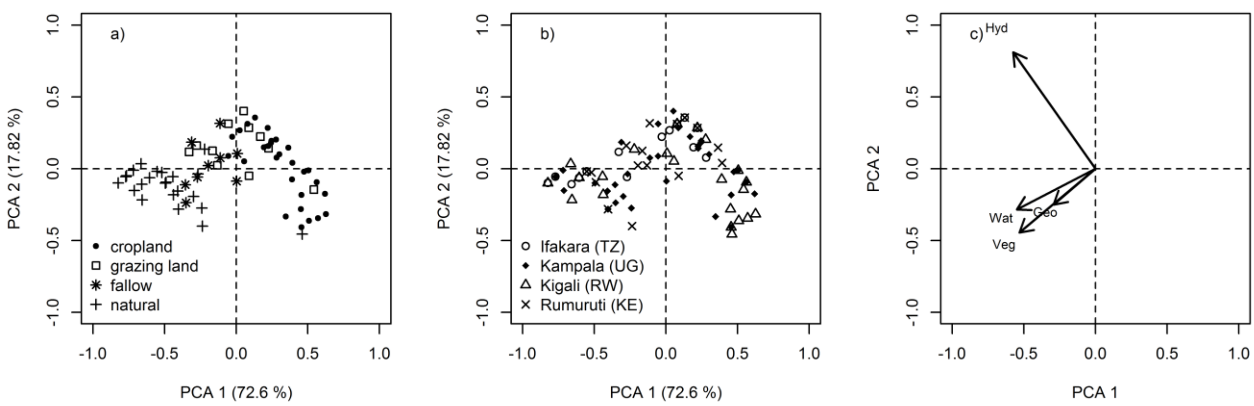

Figure 2: Principal component analysis (PCA) of the plots using the Impact scores, showing (a) the respective land use, (b) the study sites and (c) the loadings of the variables, directing from high to low impact (geo=geomorphological modification, hyd=hydrological modification, veg=vegetation disturbance, Wat=water quality).

Structure of vegetation

Largely undisturbed natural vegetation was dominated by Cyperaceae in Kigali, Kampala and Rumuruti and by Poaceae in Ifakara. To a lesser extent, swamp forest occurred in Kampala and woodland in Ifakara. Poaceae were common on grazing lands and fallows, irrespective of the study site. Croplands exhibited generally the lowest mean values for any vegetation variable, except for "relative cover of annual species" (55%). Very low shares of annual species were on the other hand associated with grazing lands (4%) and unused plots (1%). "Absolute vegetation cover" and "absolute cover of perennial species" showed opposite trends with lowest values for cropland and highest for unused plots. The shares of monocotyledonous species followed a similar trend, but with slightly higher mean values in grazing land (82%) than in unused land (78%). Woody species were generally rare at all sites, covering on average <1% in both croplands and fallows, and reaching 13% of "absolute cover of woody species" in unused plots. "Average height of vegetation" of the wetland vegetation was related to land use with mean heights of 0.2 m in croplands, 0.5 m in grazing lands, 0.8 m in fallows, and 2.5 m in unused plots, reaching up to about 20 m in one forested plot.

In terms of common species, Kigali, Kampala and Rumuruti sites were quite similar, while Ifakara shared only few species with the other sites. Typical species found on croplands and recent fallows in Kampala, Kigali and Rumuruti included *Bidens pilosa* L., *Commelina* spp., *Digitaria velutina* (Forssk.) P.Beauv. (not Rumuruti), *Galinsoga* spp., *Oxalis latifolia* Kunth (only Kigali) and *Schkuhria pinnata* (Lam.) Thell. (only Rumuruti). In grazing sites, *Centella asiatica* (L.) Urb. (not in Rumuruti) and *Cynodon dactylon* (L.) Pers. were typically found. *Cyperus latifolius* Poir. and *Leersia hexandra* Sw. frequently occurred in older fallows and lesser disturbed sites along with *Cyperus papyrus* L. on least disturbed and wettest sites. In some cases, also trees and shrubs of different species occurred, mostly on the fringe zones of the wetlands. In Ifakara, species such as *Acmella uliginosa* (Sw.) Cass., *Eragrostis ciliaris* (L.) R. Br., *Ethulia paucifructa* M.G. Gilbert, and *Paspalum scrobiculatum* L. were common in croplands and recent fallows, while tall grasses such as *Hyparrhenia rufa* (Nees) Stapf, *Panicum fluviicola* Steud., and *Phragmites mauritianus* Kunth occurred in lesser and least disturbed sites. In the fringe zone of the wetland, different shrubs were recorded.

Estimation of impacts using vegetation attributes

For each impact level indicator, predictor variables were selected in a stepwise process in which at every step one variable was added or removed until the regression model reached the optimum (lowest BIC value). Figure 3 depicts the relation between predicted and observed value. Every regression model consisted of between four (geomorphological modification and hydrological modification) and six (water quality) predictor variables. “Relative cover of monocots” was selected in all four regression models and “vertical structure”, “average height”, absolute vegetation cover” and “relative cover of annual species” were selected in three of four regression models. “Absolute cover of Cyperaceae” and “absolute cover of perennial species” were only selected in two or one regression models. “Absolute cover of Poaceae” and “absolute cover of woody species” were not chosen at all. Table 8 shows which vegetation attribute was selected as predictor variable in which regression models and the respective regression coefficients. The regression coefficients are multiplied with the value of the predictor variable for each summed up to the total impact score for the plot. The goodness-of-fit indicators RMSE and E1 varied strongly between regression models. The vegetation disturbance regression model had the lowest error and highest efficiency (RMSE=0.12, E1=0.60). In contrast, the RMSE (0.16) for the geomorphological modification regression model was low, while the efficiency E1 (0.07) was also very low. The values for error and efficiency of the hydrological modification regression model (0.26 / 0.13) and the water quality regression model (0.19/0.36) showed intermediate trends.

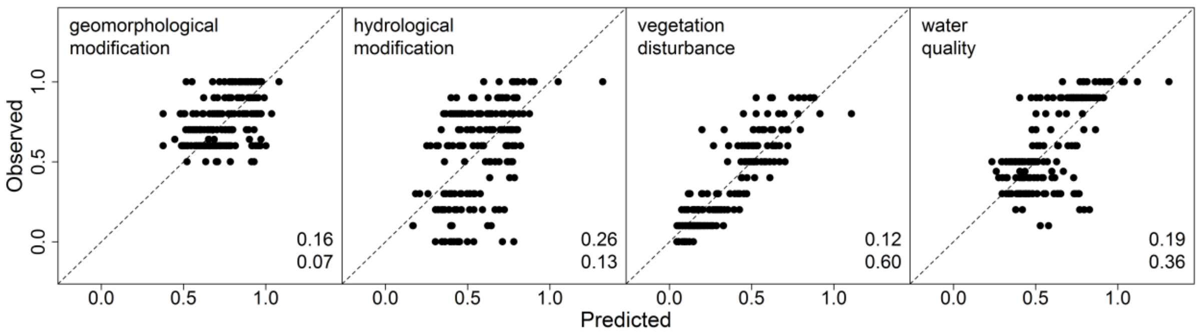

Figure 3: Observed vs. predicted values for each plot. The upper value in the bottom-right corner refers to the root mean square error (RMSE) and the lower value to the modified coefficient of efficiency (E1) of the respective regression model.

Table 10: Predictor variables used in different regression models and their coefficients. The value for each parameter has to be multiplied with the regression coefficient and summed up to the impact value of the plot. The higher the value, the lower the disturbance/degradation.

	Absolute vegetation cover	Vertical structure	Average height	Absolute cover of woody species	Relative cover of annual species	Absolute cover of perennial species	Relative cover of monocots	Absolute cover of Cyperaceae	Absolute cover of Poaceae
Regression models					**Regression coefficients**				
Geomorphological modification	0.0031	0.1773	-	-	0.0028	-	0.0031	-	-
Hydrological modification	0.0042	-	0.0380	-	0.0027	-	0.0034	-	-
Vegetation disturbance	-	0.0372	0.0326	-	-	0.0029	0.0010	0.0027	-
Water quality	0.0030	0.1195	0.0284	-	0.0011	-	0.0022	0.0018	-

Validation
Consistent with the results obtained for RMSE and E1, the regression model for vegetation disturbance turned out being the most accurate (RMSPE of 0.14) followed by the geomorphological modification (0.16), water quality regression models (0.21). Hydrological modification (0.27) had highest prediction error.

5.2.4 Discussion

Assessing wetland's biological integrity and anthropogenic impacts on wetlands facilitate decision-making regarding conservation of wetlands (U.S. EPA, 2002), and may contribute in developing sustainable land use strategies. Vegetation attributes were generally useful indicator variables and hence suitable for predicting anthropogenic impacts on wetlands, however, we observed strong variation of accuracy between the regression models referring to different impacts.

Vegetation attributes as predictor variables
Seven of the nine tested predictor variables were considered in at least one regression model. One variable regarding life span was used in each regression model; "relative cover of annual species" in three and "absolute cover of perennial species" in one. They appeared to be suitable indicators for anthropogenic disturbance in wetlands, as disturbances generally favor annuals and short-living perennials (Grime, 1974). In addition, (Miller et al., 2006) chose the proportion of annuals species with its high positive correlation with disturbance as a metric for their plant-based IBI for headwater wetlands in central Pennsylvania (USA). However, in our regression models for geomorphological modification, hydrological modification and water quality, the regression coefficient of "relative cover of annual species" was positive. This might be because plots with mostly annual plants, and hence low

values for the other predictors in the models, are not necessarily strongly disturbed in terms of geomorphology, hydrology or water quality. The structural variables "vegetation structure", referring to the number of observed layers, and "average height" were selected in most of the regression models. They appear to be useful variables that are also estimated easily in the field, unlike biomass per m^2, which is used in the vegetation-based index of biotic integrity for emergent wetlands (VIBI-EMERGENT) in Ohio (USA) by Mack (2007). In contrast, "absolute cover of woody species" was not used by our regression models, probably because most of the studied wetlands were relatively poor in woody species, independent of land use or disturbance degree. Variables regarding taxonomy were frequently selected. The high-level taxonomy variable "relative cover of monocots" proved to be a suitable indicator and was applied to all four regression models. Variables referring to the monocot-families "Cyperaceae" and "Poaceae" were less useful and could add enough additional information to be selected in the stepwise process only in two regression models ("absolute cover of Cyperaceae") or appeared to be not relevant for any ("absolute cover of Poaceae") in the context of this study. While most unused plots with semi-natural vegetation were dominated by monocots such as *Cyperus papyrus* L. and *Phragmites mauritianus* Kunth, natural swamp forests were dominated by dicotyledonous trees. In the latter case, the predictor "relative cover of monocots" can therefore be misleading. However, in models with multiple predictor variables, this effect may be compensated by variables such as "vertical structure" and "average height".

Other assessments also used taxonomy-related variables, however often on the genus or even species level. Thus, Miller et al. (2006) used the cover of *Phalaris arundinacea* L. While being native in their study area in Pennsylvania (USA), this grass reportedly invades disturbed wetlands, and hence its abundance is positively correlated to disturbance. While such variables may provide suitable indicators for wetlands' biological integrity in specific areas, they are often highly location specific and hence not applicable to broad-based approaches such as the one reported here. Although *Phalaris arundinacea* L. is reported to be introduced also in Kenya, Tanzania and Uganda (CABI, 2017), we did not record this species in any site. We consequently opted to exclude taxonomic variables below the family level. An important difference between our work and other studies refers to variables of status of species regarding origin or habitat. Thus, both numbers and relative shares of invasive and non-native species have been shown to be strongly correlated with disturbance regimes (Miller et al., 2006), and also the sum and relative cover of invasive graminoids was related to disturbance (Mack, 2007). Finally, the WET-Health approach, which was used in this work, includes introduced and invasive species as important components for assessing the vegetation integrity status (Kotze et al., 2012). As these variables were not included in the present study, our regression models cannot differentiate between native and introduced species in the vegetation cover. However, the abundance of invasive species at the study sites was low to moderate, and it may thus not affect the disturbance rating. Apart from introduced weeds in croplands, only *Psidium guajava* L. and *Mimosa pigra* L. showed in some instances relevant cover values. *Eichhornia crassipes* (Mart.) Solms, which is regarded as one of the world's most problematic invasive species in tropical regions outside its South American native range (Midgley et al., 2006), was recorded only in very few plots. Nevertheless, a parameter that covers invasive species may be suitable to improve our regression models or may be required when applying them to wetlands showing high levels of invasion. Mack (2007) applied dominance of "sensitive" and "tolerant" species referring to floristic quality assessment (DeBerry, 2015) while Miller et al. (2006) used a floristic quality assessment index. Such parameters however are currently difficult to apply for East African wetlands, as data at species level are still rare or difficult to obtain.

Prediction capacity of the models

The best performing regression model in terms of RMSPE appears to be the vegetation disturbance model with an RMSPE of 0.14. This good fit of this regression model using vegetation disturbance as a response variable is not surprising, as vegetation attributes were used as predictor variables. However, the score for the vegetation disturbance was applied according to the WET-Health method (Macfarlane et al., 2009) directly in the field before recording the vegetation attributes of which some were afterwards used to calculate biological integrity in this work. While there is some overlap, the approach is generally quite different. The WET-Health score refers to a specific theoretic natural reference state for each plot, takes species composition with an emphasis on ruderal and invasive species into account and also includes additional information such as land use. On the other hand, the regression model developed in this work solely uses vegetation attributes. A challenge regarding all regression models, but especially the vegetation disturbance model, is natural disturbance and variability of wetland vegetation on both spatial and temporal scales. Besides differences between wetlands at different localities, wetlands are generally zonated along hydrological gradients with naturally different vegetation types and hence different vegetation structure (Denny, 1993; Hood et al., 2002; Lind et al., 1974). While wet central zones typically support tall and dense vegetation consisting of graminoid species such as *Cyperus papyrus* L. or *Phragmites mauritianus* Kunth, woody species are rare. Contrarily, vegetation in fringe may be represented by woody species forming vegetation types such as Miombo woodland (Denny, 1993). Additionally, depending on the wetland type, dense swamp forests may occur in the wetland́s center. A relation between land use and spatial differences in the flooding regime can create a certain bias, as permanently flooded sites in the center of the wetland are usually unused, while the outer fringe zones and seasonally flooded wetlands are often used for cropping and / or dry season grazing. Hence, sites of little disturbance in the fringe zone are lacking in many wetlands in the region (Sakané et al., 2011). The situation was similar in our study, with all 22 permanently flooded plots unused, but only about 20 per cent of the plots with a different flooding regime. Especially at the study sites around Kigali, Rwanda, unused plots were rarely found outside the permanently flooded sites. Although this bias could be partly compensated with different ratios at the other study sites, plots of little disturbance in the fringes are still under-represented in the dataset which may lead to a trend of higher integrity values in the central zones of the wetland, independent of anthropogenic disturbances. There are also seasonal patterns in the spatial distribution of land use, as Kuria et al. (2014) described for the Malinda wetland in Tanzania, meaning that cropping and grazing occurred in the fringe zone of the wetland during the rainy season and in the central parts during the dry season. In our study area, this predominantly applied to the site of Ifakara in Tanzania. Also, temporal variability and seasonal disturbance events of natural or and anthropogenic origin other than cropping represent a big challenge in the estimation of biological integrity or degradation using vegetation attributes. This is especially the case in floodplain wetlands in "Tropical Savanna" bioclimates with bimodal rainfall distributions and significant differences between rainy and dry seasons, such as at the Ifakara site. Besides drying of plants due to lack of water during the dry season, fires may burn all above ground parts of plants and hence temporarily imply a very low biological integrity when assessed by our regression models. Although fires have always been a natural process in many ecosystems and even human-made fires have a history in southern Africa of ten thousands of years, fire events are reported to increase in frequency and are nowadays usually human-made (Heinl et al., 2004, 2007). In a study in the Okavango wetland in Botswana, Heinl et al. (2004) concluded that different habitat types in a wetland showed varying responses to fire events but especially seasonally dry floodplain habitats recovered quickly and became very close to unburned sites already in the next rainy season. During or after the rainy season flooding, especially in years with large inflows or rainfalls, flooding can be a major disturbance (Murray-Hudson et al., 2014). However, experience from the field in Ifakara suggest that natural vegetation in the central zone of the floodplain is much less affected by flooding than vegetation of sites previously disturbed by cropping. In addition, grazing activities by wildlife during the dry season, which are a key element of African wetlands, do not necessarily result in degradation (Fynn et al., 2015). They may be mistaken as anthropogenic disturbance by lower scores in the proposed regression models.

With a higher RMSPE of 0.21, the water quality regression model provided also acceptable estimates of disturbance. However, the site impacts on water quality were also linked to the vegetation disturbance as the use of agrochemicals or nutrient enrichment from grazing animals was restricted to disturbed croplands or intensively grazed rangelands and hardly occurred in areas with intact vegetation. Additionally, intact wetlands with typical plant species improve the water quality by filtering water and retaining nutrients much better than disturbed wetlands (Kansiime et al., 2007) and species such as *Cyperus papyrus* L. and *Phragmites mauritianus* Kunth are also used in constructed wetlands for water purification purposes (Okurut et al., 1999). While plant species and vegetation types that are used for water purification can obviously hardly be used as indicators for good water quality, high results in this regression model may still indicate that the respective sites improve water quality rather than decreasing it and vice versa. For detailed studies of water quality, chemical and microbial analysis or assessment methods using sensitive plant or animal species may be inevitable.

Although having the second lowest RMSPE (0.16), the geomorphological modification regression model also has limitations, as the vegetation variables we used could hardly predict disturbances that happened in the more distant past, such as the excavations and (re-)filling of the land. The very low efficiency E1 of 0.07 underlines the limitations of this regression model. Similarly, the hydrological modification regression model (0.27) could not predict past drainage. Thus, the actual conditions of drained, but formerly flooded areas may be similar to those of undrained areas that have never been flooded.

Application in the field and for ex-post analysis

We see two potential applications of the proposed vegetation-based assessment approach of wetlands:

(1) The approach can be applied in the field using a plot-based sampling strategy, whereby the plot selection can either be preferential or randomized, depending on the objective (Dengler et al., 2008). For assessing the variation of wetland conditions, a preferential selection may be preferred. In this case, the researcher delineates the plots in the field. While this approach can reduce noise, e.g. by excluding inhomogeneous plots containing different land uses or elements such as termite mounds or ditches, it is on the other side not free of bias. Hence, a randomized sampling with previously selected cells from a grid may be superior to obtain a representative value for a whole wetland or a larger hydro-geomorphological subunit (HGM; Kotze et al., 2012). A plot size of 100 m^2 (10 m by 10 m) proved to be practical and manageable in our study. To achieve ease and rapidity of wetland assessment, a full list of species at plot level may not be required, as species with low number of individuals and low cover values do not have much influence on the values of the variables. However, it is important to record the trait of species (e.g. annual, woody) and the higher taxon (e.g. Cyperaceae). Identification to species level is not necessarily required. The predictor variables used in the regression models can be directly estimated in the field ("absolute cover of perennials", "absolute cover of Cyperaceae" etc.). However, recording of dominant species is recommended.

(2) The approach may allow an ex-post application to already collected plot-based data, provided that values of the vegetation property parameters can be derived. Hence, full species lists with cover values as well as structural parameters are necessary. While values regarding vegetation cover, height or

structure are normally part of the header data of a vegetation survey, information such as the lifeform (Raunkiaer, 1907) is additionally needed. To calculate for example the “relative cover of annual species”, all cover values of therophytes recorded in the plot are added up and divided by the cover values of all species.

In both cases, values for each metric are entered into a table, multiplied with the respective regression coefficients, and summed up for the final score for each regression model. Hence, a plot has four scores for the different impacts. Depending on the objective and sampling method used, the results may be extrapolated on the whole wetland or hydro-geomorphic unit. An example for the calculation is provided as electronic supplement.

While the proposed assessment strategy may not be suited for saline wetlands, littoral regions of lakes, for inland valleys in altitudes above 2000 m (Lind et al., 1974), it has been shown to be applicable to valley bottoms and floodplains, possibly also beyond the East African region.

5.2.5 Conclusions

The findings indicate that disturbance intensity of East African wetlands can be assessed to a certain extent, using simple vegetation attributes. The assessment tool may be used as a stand-alone methodology, but also offers possibilities to support other assessment schemes, especially the WET-Health approach. The proposed methodology is based on few predictors and hence easily applicable to floodplains and valley bottom wetlands. In addition, we see a potential for an ex-post application to vegetation databases and to historical data records. Nevertheless, the method has its limitations especially when used as a stand-alone method as spatial and temporal variability of wetland vegetation can affect the accuracy of the regression models. Further, a method based on vegetation attributes is limited in assessing specific aspects of geological and hydrological modification or water quality and can therefore only give a trend. Further work aims at refining the regression models using additional data from other wetlands in the region. Along with a recalibration of the regression models, further metrics may be added or modified to achieve results that are more accurate. Data collected during different seasons may help to reduce the shortcomings caused by seasonal variability in wetlands. A validation with proxies of disturbance or biological integrity assessed with other methods than used in this work would be useful for a better evaluation of the chances and limitations of this approach. Eventually, the assessment methods might be extrapolated to cover more and different wetland types in East Africa and beyond.

Supplementary data associated with this article can be found, in the online version, at http://dx.doi.org/10.1016/j.ecolind.2018.02.017. These data include Google maps of the most important areas described in this article.

6 Diversity

Different pland associations: *Grangeo maderaspatanae-Ipomoeetum aquaticae* (top left) and *Phragmitetum mauritiani* (top right) in Kilombero floodplain, Tanzania, *Cypero denudati-Fuirenetum pubescentis* (bottom left) and *Cyperetum latifolii* (bottom right) in Namulonge valley, Uganda.

6.1 Small wetlands in East Africa: A field guide to the representative flora

This chapter refers to the aspect of floristic diversity in East African wetlands. It is a guidebook about representative species. I co-authored the species descriptions and contributed pictures. In the following, a short description of the book is given. It was published as a self-published book as:

Becker, M., Alvarez, M., **Behn, K.,** Möseler, B. M., Handa, C., Oyieke, H., Misana, S., & Mogha, N. (2014): Small wetlands in East Africa: A field guide to the representative flora. Selbstverlag, Bonn. Germany. 202 pp. ISBN 978-3-00-047349-4.

Wetlands are areas where water is the primary factor controlling the environment for plant and animal life. They harbor a huge biodiversity with many species depending on wetland ecosystems. However, a substantial share of wetlands has been transformed into sites of intensive agricultural production. Varying environmental conditions interacting with a gradient of land use intensity result in ecological niches occupied by different types of plants. In this book, 80 species plants occurring in East African wetland are presented, and are ordered in the following categories:

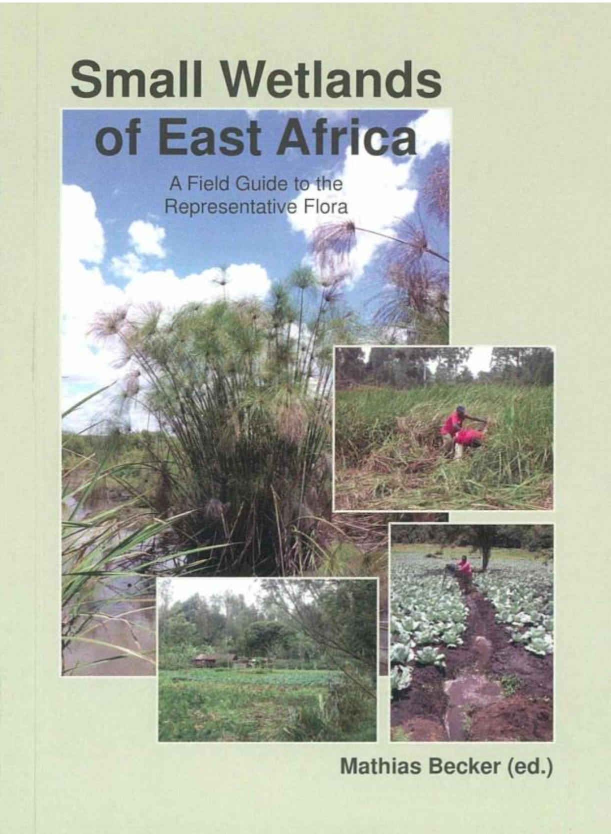

Figure 4: Cover of the book "Small Wetlands of East Africa – A Field Guide to the Representative Flora".

1. **Aquatic species** - Aquatic and amphibious species occurring in open water, either free floating plants or with floating leaves

2. **Riparian species** - Riparian, helophyte species of permanent or near permanent flooded soils

3. **Grassland species** - Species of wet grasslands and seasonally flooded soils

4. **Pioneer species** - Pioneer, opportunistic plants occurring after strong disturbances events

5. **Weeds of flood-tolerant crops** - Wetland weeds associated to flood-tolerant crops

6. **Terrestrial weeds** - Terrestrial weeds occurring in drained wetlands

All species are described regarding their growth form and morphology, their ecology, and their usefulness and importance. Additional to the scientific names, English and Swahili names were added wherever possible. The book aims at land use planers, students, development agents, and interested farmers to identify major wetland species to guide ecological assessment of wetland ecosystems.

6.2 Vegetation diversity in East African wetlands: Cocktail algorithms supported by a vegetation-plot database

This chapter is based on:

Behn, K., Alvarez, M., Mutebi, S., & Becker, M. (2022). Vegetation diversity in East African wetlands: Cocktail algorithms supported by a vegetation-plot database. *Phytocoenologia 51(3),* 199-219. https://doi.org/10.1127/phyto/2022/0392

Abstract

Aims: Wetlands in East Africa are important ecosystems for biodiversity conservation and ecosystem service provisioning yet threatened by degradation and conversion into croplands. Conservation and land use management require data on vegetation structure and dynamics. The presented work is a response to a lacking consistent classification of East African wetland vegetation. Location: Namulonge valley in Uganda and Kilombero floodplain in Tanzania. **Methods**: We sampled 431 4 m²-plots along land use intensity and flooding duration gradients. A floristic classification using the Cocktail method was performed in a two-step approach. We developed definitions for vegetation units, using plot observations from the study sites in a first step and revised them in a second step by adding data from a vegetation-plot database and complied the definitions to an expert system for classification. Resulting vegetation units were analyzed regarding their life form composition, for which we implemented a classification based on life span and growth form. Following a literature review, the identified vegetation units were assigned either to existing phytosociological associations or proposals. **Results**: We recognize eight units of marsh and reed vegetation (class *Phragmito-Magno-Caricetea*) and five units of weed and pioneer vegetation under semi-aquatic conditions (class *Oryzetea sativae*). Five of these associations were previously described in the bibliographic references. The remaining eight are newly described in this work. The associations contrast in their life form composition with the five *Oryzetea sativae* associations dominated by obligate annuals and the *Phragmito-Magno-Caricetea* associations dominated by either reed plants or lacking a dominating life form. **Conclusions**: The developed expert system enables a comparison of wetland vegetation in the East African region, and will support vegetation science and informed decision making about land use management and conservation. The two-step approach of revising a classification developed for single wetlands with a database is promising for data-scarce regions.

Keywords: Braun-Blanquet, Cocktail classification, floodplain, formalized classification, functional diversity, inland valley, phytosociology, semi-aquatic vegetation, syntaxonomy.

6.2.1 Introduction

Wetlands are important ecosystems for biodiversity conservation (Denny, 1994), supporting water regulation and carbon sequestration, and contributing to local people´s livelihoods. For instance, they provide food and medicinal plants, building material, are sites for hunting and fishing as well as grazing sites for animals (Dam & Kipkemboi, 2011; Mombo et al., 2011). Beyond that, wetlands can be of cultural or spiritual importance (Gardner & Finlayson, 2018). Wetlands are increasingly used for crop production due to prolonged water availability and usually fertile soils (Sakané et al., 2011). Main drivers of these land use changes have been population growth, lack of arable uplands and alternative livelihood strategies (Namaalwa et al., 2013). Policy development programs may explicitly focus on using wetlands for agricultural production to meet the countries´ food needs or for international trade (Dixon & Wood, 2003). In turn, wetland protection policies are often either weak or poorly enforced (Mombo et al., 2011). Other threats to wetlands comprise land filling, construction of dams, extraction of water and sediments, excessive applications of agro-chemicals, and the introduction of invasive species (Kotze et al., 2012), potentially leading to their degradation, loss of biodiversity, and diminish their ability of provisioning ecosystem services (Schuyt, 2005). For informed decision-making, data on the dynamics, diversity and structures of wetlands are required. Vegetation types can hereby serve as a useful tool, both for research and ecosystem management as they can indicate site conditions, hemeroby or ecological processes. For instance, phytosociological units according to the Braun-Blanquet approach play a very important role in the legislation and practical implementation of conservation network Natura 2000 in the European Union (Dengler et al., 2008).

Diverse procedures have been used to classify vegetation units, ranging from purely numerical methods (unsupervised classification) such as hierarchical clustering, over supervised classification to expert-based definitions (semi-supervised and supervised classifications). These classification methods may be based on different criteria such as floristic composition, physiognomy or functional traits (de Cáceres et al., 2018; de Cáceres & Wiser, 2012). In this work, we follow the Braun-Blanquet approach using species composition to define syntaxa (Braun-Blanquet, 1964) and apply the Cocktail Classification (Bruelheide, 1997; Kočí et al., 2003). Available wetland classifications following the Braun-Blanquet approach have been formerly conducted in the Democratic Republic of the Congo (incl. the former Belgian Congo and Zaire, in the following referred to as DRC) (e.g., Lebrun, 1947; Nyakabwa, 1981), in South Africa (e.g., (Furness & Breen, 1980), and in East Africa (Alvarez, 2017).

To complement, improve, and ease the vegetation classification in East Africa, we applied an approach starting by classifying data from two wetlands and revising the outcome, using available vegetation-plot data with the following objectives: (1) to classify the vegetation of East African wetlands using the

Cocktail method; (2) to consolidate this classification in the context of the Braun-Blanquet approach comparing surveys' data with plot-observations stored in a database; and (3) to find the correspondence of this floristic classification with life forms and chorology.

6.2.2 Material and methods

Study sites

The data were collected at two study sites, Namulonge in Uganda and Ifakara in Tanzania (Figure 5), representing an inland valley and a floodplain, the dominant wetland types in East Africa (Leemhuis et al., 2016).

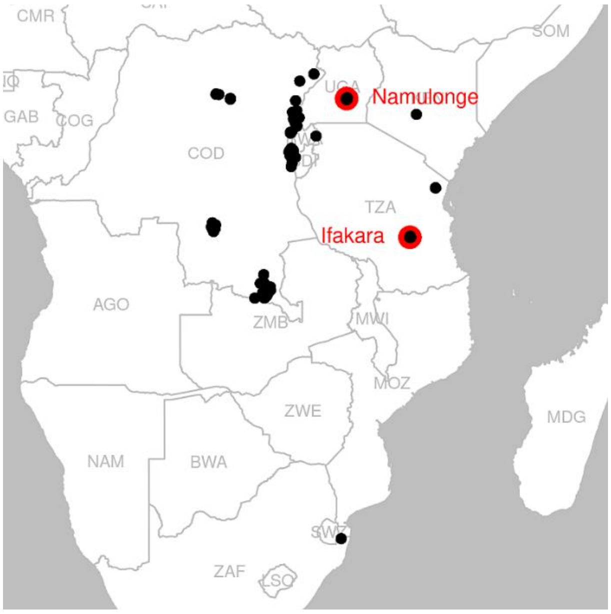

Figure 5: Location of assessed plot observations in Sub-Saharan Africa. In gray color are oceans, borderlines and the abbreviation of the respective countries. Red circles and labels indicate the location and name of field surveys in Uganda and Tanzania. Black dots indicate the location of plot observations used in the database assessment.

Namulonge is situated in Central Uganda, about 30 km northeast of Kampala. It lies at an elevation of approximately 1,100 m a.s.l. and consists of the Namulonge valley and adjacent smaller inland valleys. According to the classification of Köppen-Geiger, Namulonge is at the transition between the "Tropical Monsoon" and the "Tropical Rainforest" bioclimates (Peel et al., 2007). It has an average annual rainfall of 1,291 mm with a bimodal pattern and an annual average temperature of 22 °C (Behn et al., 2018; Hijmans et al., 2005)Soils in the valley bottom lands belong the groups of Gleysol, Fluvisol and Histosol in the classification of the World Reference Base for soil resources(IUSS Working Group, 2015) . Most of the study locality belongs to the National Crops Resources Research Institute (NaCCRI) and has a long history of crop cultivation (mainly maize, tomato and sweet potato on valley slopes and rice in the lowlands). While the central stream of the Namulonge valley was modified to provide drainage and stream derivation irrigation for crop growth in the wetland (Gabiri et al., 2018b), large areas are left to fallow in different succession stages, and also patches of pristine vegetation occur. The latter ones are characterized by papyrus marshes and swamp forests.

Ifakara is located in the floodplain of the Kilombero River, close to the city of Ifakara in Tanzania at an elevation of 250 m a.s.l. The bioclimate is considered a "Tropical Savanna" with an average annual rainfall of 1,427 mm with a distinct dry season from June to October and an annual average temperature of 25 °C (Hijmans et al., 2005). The predominant Fluvisols have silt loam and silty clay loam textures with the clay content increasing towards the river (Gabiri et al., 2018a). Large parts of the floodplain are submerged during the long rainy season from March to May and are widely used for rice cultivation. Maize and sweet potatoes are often grown in the drought-prone fringes, as well as during the dry season. While the cropland area has increased dramatically in the last decades (Leemhuis et al., 2017), some parts remain largely undisturbed or are used for extensive dry season grazing. These parts are characterized by edaphic grasslands dominated by tall grasses such as *Phragmites australis* and *Panicum fluviicola*. Towards the fringes of the floodplain, the duration and depth of soil submergence decreases and grasslands are gradually replaced by Miombo woodland (Hood et al., 2002).

Vegetation sampling

Vegetation was sampled at both localities between September 2014 and December 2016. Plots were chosen preferentially (Dengler et al., 2008) along gradients of land use (cultivated, recent and older fallows, unused or recovered sites) at different positions in the wetland (drought-prone fringe to submergence-prone riparian zone). In 431 plots of 4 m² (2 m by 2 m), all vascular plants were recorded and their abundance was estimated as cover percentage. Besides species, structural data such as height of the stands, total cover, as well as available information on site conditions such as flooding intensity or anthropogenic influences such as land use were recorded. If feasible, plant species were identified directly in the field. In the cases where this was not possible on the field, specimens were collected, pressed and mounted for their determination at the East African Herbarium, National Museums of Kenya, in Nairobi.

Life forms and chorology of species

Habit and lifespan of species were derived from Flora of Tropical East Africa (Polhill, 1949-2010), The IUCN Red List of Threatened Species (IUCN, 2020; POWO, 2021), and Plants of the World Online (POWO, 2021). Based on these data and considering the Raunkiær system (Mueller-Dombois & Ellenberg, 1974), the works of Den Hartog & Segal, 1964), Boutin & Keddy (1993) and Ewel & Bigelow (1996), we developed a life form classification, defining eight major life forms to which species were assigned (Table 5). We further classified species by their origin in Sub-Saharan Africa. Species were considered as “native” if their native range following POWO (2021) includes parts of Sub-Saharan Africa. Otherwise, species were classified as “introduced”.

Table 11: Overview of life forms used in this work for classifying East African wetland vegetation with their description

Life form classes	Description
Obligate annual	Plant species completing their life cycle in one season without the capacity to persist for longer.
Facultative annual	Short living perennials (including biennial plants) without lateral spread and relatively weak root system. Includes perennial plants able to complete a life cycle in one season under adverse conditions or annuals able to persist for longer than one season if the conditions allow it.
Tussock plant	Perennial species with little lateral spread due to longitudinally compressed rhizomes. Includes also perennial herbs with woody base.
Reptant plant	Prostrate plants developing long rhizome or stolons.
Phanerophyte	Species with woody stems, growing as tree or shrub, including palms
Climbing plant	Climbing species, herbaceous or woody.
Reed plant	Tall herbs with clonal spread by rhizomes and well developed aerenchyma in their tissues as adaptation to saturated conditions in the ground.
Acropleustophyte	Plants growing in or on the water surface, not sessile to the ground.

Data preparation

Besides the collected field data, we used relevés collected from nine publications (Alvarez, 2017; Furness & Breen, 1980; Germain, 1951; Lebrun, 1947; Mullenders, 1954; Nyakabwa, 1981; Schmitz, 1971; Szafranski & Apema, 1983; Taton & Risopoulos, 1955). The localities of these works are shown in Figure 5. The relevés were imported to R (R Core Team, 2019) from SWEA-Dataveg (GIVD ID AF-00-006) (Alvarez et al., 2021) and subsequently unified to a common taxonomy. As different cover scales were used in the sources, cover values were converted to percent values using the “transform()” function with the rule “middle” (i.e. midpoint transformation). For further statistical analysis, we reclassified all cover values into four classes, namely 1 (0-25%), 2 (25-50%), 3 (50- 75%), and 4 (75-100%), to achieve a better comparability of data recorded in different scales and enhancing the floristic contrast between plots. Further, sub-specific taxa were merged at species level using the R-packages “vegtable” (Alvarez, 2021) and “taxlist” (Alvarez & Luebert, 2018).

Vegetation classification

We classified vegetation using the Cocktail method (Bruelheide, 1997), a supervised classification, merging external information on species ecology with statistically proven co-occurrence of species in the data set to obtain species groups. Based on these species groups, definitions of vegetation units were developed (Dengler et al., 2008). We focused on wetland vegetation and disregarded plots of aquatic vegetation and those of terrestrial weed communities. The classification was constructed through an iterative process (Figure 6). The process started with an experience-based preliminary classification (1) and the identification of species groups (2) based on ecological preferences and co-occurrence following (Kočí et al., 2003). In steps (3) and (4), a classification was revised using the reviewed species groups. To recognize vegetation units according to the occurrence of a species group, the group was considered to be present in a relevé if at least half of the species occurred (Kočí et al., 2003).

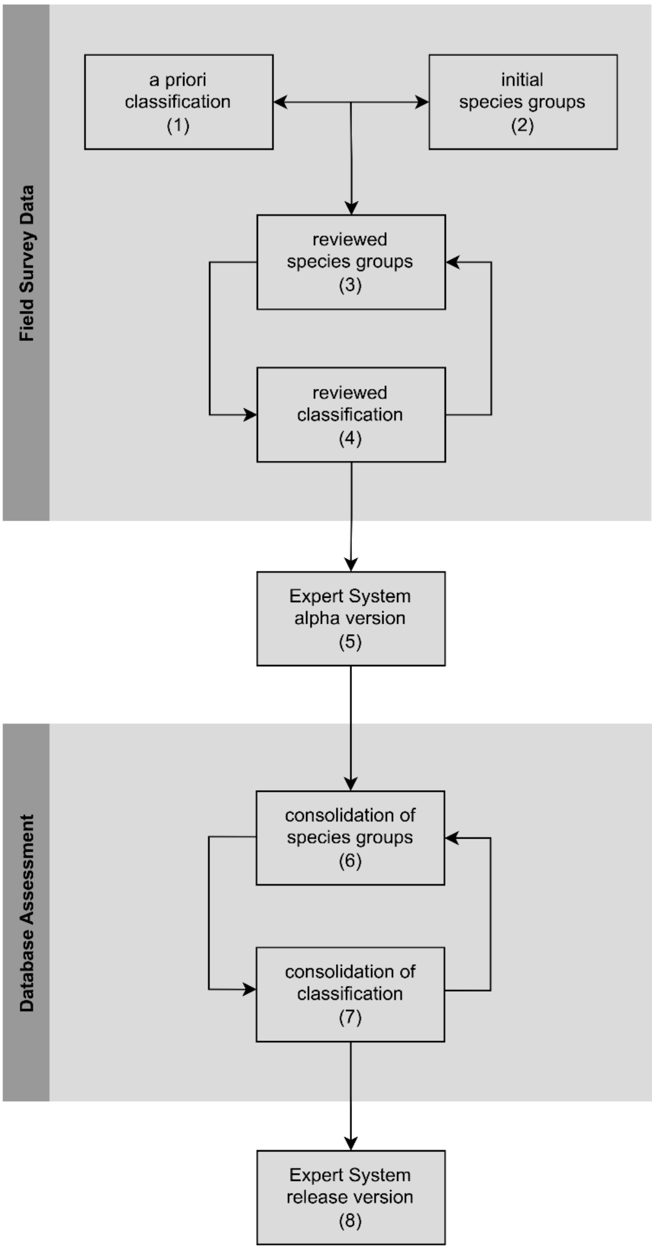

Figure 6: Workflow for the design of classification algorithms and their compilation in an expert system for wetland vegetation in East Africa. The classification is restricted to a field survey in the first stage and in a second stage expanded to data stored in a vegetation-plot database. After digitizing data, a table is produced, arranging plots according to a classification based on the experience of collectors in the field (1), at the same time species groups discriminating these a-priori vegetation units are preliminarily selected (2). Cocktail definitions are developed in an iterative process of improving classification and finding diagnostic species according to fidelity measurements (3 and 4). This step results in an expert system optimized for the field survey data (5). In a second step the classification will be extended to data stored in a vegetation-plot database in order to recognize related vegetation units. Both, classification and definition of species groups (6 and 7) will be done in an iterative process including the calculation of fidelity measures and an exhaustive review of bibliographic references. This procedure results in an improved expert system (8) exploiting the maximum of available data.

The species groups were subsequently adjusted by adding species with higher and removing species with lower phi-value. Threshold phi-value slightly differed between species groups as we aimed at creating ecologically coherent groups of three to six species. The fidelity of species to a vegetation unit was calculated using the phi-coefficient with an equalization of the group sizes (Tichý & Chytrý, 2006) and tested for significance using Fischer´s exact test at $p < 0.001$ (Chytrý et al., 2002) as implemented in JUICE (Tichý, 2002). Steps (3) and (4) were repeated until meaningful and sound species groups emerged with no other species having a higher phi-value than those in the defining group. Since wetland vegetation is often characterized by species-poor stands, dominated by perennial grasses or sedges (Landucci et al., 2013), cover values of single species were used in the definition of Cocktail algorithms, setting threshold levels to 25 and 50% (Kočí et al., 2003) resulting in a preliminary expert system (5). The algorithm was applied to the dataset, species groups and unit definitions were manually adjusted, and the previous steps were repeated (6 and 7). The aim was to clearly separate units and to reduce double-classifications. In later steps, also exclusion criteria were added to avoid the classification of unsuitable plots. For the vegetation units as classified by the final expert system (8), we then determined diagnostic, constant, and dominant species. The species were considered diagnostic when their phi-value exceed 0.3 and was significant at $p < 0.001$ (Fisher´s exact test) (Chytrý et al., 2002). Constant species were defined as species occurring in more than 50% of the plots of a vegetation unit. Dominant species had an average non-zero cover higher than 25% and occurred in at least 25% of the plots.

Nomenclature review

In a final step, all units were assigned to a phytosociological association according to Braun-Blanquet (Westhoff & Van Der Maarel, 1978). Whenever possible, we used associations that had already been described and had been assigned a valid name. For the remaining units, we gave new names according to the International Code of Phytosociological Nomenclature 4th edition (Theurillat et al., 2021). For new described associations, holotypes were assigned. In cases of previously described associations without assigned types, lectotypes were selected among plot observations containing most of the diagnostic species for the respective association. The arrangement of the higher syntaxa (class, order, and alliance) considered physiognomy, characteristic species composition, and ecological preferences of the associations, following Schmitz (1988) and the critical revision of higher syntaxonomic ranks by (Alvarez, 2017).

Diversity assessment

In order to display floristic relationships between vegetation units and to infer ecological gradients, we used a detrended correspondence analysis (DCA), considering the heterogeneity of the assessed data set and the expected unimodal response of species composition to environmental gradients (Lepš

& Šmilauer, 2003). For this, we used the function “decorana()” of the R-package “vegan” (Oksanen et al., 2020).

We used reclassified cover values and only diagnostic species for ordinations to stress the differences between vegetation units, excluding both species with broad ecological amplitude and rare species.

The goodness of the final classification was tested by multiple response permutation procedure (MRPP). We applied the function “mrpp()” of the package “vegan”, setting the dissimilarity to “Bray-Curtis” weighted on group size and the permutation number to 500 (Oksanen et al., 2020). Reclassified cover values were used also here. To assess the contrasts between the vegetation units, we further calculated the proportions of each life form and the proportion of introduced species for every plot weighted by their cover value with the function “trait_proportion()” of the package “vegtable” (Alvarez, 2021). To test for significant differences between the vegetation units regarding the proportions of each life form and of introduced species, we used the Kruskal-Wallis test (function “kruskal.test()” of the package “stats”) (R Core Team, 2019). For a pairwise comparison we used the Kruskal pairwise test (function “kruskal()” from the package “agricolae”) (de Mendiburu, 2019). We further calculated the proportion of dominant families weighed on cover for each association.

6.2.3 Results

Assessed data set

In total, we pre-selected 1,566 plot observations, which were used for fine-tuning the classification. Some 431 of them were collected in the field at the two described sites (Ifakara and Namulonge). The final classification considers a subset of 289 plot observations collected nine sources (Supplement S5) and distributed in seven countries. This subset includes records of 335 vascular plant species classified in 62 families (see Supplement S1 for a checklist and Supplement S2 for a list of used synonyms).

Syntaxonomic classification

We defined eight distinct species groups (Table 12) and formal definitions for 13 vegetation units corresponding to phytosociological associations (Table 13). These groups are related to both the wetlands hydrology types (floodplain vs. inland valley) and to the type and level of anthropogenic disturbances.

Table 12: Sociological species groups used in the classification, their member species and the respective family and life form (based on field survey in an inland valley in Uganda and a floodplain wetland in Tanzania, 2014-2016 and secondary data sources)

Species group	Species	Family	Lifeform
***Centrostachys aquatica* Group**	*Centrostachys aquatica*	Amaranthaceae	obligate annual
	Coldenia procumbens	Boraginaceae	obligate annual
	Glinus lotoides	Molluginaceae	obligate annual
	Heliotropium indicum	Boraginaceae	obligate annual
	Pycreus polystachyos	Cyperaceae	obligate annual
***Corchorus fascicularis* Group**	*Corchorus fascicularis*	Malvaceae	obligate annual
	Hibiscus cannabinus	Malvaceae	obligate annual
	Hyptis spicigera	Lamiaceae	obligate annual
	Ipomoea eriocarpa	Convolvulaceae	obligate annual
	Melochia corchorifolia	Malvaceae	obligate annual
	Panicum hanningtonii	Poaceae	obligate annual
***Cyperus difformis* Group**	*Cyperus difformis*	Cyperaceae	obligate annual
	Cyperus distans	Cyperaceae	facultative annual
	Echinochloa haploclada	Poaceae	tussock plant
	Kyllinga odorata	Cyperaceae	tussock plant
	Panicum subalbidum	Poaceae	facultative annual
***Cyperus papyrus* Group**	*Cyclosorus interruptus*	Thelypteridaceae	tussock plant
	Cyperus papyrus	Cyperaceae	reed plant
	Desmodium salicifolium	Fabaceae	climbing plant
***Fuirena ciliaris* Group**	*Ammannia senegalensis*	Lythraceae	obligate annual
	Fimbristylis bisumbellata	Cyperaceae	obligate annual
	Fimbristylis quinquangularis	Cyperaceae	obligate annual
	Fuirena ciliaris	Cyperaceae	obligate annual
	Pycreus pumilus	Cyperaceae	obligate annual
***Fuirena pubescens* Group**	*Cyperus denudatus*	Cyperaceae	reptant plant
	Fuirena pubescens	Cyperaceae	tussock plant
	Torenia thouarsii	Linderniaceae	tussock plant
***Ischaemum rugosum* Group**	*Acmella uliginosa*	Asteraceae	obligate annual
	Courtoisina cyperoides	Cyperaceae	obligate annual
	Schizachyrium brevifolium	Poaceae	obligate annual
	Ischaemum rugosum	Poaceae	obligate annual
	Pycreus macrostachyos	Cyperaceae	obligate annual
***Melanthera scandens* Group**	*Hyptis lanceolata*	Lamiaceae	facultative annual
	Ipomoea cairica	Convolvulaceae	climbing plant
	Melanthera scandens	Asteraceae	climbing plant

Table 13: Cocktail definition for each unit identified from field surveys in an inland valley in Uganda and a floodplain wetland in Tanzania, 2014-2016, as well as from secondary data sources.

Number	Cocktail definition
1	*Ischaemum rugosum* GROUP AND NOT *Panicum hanningtonii* > 50%
2	*Fuirena ciliaris* GROUP
3	*Corchorus fascicularis* group AND *Panicum hanningtonii* > 25%
4	*Ipomoea aquatica* > 25%
5	(*Centrostachys aquatica* GROUP OR *Centrostachys aquatica* > 25%) AND NOT *Cyperus fastigiatus* > 25%
6	*Cyperus difformis* GROUP
7	*Fuirena pubescens* GROUP OR *Fuirena pubescens* > 25%
8	*Melanthera scandens* GROUP AND NOT *Cyperus papyrus* > 50%
9	*Cyperus latifolius* > 25%
10	(*Cyperus papyrus* GROUP AND (*Cyperus papyrus* > 25% OR *Cyclosorus interruptus* > 25%)) OR *Cyperus papyrus* > 50%
11	*Phragmites australis* > 50% AND NOT *Echinochloa pyramidalis* > 25%
12	*Phragmites australis* > 25% AND *Echinochloa pyramidalis* > 25%
13	*Panicum fluviicola* > 25%

Table 14: Table of holotypes of associations newly described in this work. All cover values are in percent. Percent values in bold indicate that this species is in this work regarded as a diagnostic species for the respective association.

Column number	1	2	3	4	5	6	7	8
Association.	1	2	3	4	6	7	8	13
Relevé number	3467	3532	3488	3596	3664	3692	3733	3576
Country	TZ	TZ	TZ	TZ	UG	UG	UG	TZ
Record date	07.05. 2015	24.06. 2015	24.06. 2015	31.07. 2016	09.01. 2015	19.10. 2015	06.08. 2016	22.06. 2015
Plot size (m²)	4	4	4	4	4	4	4	4
Elevation (m a.s.l.)	255	250	249	250	1105	1107	1105	250
Longitude (degr.)	36.712	36.701	36.690	36.690	32.642	32.641	32.642	36.696
Latitude (degr.)	-8.128	-8.155	-8.172	-8.173	0.521	0.520	0.521	-8.176
Ischaemum rugosum	**40**	.	.	.	.	.	.	.
Pycreus macrostachyos	**20**	.	.	.	.	.	.	.
Acmella uliginosa	**5**	.	.	.	.	.	.	.
Echinochloa colona	**5**	.	.	.	.	.	.	.
Eragrostis japonica	**3**	.	.	.	.	.	.	.
Basilicum polystachyon	**2**	.	.	.	.	.	.	.
Courtoisina cyperoides	**2**	.	.	.	.	.	.	.
Aeschynomene indica	2	.	.	.	.	.	.	.

Azolla pinnata	1	.	.	.	.	.	.	.
Corchorus olitorius	1	.	.	.	.	.	.	.
Oryza sativa	**2**	**35**	.	.	2	.	.	.
Fuirena ciliaris	.	**10**	.	.	.	.	.	.
Fimbristylis quinquangularis	.	**10**	.	.	.	.	.	.
Fimbristylis bisumbellata	2	**5**	.	.	.	.	.	.
Bulbostylis hispidula	.	5	1	.	.	.	.	.
Pycreus pumilus	.	**3**	1	.	.	.	.	.
Oldenlandia fastigiata	.	2	.	.	.	.	.	.
Cyperus foliaceus	.	**2**	1	.	.	.	.	.
Ammannia senegalensis	.	**1**	.	.	.	.	.	.
Ammannia auriculata	.	**1**	.	.	.	.	.	.
Phyllanthus spec.	.	1	.	.	.	.	.	.
Panicum hanningtonii	.	**3**	**87**	.	.	.	.	.
Hibiscus cannabinus	.	.	**3**	.	.	.	.	.
Hygrophila auriculata	.	1	**3**	.	.	.	.	.
Melochia corchorifolia	1	.	**3**	.	.	.	.	.
Corchorus fascicularis	.	1	**2**	.	.	.	.	.
Ipomoea eriocarpa	.	.	**2**	.	.	.	.	.
Oryza longistaminata	.	.	**2**	.	.	.	.	.
Hyptis spicigera	.	.	**1**	.	.	.	.	.
Indigofera spec.	.	.	1	.	.	.	.	.
Ipomoea aquatica	.	3	.	**65**	.	.	.	.
Grangea maderaspatana	.	.	.	**10**	.	.	.	.
Leptochloa panicea	.	.	.	**5**	.	.	.	.
Merremia hederacea	.	.	.	**5**	.	.	.	2
Paspalum scrobiculatum	.	.	.	2	2	1	.	1
Sphaeranthus africanus	.	.	.	2	.	.	.	.
Persicaria senegalensis	.	.	.	1	.	.	.	.
Cyperus difformis	.	.	.	.	**40**	.	.	.
Cyperus distans	.	.	.	.	**30**	.	.	.
Panicum subalbidum	.	.	.	.	**20**	.	.	.

Ageratum conyzoides	.	.	.	.	10	2	.	.
Echinochloa haploclada	.	.	.	.	**5**	.	.	.
Digitaria abyssinica	.	.	.	.	**5**	.	.	.
Eleusine indica	.	.	.	.	5	.	.	.
Diplachne caudata	.	.	.	.	5	.	.	.
Kyllinga odorata	.	.	.	.	**2**	.	.	.
Kyllinga bulbosa	.	.	.	.	1	.	.	.
Eclipta prostrata	.	.	.	.	1	.	.	.
Fuirena pubescens	.	.	.	.	.	**65**	.	.
Vigna heterophylla	.	.	.	.	.	30	.	.
Cyperus denudatus	.	.	.	.	.	**5**	.	.
Crassocephalum vitellinum	.	.	.	.	.	**5**	.	.
Torenia thouarsii	.	.	.	.	.	**2**	.	.
Commelina diffusa	.	.	.	.	.	1	.	.
Oldenlandia corymbosa	.	.	.	.	.	1	.	.
Desmodium setigerum	.	.	.	.	.	1	.	.
Phyllanthus amarus	.	.	.	.	.	1	.	.
Ipomoea cairica	.	.	.	.	.	.	**35**	.
Triumfetta brachyceras	.	.	.	.	.	.	**30**	.
Ludwigia abyssinica	.	2	.	.	.	1	15	.
Melanthera scandens	.	.	.	.	.	.	**10**	.
Polygonum pulchrum	.	.	.	.	.	.	10	.
Leersia hexandra	.	.	.	.	.	.	5	.
Persicaria decipiens	.	.	.	.	.	.	5	.
Hyptis lanceolata	.	.	.	.	.	.	2	.
Panicum trichocladum	.	.	.	.	.	.	2	.
Panicum fluviicola	.	.	.	.	.	.	.	**100**
Vigna vexillata	.	.	.	.	.	.	.	**5**

TZ = Tanzania, UG = Uganda, degr. = degrees

01. ***Pycreo macrostachyos-Ischaemetum rugosum*** ass. nova hoc loco

Holotypus: column 1 in Table 14; relevé ID 3467 in AF-00-006

Iconography: Supplement S3 / Appendix A1, Plate 1

Diagnostic species (phi-value x 100): *Ischaemum rugosum* (73), *Courtoisina cyperoides* (72), *Acmella uliginosa* (57), *Pycreus macrostachyos* (49), *Oryza sativa* (45), *Basilicum polystachyon* (44), *Fimbristylis bisumbellata* (44), *Echnichloa colona* (41), *Eragrostis japonica* (39), *Ethulia paucifructa* (34), *Ammannia auriculata* (33), *Stemodia serrata* (33).

Constant species (percentage frequency): *Ischaemum rugosum* (100), Courtoisina cyperoides (100), *Oryza sativa* (91), *Acmella uliginosa* (82), *Echinochloa colona* (82), *Pycreus macrostachyos* (73), *Basilicum polystachyos* (73), *Fimbristylis bisumbellata* (64), *Oldenlandia corymbosa* (64).

Dominant species (average non-zero cover): none

This association is characterized by relatively tall (>30 cm) annual grasses (average proportion 0.68) and sedges (0.15). It is a pioneer community on recently disturbed sites, such as fallows after rice cultivation or rice fields with little or no weed control. Lacking dominant species, it is relatively species-rich for wetland vegetation (8-21 species on 4 m² plots). This association was only found at the Ifakara floodplain, where it is a temporary community of the rainy and early dry seasons. The frequently encountered Asteraceae *Acmella uliginosa* is consumed as a wild vegetable and used in traditional medicine (Fern, 2021).

02. *Fuireno ciliari-Ammannietum senegalensis* ass. nova hoc loco

Holotypus: column 2 in Table 14; relevé ID 3532 in AF-00-006

Iconography: Supplement S3 / Appendix A1, Plate 2

Diagnostic species (phi-value x 100): *Ammannia senegalensis* (76), *Fuirena ciliaris* (66), *Fimbristylis bisumbellata* (61), *Pycreus pumilus* (60), *Fimbristylis quinquangularis* (55), *Cyperus foliaceus* (51), *Panicum hanningtonii* (37), *Oryza sativa* (37), *Ammannia auriculata* (36), *Courtoisina cyperoides* (35), *Ipomoea aquatica* (32), *Echinochloa colona* (31), *Stemodia serrata* (30).

Constant species (percentage frequency): *Ammannia senegalensis* (100), *Fimbristylis bisumbellata* (88), *Pycreus pumilus* (75), *Fimbristylis quinquangularis* (75), *Panicum hanningtonii* (75), *Ipomoea aquatica* (75), *Ludwigia abyssinica* (75), *Oryza sativa* (75), *Echinochloa colona* (63), Fuirena ciliaris (63), *Courtoisina cyperoides* (50), *Hygrophila auriculata* (50), *Bulbustylis hispidula* (50).

Dominant species (average non-zero cover): *Oryza sativa* (41).

This association is similar to the *Pycreo macrostachyos–Ischaemetum rugosum* community and shares many diagnostic species. It was only observed at the Ifakara floodplain, and only during or shortly after the rainy season. The high proportion of Poaceae (0.50) is mainly resulting from the rice crop. All plots from this association were either rice fields or recently disturbed sites close to them. Most of the species are considered typical weeds of rice paddies (Makokha et al., 2017). Thus, despite the low number of plots, this association is likely to be widespread in cultivated wetlands of East Africa.

03. *Corchoro fascicularis–Panicetum hanningtonii* ass. nova hoc loco

Holotypus: column 3 in Table 14, relevé ID 3488 in AF-00-006

Iconography: Supplement S3 / Appendix A1, Plate 3

Diagnostic species (phi-value x 100): *Corchorus fascicularis* (64), *Hyptis spicigera* (55), *Ipomoea eriocarpa* (54), *Melochia corchorifolia* (52), *Panicum hanningtonii* (51), *Hibiscus cannabinus* (43), *Hygrophila auriculata* (34), *Crotalaria bernieri* (34), *Pycreus macrostachyos* (31), *Oryza* *longistaminata* (30). **Constant species** (percentage frequency): *Panicum hanningtonii* (100), *Corchorus fascicularis* (71), *Hibiscus cannabinus* (76), *Melochia corchorifolia* (76), *Hyptis spicigera* (76), *Hygrophila auriculata* (59), *Ipomoea eriocarpa* (53).

Dominant species (average non-zero cover): *Panicum hanningtonii* (65).

This association is dominated by annual species, mainly by the tall grass *Panicum hanningtonii*. The family Poaceae has an average proportion of 0.79. It has a denser structure and contains also tall herbs and climbing plants. Plots of this association are all fallows of former rice paddies, although *Oryza sativa* is surprisingly absent in them. It is thriving during or after the rainy season in the Kilombero floodplain and is completely dying off during the dry season, leaving large amounts of dry matter susceptible to burning. We did not encounter any specific use of the dominating *Panicum hanningtonii*, while associated species such as *Corchorus fascicularis* or *Hyptis spicigera* provide food, medicine or fiber (Fern, 2021). According to our field observation, this association is likely to be of importance as nesting site for birds. While some species of this association are common and widespread, the dominant *Panicum hanningtonii* is only found in South East of Tropical Africa (Malawi, Mozambique, Tanzania and Zambia) (POWO, 2021).

04. *Grangeo maderaspatanae-Ipomoeetum aquaticae* ass. nova hoc loco

Holotypus: column 4 in Table 14, relevé ID 3596 in AF-00-006

Iconography: Supplement S3 / Appendix A1, Plate 4

Diagnostic species (phi-value x 100): *Leptochloa panicea* (49), *Ipomoea aquatica* (44), *Aeschynomene afraspera* (38), *Merremia hederacea* (37), *Grangea maderaspatana* (33).

Constant species (percentage frequency): *Ipomoea aquatica* (100), *Paspalum scrobiculatum* (88), *Leptochloa panicea* (50), *Grangea maderaspatana* (50).

Dominant species (average non-zero cover): *Ipomoea aquatica* (54).

The *Grangeo maderaspatanae-Ipomoeetum aquaticae* is found in the floodplain at Ifakara on disturbed sites close to the river and occurs shortly after flooding. It is dominated by the name-giving species *Ipomoea aquatica*. While being common in wet sites including paddy rice fields (Fern, 2021), we did not find a description of a vegetation association dominated by this species. It can, depending on the ecological conditions, grow as an annual or perennial (POWO, 2021), hence the “facultative annual” life form and the family of Convolvulaceae (0.65) dominate this association. *Ipomoea aquatica* is consumed as a wild vegetable.

05. *Centrostachyo aquaticae-Persicarietum senegalensis* Alvarez 2017

Holotypus: plot 256 in Table 8 in Alvarez (2017); relevé ID 256 in AF-00-006

Iconography: Supplement S3 / Appendix A1, Plate 5

Diagnostic species (phi-value x 100): *Coldenia procumbens* (91), *Centrostachys aquatica* (91), *Pycreus polystachyos* (72), *Sphaeranthus bullatus* (54), *Alternathera nodiflora* (53), *Heliotropium indicum* (47), *Neptunia oleracea* (47), *Glinus lotoides* (46), *Persicaria senegalensis* (38), *Glinus oppositifolius* (36), *Ludwigia adscendens* (35), *Physalis angulata* (33).

Constant species (percentage frequency): *Coldenia procumbens* (92), *Persicaria senegalensis* (83), *Centrostachys aquatica* (83), *Pycreus polystachyos* (75), *Heliotropium indicum* (75), *Glinus lotoides* (75), *Ludwigia adscendens* (58), *Ipomoea aquatica (*58), *Physalis angulata* (50).

Dominant species (average non-zero cover): none

Centrostachyo aquaticae-Persicarietum senegalensis was described for Kwasunga, Tanzania by Alvarez (2017). It is found at riverbanks under the influence of seasonal flooding and disturbance by fishing activities. In our study area, we found similar conditions, though the disturbance was a result of agricultural activities. It is characterized by hydro-therophytes and amphibious perennials (such as *Coldenia procumbens, Persicaria senegalensis, Neptunia olearacea*). This association may replace associations of the *PhragmitoMagno-Caricetea*, such as *Phragmitetum mauritiani* and *Vigno vexillatae-Panicetum fluviicolae*. It is rich in species that are rather evenly distributed, hence lacking dominant species. Unlike other vegetation units, important families are Amaranthaceae (0.20), Boraginaceae (0.25), Molluginaceae (0.10) and Polygonaceae (0.19) rather than Poaceae (0.10) and Cyperaceae (0.03). However, the proportions of families differ between plots. Some species in this association, such as *Ipomoea aquatica* and *Neptunia oleracea* are consumed as vegetables or used as medicinal plants.

06. *Cypero distantis-Cyperetum difformis* ass. nova hoc loco

Holotypus: column 5 in Table 14, relevé ID 3664 in AF-00-006

Iconography: Supplement S3 / Appendix A1, Plate 6

Diagnostic species (phi-value x 100): *Panicum subalbidum* (53), *Echinochloa haploclada* (48), *Cyperus difformis* (45), *Kyllinga odorata* (43), *Cyperus distans* (40), *Digitaria abyssinica* (32)

Constant species (percentage frequency): *Cyperus distans* (95), *Ageratum conyzoides* (92), *Cyperus difformis* (90), *Commelina diffusa* (81), *Panicum subalbidum* (75), *Kyllinga odorata* (73), *Echinochloa haploclada* (63), *Digitaria abyssinica* (61), *Acmella caulirhiza* (58), *Ludwigia abyssinica* (51)

Dominant species (average non-zero cover): none

This association is found in Namulonge valley in Uganda on recently disturbed sites, including rice paddies. While the association is dominated by annual plants and contains typical weeds of paddy rice (Makokha et al., 2017), the proportion of perennials is much higher than in the previously described associations of the floodplain wetlands (Figure 8). At Namulonge, plots of this association are shallowly flooded during the rainy season, but not submerged. The *Cypero distantis-Cyperetum difformis* appears to be an association of early stages of succession, which can be quickly replaced by other associations if not disturbed. (Nyakabwa (1981) described a similar association, the *Echinochloo-Cypertum difformis*, for the area of Kisangani (DRC) as a ruderal community on humid or temporary muddy soils during the rainy season. However, we decided not to merge these two associations, as there are also notable differences in species composition, such as the absence of the annual *Echinochloa colona* in our association, which is a key species in the association of the *Echinochloo-Cyperetum difformis*. We did not find any other association described in the literature, which resembles the newly described association here, although we suspect it to be quite common in East Africa, as both the species and the habitat are widespread. Most abundant families are Cyperaceae (0.37), Poaceae (0.37) and Asteraceae (0.14). Many plants occurring in this association are reported having medicinal properties or are used in other ways (Makokha et al., 2017).

07. *Cypero denudati-Fuirenetum pubescentis* ass. nova hoc loco

Holotypus: column 6 in Table 14, relevé ID 3692 in AF-00-006

Iconography: Supplement S3 / Appendix A1, Plate 7

Diagnostic species (phi-value x 100): *Fuirena pubescens* (58), *Torenia thouarsii* (54), *Cyperus denudatus* (53), *Crassocephalum vitellinum* (30).

Constant species (percentage frequency): *Fuirena pubescens* (90), *Cyperus denudatus* (81), *Torenia thouarsii* (69), *Commelina diffusa* (60), *Ludwigia abyssinica* (57), *Leersia hexandra* (52), *Crassocephalum vitellinum* (50).

Dominant species (average non-zero cover): *Panicum maximum* (40), *Fuirena pubenscens* (36), *Mimosa pigra* (35).

The *Cypero denudati-Fuirenetum pubescentis* association is a fallow vegetation in wetlands. However, it has only few annual species and is dominated by perennial reptant and tussock plants and therefore not directly following disturbance. It appears to occur under dryer conditions than the *Melanthero scandentis-Leersietum hexandrae*. Important families in this association were Cyperaceae (0.40), Poaceae (0.24) and Asteraceae (0.10). In some plots of this association, invasive *Mimosa pigra* (Witt et al., 2020) and consequently Fabaceae (0.12) are dominant. Although most species are common in the region, we did not find similar vegetation described in the consulted literature.

08. *Melanthero scandentis-Leersietum hexandrae* ass. nova hoc loco

Holotypus: column 7 in Table 14; relevé ID 3733 in AF-00-006

Iconography: Supplement S3 / Appendix A1, Plate 8

Diagnostic species (phi-value x 100): *Melanthera scandens* (55), *Ipomoea cairica* (45), *Hyptis lanceolata* (38), *Triumfetta brachyceras* (32).

Constant species (percentage frequency): *Melanthera scandens* (95), *Ipomoea cairica* (89), *Leersia hexandra* (79), *Ludwigia abyssinica* (53).

Dominant species (average non-zero cover): *Triumfetta brachyceras* (35), *Leersia hexandra* (28).

This association is a fallow vegetation under wet conditions. It is characterized by erect or climbing perennial dicotyledonous plants and the reptant perennial grass *Leersia hexandra*. Even though most of the species are common in the region, we did not find a suitable association described in literature. This association shares diagnostic species with *Cyperetum latifolii*, such as *Melanthera scandens* and *Cyperus latifolius* (Germain, 1951). Both associations seem to coat *Cyperus papyrus* communities or replace them after disturbance or drainage (Alvarez, 2017). *Cyperus papyrus* is found in low abundance in some of the plots. Diagnostic species such as *Melanthera scandens* and *Ipomoea cairica* are also found on the edges of Papyrus swamps. Possibly this association represents a regeneration stage for Papyrus swamps and may succeed when drainage infrastructure is removed. Important families were Poaceae (0.39) and Convolvulaceae (0.11). In some plots also Malvaceae (0.10) with the species *Triumfetta brachyceras* were dominant. Regarding ecosystem services, *Leersia hexandra* may be used as fodder plant. *Melanthera scandens* or *Ipomoea cairica* are important medicinal plants.

09. *Cyperetum latifolii* (Germain 1951) Schmitz 1988

Lectotypus: plot 1, Table 30 in Germain 1951, designated by Alvarez 2017, relevé ID 4764 in AF-00-006

Iconography: Supplement S3 / Appendix A1, Plate 9

Diagnostic species (phi-value x 100): *Lythrum rotundifolium* (49), *Cyperus latifolius* (45), *Panicum hymeniochilum* (35).

Constant species (percentage frequency): *Cyperus latifolius* (100), *Leersia hexandra* (64), *Ludwigia abyssinica* (64)

Dominant species (average non-zero cover): *Cyperus latifolius* (60)

This association, typically dominated by *Cyperus latifolius* and accompanied by *Leersia hexandra* and other nitrophilous, therophyte species (Germain, 1951), occurs in different countries in East and East-Central Africa. It fringes *Cyperus papyrus* communities or replaces them as secondary vegetation after clear cut or drainage (Alvarez, 2017). In the Namulonge valley, it is mainly found on fallow land. For South-Western Ethiopia, (Woldu & Yeshitela, 2003) mention a *Cyperus latifolius-Aeschynomene abyssinica* community as pristine wetland vegetation. The dominating species *Cyperus latifolius* is used for different purposes, e.g. as livestock fodder (Alvarez, 2017) or for craft production (Kotze & Traynor, 2011). Cyperaceae (0.63) and Poaceae (0.15) are the most important families.

10. *Cypero papyri-Dryopteridetum gongylodes* (Germain 1951) Schmitz 1963

Lectotypus: plot 1, Table 28 in Germain 1951, designated by Alvarez 2017; relevé ID 4759 in AF-00-006

Iconography: Supplement S3 / Appendix A1, Plate 10

Diagnostic species (phi-value x 100): *Cyperus papyrus* (64), *Cyclosorus interruptus* (47), *Carex mannii* (34), *Persicaria strigosa* (33), *Pilogyne minutiflora* (31).

Constant species (percentage frequency): *Cyperus papyrus* (100), *Cyclosorus interruptus* (54).

Dominant species (average non-zero cover): *Cyperus papyrus* (71), *Cyclosorus interruptus* (32).

This association is common in the headwaters of the Nile and the upper Nile. It covers large areas particularly in Uganda and South Sudan (Denny, 1993). *Cyperus papyrus* builds floating mats on the water surface or grows on permanently waterlogged soil at the edge of rivers and lakes. Being a widespread association, it was already described in 1951 by Germain (1951).

Papyrus is largely considered to be iconic for natural wetland vegetation, and the ecology of this association has been extensively described. While dominated by *Cyperus papyrus*, an increased abundance of the fern *Cyclosorus interruptus* is observed at the fringes of the Papyrus marsh. This probably indicates drier conditions and sparser canopy than in the middle of stands as well as disturbances in the cover and hydrology due to human activities (e.g. grazing and watering places, harvest of papyrus or clearing and drainage for cultivation). It is frequently harvested and used as material for thatching, for mats, boats or baskets (Lind et al., 1974), but the most known purpose is probably for the historic Papyrus paper in ancient Egypt. If not overused, Papyrus stands can recover quickly (Alvarez, 2017). They are also very important for many other ecosystem services such as water regulation (Kayendeke et al., 2018) and purification and as habitat for many animal species. Reeds (*Cyperus papyrus*) and reptant plants (*Cycolosorus interruptus*) dominate the lifeforms (see also Figure 8). Several climbers such as *Desmodium salicifolium*, *Ipomoea* spp. or *Zehneria* spp. occur in these stands, indicating a high competition for light in the understory. The dominating families are Cyperaceae (0.64) and Thelypteridaceae (0.17).

11. *Phragmitetum mauritiani* (Lebrun 1947) Schmitz 1988

Synonym: *Phragmitetum afro-lacustre* Lebrun 1947

Iconography: Supplement S3 / Appendix A1, Plate 11

Lectotypus: plot 2, Table 29 in Lebrun 1947, designated by Alvarez 2017; relevé ID 3891 in AF-00-006

Diagnostic species (phi-value x 100): *Phragmites australis* (48), *Kosteletzkya adoensis* (34).

Constant species (percentage frequency): *Phragmites australis* (100).

Dominant species (average non-zero cover): *Phragmites australis* (80).

Phragmites australis is a species of almost worldwide distribution. In East Africa, it is replaced by *P. mauritianus* (POWO, 2021). It is, however, disputed, whether *P. australis* and *P. mauritianus* are two distinct species (The Plant List, 2013) or synonyms (CJBG & SANBI, 2012). While some scholars (e.g., Furness & Breen, 1980) mention ecological differences between *P. australis* and *P. mauritianus*, *P. australis* is recognized as a highly variable species (Saltonstall, 2002). As we follow the nomenclature of the African Plant Database (CJBG & SANBI, 2012), we treat the names here as synonymous. Following the suggestion of (Alvarez, 2017), we decided to keep the name *Phragmitetum mauritiani* (Lebrun 1947) Schmitz 1988 anyway, to differentiate this *Phragmites australis* community from Tropical Africa from those of other continents.

For the *Phragmitetum mauritiani* or similar communities, there are several descriptions from DRC and also from Tanzania (see Alvarez (2017) for an overview). They occur on the fringes of lakes or streams and reach a height of up to 5 m. In the floodplain at Ifakara, they form a belt along the Kilombero River that is flooded every year for several months. In Hood et al. (2002), they are mentioned as "Riverside community" dominated by *P. mauritianus*. With increasing distance from the river and shorter flooding duration, the *Phragmitetum mauritiani* is replaced by "low lying valley grassland" (Hood et al., 2002) which equals the *Vigno vexillatae-Panicetum fluviicolae* of this work. This association is dominated by reed plants from the Poaceae (0.85) family, but also climbing species of the Convolvulaceae family such as *Ipomoea rubens* occur. *P. australis* is often used as construction or thatching material.

12. *Echninochloo pyramidali-Phragmitetum australis* (Furness & Breen 1980) ass. nova hoc loco

Lectotypus hoc loco designates, relevé 101 in Table 3 in Furness & Breen 1980; relevé ID 3366 in AF-00-006

Diagnostic species (phi-value x 100): *Phragmites australis* (48), *Echinochloa pyramidalis* (48), *Grewia caffra* (40).

Constant species (percentage frequency): *Phragmites australis* (100), *Echinochloa pyramidalis* (100), *Alternanthera sessilis* (80).

Dominant species (average non-zero cover): *Phragmites australis* (67), *Echinochloa pyramidalis* (47)

This association was described for the Pongolo floodplain in South Africa by Furness & Breen (1980) as "*Phragmites mauritianus*-community". While this community was recorded neither in Ifakara nor in Namulonge, it is included here due to its floristic relationship with *Phragmitetum mauritiani*. It is differentiated from the "*Phragmites australis* community" by the presence and of the respective *Phragmites* species. We separated between the associations using the abundance of *Echinochloa pyramidalis*, which needs to cover at least 25% for this association. Irrespective of the different definition, the results are the same, apart from one plot in which *Echinochloa pyramidalis* covers less than 25%. According to Furness & Breen (1980), this association occurs in the lower lying areas of the floodplain and is dominated by *Phragmites australis (P. mauritianus* in the reference*)* which forms dense mats and reaches up 3.5 m height, together with *Echinochloa pyramidalis* and *Alternanthera sessilis*. Poaceae have the highest proportion of all associations (0.97).

13. *Vigno vexillatae-Panicetum fluviicolae* ass. nova hoc loco
Holotypus: column 8 in Table 14, 3576 in AF-00-006
Iconography: Supplement S3 / Appendix A1, Plate 12
Diagnostic species (phi-value x 100): *Panicum fluviicola* (86), *Vigna vexillata* (37), *Chrysopogon nigritanus* (32).
Constant species (percentage frequency): *Panicum fluviicola* (100).
Dominant species (average non-zero cover): *Panicum fluviicola* (79), *Phragmites australis* (27).
Although *Panicum fluviicola* occurs in most parts of Tropical Africa, we did not find any other reference for a description of a *Panicum fluviicola* association. Only for the Kilombero valley (Hood et al., 2002) describe a "Low lying valley grassland" that is characterized by the dominance of *Panicum fluviicola*. It grows in a zone around the river that has seasonal flooding, but shorter and less deep than the zone of *Phragmites australis*. From our fieldwork that was done in the same locality, we can confirm this, although there are overlaps between these two species. The second reference from Mahango Game Reserve in northeast Namibia (Hines, 1993) mentions depressions with tall, flooded grasslands that are dominated by *Panicum fluviicola* and other grasses, but the source does not provide vegetation relevés. The dominating lifeform is reed plant. In addition, climbers occur frequently. Most important family is Poaceae (0.93). The dominating species, *Panicum fluviicola*, is used as thatching material and for fish traps (own field observations), while the other common species *Vigna vexillata* is an important wild vegetable and

For the arrangement of the associations into higher syntaxa, we followed Schmitz (1988) and the critical revision by Alvarez (2017) and the descriptions of the alliances in both references. The newly described associations *Pycreo macrostachyos-Ischaemetum rugosum*, *Fuireno ciliari-Ammannietum senegalensis*, *Corchoro fascicularis–Panicetum hanningtonii, Grangeo maderaspatanae-Ipomoeetum aquaticae* were all assigned to the *Ecliption albae*, an alliance comprising semi-aquatic pioneer and weed communities. *Cypero distantis-Cyperetum difformis and Cypero denudati-Fuirenetum pubescentis* were assigned to the same alliance as *Cyperetum latifolii*, the alliance *Magno-Cyperion divitis* representing associations dominated by tall sedges and growing on moist soils in the fringes of papyrus marshes. Even though *Melanthero scandentis-Leersietum hexandrae* shares similar ecological conditions, we assigned it to *Echinochloion crus-pavonis* as sedges are largely lacking and *Leersia* *hexandra*, a typical species for this association, dominates instead. *Echninochloo pyramidali-Phragmitetum australis* and *Vigno vexillatae-Panicetum fluviicolae* were assigned to *Phragmition communis*, as they are also dominated by tall grasses and occur in the seasonally flooded riverbanks as well as the *Phragmitetum mauritiani*. Table 15 provides an overview of the complete syntaxonomy of the associations described in this work.

Table 15: Overview of all associations studied in this work based on wetlands of East Africa (inland valley swamp in Uganda and floodplain wetland in Tanzania) and secondary data sources and their assignments to higher syntaxa. The abbreviation "ass. nova hoc loco" indicates that this association was first described in this work. In the squared brackets the number of each association as used in this work is provided

Oryzetea sativae Miyawaki 1960

- ***Amarantho-Ecliptetalia*** Schmitz 1971
  - ***Ecliption albae*** Lebrun 1947
    - ***Pycreo macrostachyos-Ischaemetum rugosum*** ass. nova hoc loco **[1]**
    - ***Fuireno ciliari–Ammanietum senegalensis*** ass. nova hoc loco **[2]**
    - ***Corchoro fascicularis–Panicetum hanningtonii*** ass. nova hoc loco **[3]**
    - ***Grangeo maderaspatanae-Ipomoeetum aquaticae*** ass. nova hoc loco **[4]**
    - ***Centrostachyo aquaticae-Persicarietum senegalensis*** Alvarez 2017 **[5]**

Phragmito-Magno-Caricetea Klika ex Klika & Novák 1941

- ***Phragmitetalia communis*** Koch 1926
- ***Magno-Cyperion divitis*** (Lebrun 1947) Schmitz 1988
    - ***Cypero distantis–Cyperetum difformis*** ass. nova hoc. loco **[6]**
    - ***Cypero denudati-Fuirenetum pubescentis*** ass. nova hoc loco **[7]**
    - ***Cyperetum latifolii*** (Germain 1951) Schmitz 1988 **[9]**
  - ***Echinochloion crus-pavonis*** (Léonard 1950) Schmitz 1988
    - ***Melanthero scandentis-Leersietum hexandrae*** ass. nova hoc loco **[8]**
  - ***Phragmition communis*** Koch 1926
    - ***Phragmitetum mauritiani*** (Lebrun 1947) Schmitz 1988 **[11]**
    - ***Echinochloo pyramidalis–Phragmitetum australis*** (Furness and Breen 1980) nomen novum hoc loco **[12]**
    - ***Vigno vexillatae-Panicetum fluviicolae*** ass. nova hoc loco **[13]**
- ***Cyperetalia papyri*** (Lebrun 1947) Alvarez 2017
  - ***Cyperion papyri*** (Lebrun 1947) Alvarez 2017
    - ***Cypero papyri-Dryopteridetum gongylodes*** (Germain 1951) Schmitz 1963 **[10]**

Ordination and classification goodness

The ordination by DCA supports the classification of communities in two classes, namely *Phragmito-Magno-Caricetea* and *Oryzetea sativae* (Figure 7). As expected, the length of the first DCA axis of about 10 indicates, that the data set is very heterogeneous, and the species are not linearly distributed along environmental gradients (Lepš & Šmilauer, 2003). It is further visible that the proportion of annual species and the proportion of reed plants have a strong negative correlation, while they hardly correlate with the proportion of tussock plants. The DCA axis 1 appears to be strongly linked to flooding duration. Although not enough data were available for a proper analysis with all plots, it is known from literature (e. g. Lind et al., 1974) that the *Cypero papyri-Dryopteridetum gongylodes* requires permanently waterlogged soils, while the associations on the other side (particularly *Pycreo macrostachyos-Ischaemetum rugosum*, *Fuireno ciliari-Ammannietum senegalensis* and *Corchoro fascicularis–Panicetum hanningtonii*) are seasonal communities during the rainy season. Disturbance, both anthropogenic (tillage and weeding for cultivation) and natural (flooding, fire), seem to be correlated to axis 1 and axis 2. This is supported by the previously mentioned proportion of annual species indicating high disturbance in contrast to a high abundance of tall perennial species (Behn et al., 2018).

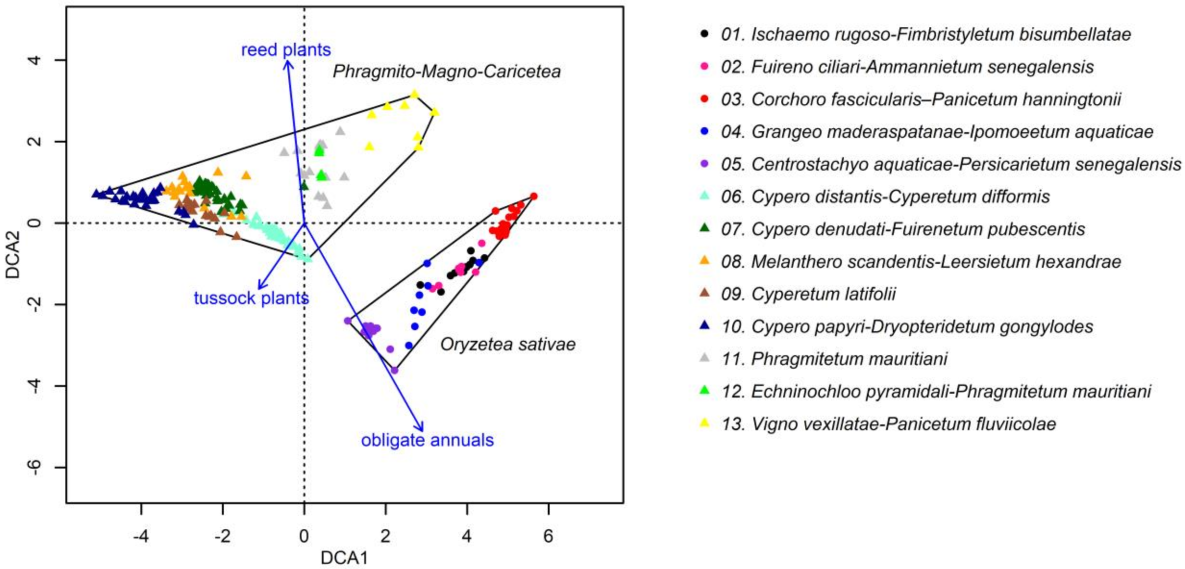

Figure 7: Detrended correspondence analysis (DCA) of all classified plots in this work based on an inland valley swamp of Uganda and a floodplain wetland in Tanzania (2014–2016) and secondary data sources using the diagnostic species of one or more vegetation units. Hulls connect all plots belonging to the phytosociological classes of *Phragmito-Magno-Caricetea* and *Oryzetea sativae*.

Results of the MRPP show an average dissimilarity of 0.59, which is lower than the expected (random) dissimilarity (0.90). The significant (P-value < 0.01) group weighted A-value of 0.35 hence validates the classification. For the life forms, the result is similar with a significant (P-value < 0.01) A-value of 0.46. However, differences within the group and between groups are obviously lower than for species (observed Delta: 0.37, expected delta 0.69).

Life form and introduced species analysis

The proportions of each life form as well as the proportion of introduced species differed between associations according to Kruskal-Wallis test (P-value < 0.01). While not all associations differed significantly from each other, we observed significant differences between groups of associations (see Figure 8 for selected life forms). Regarding obligate annual species, the associations of the *Oryzetea sativae* (1-5) and the *Cypero distantis-Cypertum difformis* differed significantly from the other associations of the *Phragmito-Magno-Caricetea*.

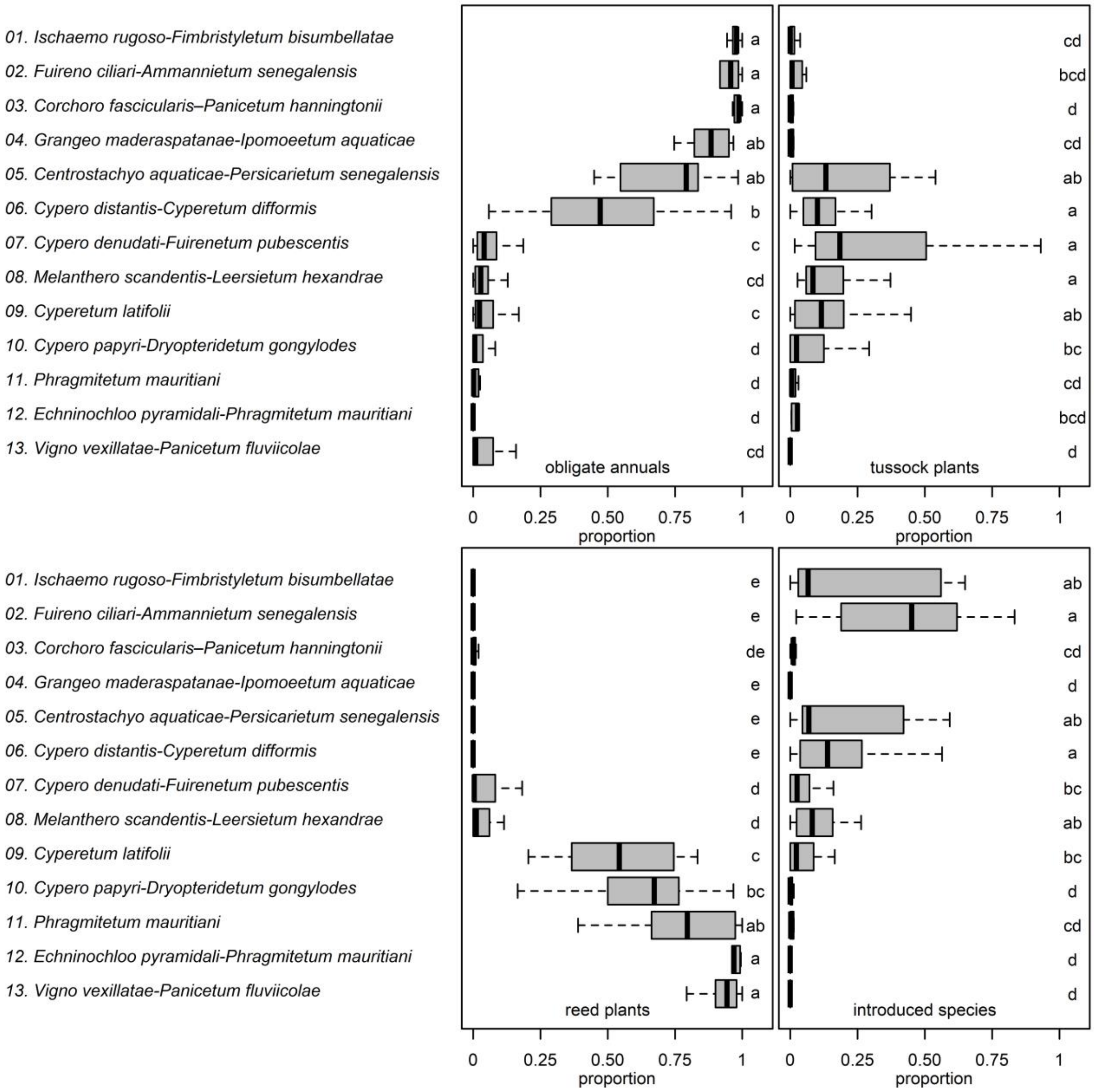

Figure 8: Proportion of obligate annuals, tussock plants, reed plants and introduced species for each association in this work based on wetlands of East Africa (inland valley swamp in Uganda and floodplain in Tanzania, 2014–2016 and secondary data sources). Letters on the right indicate significant (p>0.05) differences between the associations.

The five associations dominated by reed plants (9, 10, 11, 12, 13) differed significantly from all the other associations. Particularly in associations with the tall grasses *Panicum fluviicola* and *Phragmites australis* (11-13) other life forms are rare. However, we did observe several species of climbing plants in the associations dominated by reed plants. For the tussock plants, the trend is not clear, however, some associations differed from those dominated by annuals (1-5) and from those dominated by reed plants (9-13). Associations also differed regarding the proportion of introduced species (Figure 8). Introduced species tended to be more abundant in the *Oryzetea sativae* class than in the *Phragmito-*

Magno-Caricetea class. While they were rare in units dominated by one native species (especially associations 3, 9, 10, and 11), others show a strong variation. Important introduced species are cultivated rice (*Oryza sativa*), mainly in the *Fuireno cliliari-Ammanietum senegalensis*, the annual pioneer / weed species *Ageratum conyzoides*, mainly in the *Cypero distantis–Cyperetum difformis,* and the invasive shrub *Mimosa pigra* that occurred mainly in the *Cypero denudati-Fuirenetum pubescentis*. Particularly the latter one is considered to be a problematic invasive species with negative socio-ecological impacts (Witt et al., 2020).

6.2.4 Discussion

Differences between associations

The newly described associations have been observed only in one of the two study sites (Ifakara or Namulonge). These represent pioneer or early succession stages in wetlands that to our best knowledge have rarely been researched from a phytosociological perspective on the African continent. Wittig et al. 2011) did an extensive study on weed communities in West Africa, but wetlands and irrigated fields are not covered in their work. Similar associations for rice-weed communities have been described mainly elsewhere, for example in Japan (Miyawaki, 1960) or more recently for Thailand (Nowak et al., 2015).

As the present classification is based on floristic differences, it is obvious that the associations differ in terms of species composition. The big differences regarding dominant life forms, resulting from disturbance regimes including cropping activities and/or ecological differences supports the separation of many associations additionally. However, in some cases there are overlaps between associations both in terms of life forms and species. Associations were spatially close and occurred presumably under similar or same environmental conditions, therefore some associations may be predominantly a result of different disturbance regimes. In line with observations done for instance by Alvarez (2017) and Behn et al. (2018), plots dominated by annual plants have recently and intensively been disturbed. Those with smaller perennials such as tussock or reptant plants are disturbed less frequently and the reed plant-dominated associations were largely undisturbed or recovered. Particularly the associations *Pycreo macrostachyos-Ischaemetum rugosum, Fuireno ciliari-Ammannietum senegalensis,* and *Corchoro fascicularis-Panicetum hanningtonii*, all dominated by obligate annual species, have many species in common resulting in some double classifications (Kočí et al., 2003). There are also overlaps between *Cypero distantis-Cyperetum difformis* and *Cypero denudati-Fuirenetum pubescentis.* These associations may represent different successional stages. All the above-mentioned associations were defined by the occurrence of a respective species group that often includes generalist species, which makes overlaps more likely than between associations defined by cover of dominant species.

While the two study sites had few species in common, most of the species in the Cocktail groups occur throughout Africa, many have a paleotropical or pantropical distribution (POWO, 2021). Hence, the difference in the flora of the study site may rather be explained by the site conditions including elevation than by biogeography. Only *Panicum hanningtonii*, the dominating species of the *Corchoro fascicularis-Panicetum hanningtonii* is limited to Tanzania, Malawi, Mozambique and Zambia (POWO, 2021). Hence, this association may be geographically much more limited than the other two associations.

Regarding the two associations dominated by *Phragmites australis*, we decided to use the high abundance of *Echinochloa pyramidalis* for the separation. This resembles the separation of the two associations in (Furness & Breen, 1980), even though their separation was based on the taxonomic separation of *Phragmites australis* and *P. mauritianus*, which were despite the high intraspecific variability (Saltonstall, 2002) considered synonyms in this work following African Plant database (CJBG & SANBI, 2012).

Although not found in literature, the associations newly described here may be common and currently not of high conservation value, particularly those associations with small perennials that represent early succession. With increasing land use intensity including a potentially increasing use of herbicides as well as stricter conservation reducing disturbance, this may however change in the future.

Consolidating classification by this novel method

In this work, the Cocktail method proved to be suitable for classifying vegetation in the studied wetlands and beyond, when its challenges and limitations as described in the following are recognized. Wetlands are often species-poor and consist only of one dominating species with very few accompanying species. In this work and in previous ones (Kočí et al., 2003; Landucci et al., 2013), this problem was solved with cover value thresholds for dominating species that that are needed in addition to or replacing the species group occurrence in the formal definition. While this appears to be generally a suitable solution, there is the risk of aggregating plots with different ecological conditions, when the dominant species has a broad ecological amplitude. In our case, it seems to apply to *Cyperus papyrus*, although we did not find clear evidence in this work to justify a differentiation of *Cyperus papyrus* associations.

Furthermore, the assessed plots may be quite different in terms of plot sizes, and in some cases, this information is even not available (Alvarez et al., 2021). Such heterogeneity may be critical for statistical assessments (Chytrý & Otýpková, 2003).

In general, both double-classified and unclassified plots are an important feature of the Cocktail approach (Kočí et al., 2003). Double classification can make sense along an ecological gradient or in the transition between succession stages. To reduce double classification, Cocktail definitions should be narrow and focus on the core relevés of a vegetation unit (Kočí et al., 2003). This leads to large numbers of unclassified relevés that lack specialist species or are sparsely vegetated because of recent disturbance such as weeding, flooding or fire. In our case, we focused on semi-aquatic vegetation and developed definitions only for the classes of *Phragmito-Magno-Caricetea* and *Oryzetea sativae*, even though some relevés recorded at the fringes of our study area contained aquatic or upland vegetation. While previous works in Europe (e.g., Kočí et al., 2003; Landucci et al., 2013) had the advantage of a big existing databases and an already existing classification as a baseline, studies in East African wetlands using Cocktail classification (Alvarez, 2017) or numerical classifications (Alvarez et al., 2012; Hood et al., 2002) work only with one or few sites. The novelty of our approach is the combination of the classification of the vegetation in two wetlands and the application to a vegetation-plot database recognizing in an objective way syntaxa previously defined for other localities. This is consequently a more constructive approach for the classification of semi-aquatic vegetation at the local as well as at the regional or even continental level. The classification using the database and the formal Cocktail definitions have an important advantage: It is less prone to local bias than numerical classification approaches such as hierarchical clustering or TWINSPAN (Bruelheide & Chytrý, 2000). Incremental assessment of syntaxa by adding new data in the future may require some fine-tuning in Cocktail algorithms but in turn provide a more consolidated classification. Hence, the proposed method and the resulting expert system may help to provide an easy classification for future vegetation studies in wetlands. It appeared to be a suitable approach for our study area and further regions where vegetation plot data are scarce. Similarly, it can be used for the comparison of different wetlands.

Electronic supplements:

Supplement S1: List of recorded vascular plant species sorted by phylums and families (https://doi.org/10.5281/zenodo.5109982).

Supplement S2: List of synonyms used for vascular plant species and sub-specific taxa in the assessed plot observations (https://doi.org/10.5281/zenodo.5110121).

Supplement S3: Color plates of the described associations (https://doi.org/10.5281/zenodo.5111455).

Supplement S4: Tutorial for the work with the vegetation data in R (https://doi.org/10.5281/zenodo.5111478).

Supplement S5: R-image with the assessed plot-observations (https://doi.org/10.5281/zenodo.5111485).

7 Recovery dynamics

Recovery dynamic in the riparian zone in the Namulonge inland valley, Uganda, after tillage in September 2014. Pictures taken in the same plot in October 2014 (top left), December 2014 (top right), April 2015 (bottom left), and November 2015 (bottom right).

7.1 Recovery dynamics of wetland vegetation along a hydrological gradient in an agriculturally used inland valley in Uganda

This chapter is based on:

Behn, K., Alvarez, M., Mutebi, S., & Becker, M. (2024). Recovery dynamics of wetland vegetation along a hydrological gradient in an agriculturally used inland valley in Uganda. *Wetlands Ecology and Management*, *32*(6), 959–974. https://doi.org/10.1007/s11273-024-10011-6

Abstract

Wetlands in East Africa are important for providing ecosystem services and for conserving biodiversity. They are also suitable and increasingly used for agriculture. Between cropping cycles, spontaneous vegetation regrows on fallow plots. We hypothesize that recovery is affected by hydro-edaphic conditions and the duration of the fallow period. Land use intensification reduces fallow durations. A multi-year field study investigated the dynamics, biodiversity, and potential uses of fallow vegetation species after a disturbance event in an inland valley wetland in Central Uganda. The wetland was stratified into three hydrological positions along a gradient comprising the valley fringe, the mid-valley, and the riparian zone. In each zone, biomass was removed, and the soil was tilled, simulating a common disturbance event. Subsequently, four plots of 4 x 4 m size were delineated in each zone. Vegetation regrowth was subsequently monitored over a period of two years. We recorded and analyzed changes in aboveground live biomass, abundance of selected plant species, taxonomic and functional composition, and evenness during a 27-months recovery phase. While annual species dominated the vegetation initially, these were gradually replaced by herbaceous perennials, and eventually by tall reeds and woody plants, constituting three successional stages. The dynamics were similar, but species composition differed across the positions. At all successional stages, we observed the presence of useful wild plants, but also invasive species such as *Mimosa pigra* were recorded. While temporary fallows are important for biodiversity in tropical wetlands, such successions cannot substitute for the functions and services provided by natural vegetation and may promote invasive species.

Keywords: Biodiversity, invasive species, Namulonge, recovery, succession, useful wild plants

7.1.1 Introduction

Wetlands cover about 11% of Uganda´s land area. Thus, they play a major role in shaping the country´s landscape and natural resource base (Government of Uganda, 2016). Wetlands provide numerous ecosystem services (ESS, Millennium Ecosystem Assessment, 2005) and are of high relevance for biodiversity conservation as habitat for various species. They are important for water regulation and purification. They store large amounts of carbon in the above-ground living biomass, but also contribute to peat accumulation in permanently waterlogged soils. Wetlands are sites for hunting and fishing, and further provide wild plants for food, fiber, and medicinal plants. They support pollinating insects and livestock grazing (Mombo et al., 2011; Behn et al., 2022). Tropical wetlands, which are generally highly productive ecosystems (Jones et al., 2018), have become focal areas for food production (Sakané et al., 2011).

Driven by several factors, including population growth, climate change, and degradation of upland fields, as well as for improving food security and sovereignty in many tropical countries (Behn et al., 2022), wetlands are increasingly used as croplands for suitable crops such as rice (*Oryza sativa*) or taro (*Colocasia esculenta*). Drainage and irrigation also enable the cultivation of higher value vegetables, such as tomatoes (*Solanum lycopersicum*), to supply the growing urban markets (Sakané et al., 2011). For wetlands, such land use intensification often implies the use of fertilizers and pesticides, short fallow periods between cultivation cycles, and modified ecological conditions (Sakané et al., 2014). Simultaneously, awareness about the importance of undisturbed wetlands for especially regulating ESS is increasing. Flood protection, water purification, and carbon storage require little-disturbed wetlands. Thus, wetland protection becomes a priority task (Donde et al., 2023).

Processes, structure, diversity, and ESS provision of wetland vegetation are strongly influenced by land use practices and their intensification or abandonment (Behn et al., 2022). Natural disturbances and those caused by agricultural activity can temporarily or permanently destroy habitats. For example, when tall sedges such as *Cyperus papyrus* are removed, also climbing herbs lose their supporting structure. Loss of wetland habitats also strongly affects faunal diversity (Pomeroy et al., 2017; Stephenson et al., 2020). On the other hand, disturbance, for instance from infrequent and spatially restricted agricultural use, can also create “new” habitats. Several plant species need open ground and light to germinate and grow. On the landscape level, a mosaic of patches of different successional stages following a disturbance is important for biodiversity (Levin, 2000), hence, reducing or preventing disturbances can also negatively affect habitat diversity. Depending on the type, intensity, frequency, and spatial scale of disturbance, effects on biodiversity and vegetation vary. Plants can easily regrow after partial biomass removal, or a new cycle of secondary succession is initiated (Chang et al., 2019), or severe and permanent losses of biodiversity occur, for instance when wetland sites are used for mining activities or for intensive agricultural production (Beuel et al., 2016). The latter one is particularly relevant when agricultural intensification is associated with drainage and increased use of agrochemicals with a permanent cultivation of upland crops, as opposed to seasonal cultivation with wetland-adapted crops that require little habitat modification (Beuel et al., 2016, Sakané et al., 2014). Any habitat alteration also affects the provision of ESS, such as the supply of wild medicinal plants that are collected from various habitat types. In Southern Uganda, these habitat types include forests, swamps, and (wet) grasslands, but also cultivated areas, and post-cultivation fallows (Ssegawa & Kasenene, 2007), while Kadoma et al. (2023) cite an herbalist from Central Uganda complaining about decrease in the supply of medicinal plants from wetlands due to farming activities.

Studies focusing on wetland regeneration from soil seedbanks have been conducted in Europe, Australia or America, but are limited in Eastern Africa. A recent study about seed banks in wetland soils in South Sudan stressed their importance for the regeneration of cultivated wetlands (Esaete et al., 2021), but the authors did not study the succession process. Terer et al. (2012) did research effects of biomass harvesting in *Cyperus papyrus* in Kenyan wetlands, but this study investigated regrowth of *Cyperus papyrus* and not succession. While many studies exist on succession globally (e.g., Prach & Walker 2019), studies in tropical environments often focus on forests (e.g., Makelele et al., 2021) however rarely on non-forested wetlands. Studies often use space-for time substitution (Johnson & Miyanishi, 2021) or annual sampling intervals (Chang et al., 2019). Particularly little is known about effects of changing hydro-edaphic attributes at different wetland positions or along the gradient from the valley fringe to the center positions.

The aims of this work are therefore to contribute to a better understanding of the early vegetation dynamics in a tropical wetland ecosystem after an induced disturbance in relation to the hydrological position in the wetlands. A second aim was to evaluate the possible implications on biodiversity and ESS provision We conducted a 27-month-long experiment in an inland valley wetland in Central Uganda. Inland valley wetlands are the main wetland type in Central Uganda. They are typically found in narrow valleys with a central stream bisecting the wetland. They comprise a seasonally slightly inundated valley bottom and hydromorphic fringes which are the lower part of the slope and limited by the upper parts of the slopes on both sides (Sakané et al. 2011; Gabiri et al., 2018). With this background, we addressed the following research questions:

1. Are vegetation recovery processes affected by position along a hydrological gradient in a tropical inland valley?

2. Do position and time affect taxonomic and functional composition during the recovery process?

3. What do potential changes in plant species occurrence and abundance imply for ESS provision?

7.1.2 Material and Methods

Study site

The study was conducted in the Namulonge valley, within the premises of the Namulonge Research Station of the National Crop Resources Research Institute (NaCRRI) in Uganda. The site is located about 25 km north of the capital city of Kampala in the Wakiso district at an elevation of about 1100 m a.s.l. The area is located in the transitional zone between the tropical monsoon ("Am") and tropical rainforest ("Af") bio-climates (Peel et al., 2007) with two rainy seasons per year, from March to May and from August to November (Gabiri et al., 2018). The average annual rainfall is 1291 mm and the average annual temperature 22°C (Behn et al., 2018). The seasonal wetlands in the Namulonge valley are mainly used for subsistence farming under a variety of management systems, including fallow rotations in previously used croplands. Major crops grown in the wetland include rice (*Oryza sativa*), maize (*Zea mays*), taro (*Colocasia esculenta*), cassava (*Manihot esculenta*), and tomatoes (*Solanum lycopersicon*) (Gabiri et al. 2018). In this part of the wetland, experimental plots were located. Natural and little disturbed vegetation also occurred, mostly as papyrus marsh in the riparian zone, where wetlands tended to be permanent. Here, and in the neighboring valley outside of the research station within a radius of less than 2 km from the experimental plots, we assessed reference sites. Apart from the papyrus marshes, long-term undisturbed sites were rare at the study site, although observations from the broader surroundings indicate evergreen forests in the fringe and tall grasses, bushes, and *Phoenix reclinata* palms in the middle zone as natural vegetation.

Experimental set up

Three hydrological positions within the inland valley were differentiated as "valley fringe", "mid-valley", and "riparian zone". These positions are typical for this type of wetlands and differ regarding their water source with valley fringe positions receiving water predominantly from slope run-off or subsurface interflow, while the main water source in the riparian zone is overflow from the stream (Sakané et al., 2011). At our study site in Namulonge, the transect from the slope to the stream on which "valley fringe", "mid-valley", and "riparian zone" were located is about 200 m long. While the increasing steepness of the slope on the one side and the river on the other side clearly limited the transect, a strict delineation between zones with was not possible. The zoning therefore represents a simplification of the complex wetland system. In a study in the same valley, Gabiri et al. (2018) found that these positions do not significantly correlate to specific hydrological regimes, however soil-moisture throughout the year was significantly higher in the riparian zone and mid-valley as compared to the fringe zones. They also observed position-specific differences in soil properties. While the texture class was generally silty loam, the bulk density was highest at the valley fringe (1.33 ± 0.32 g

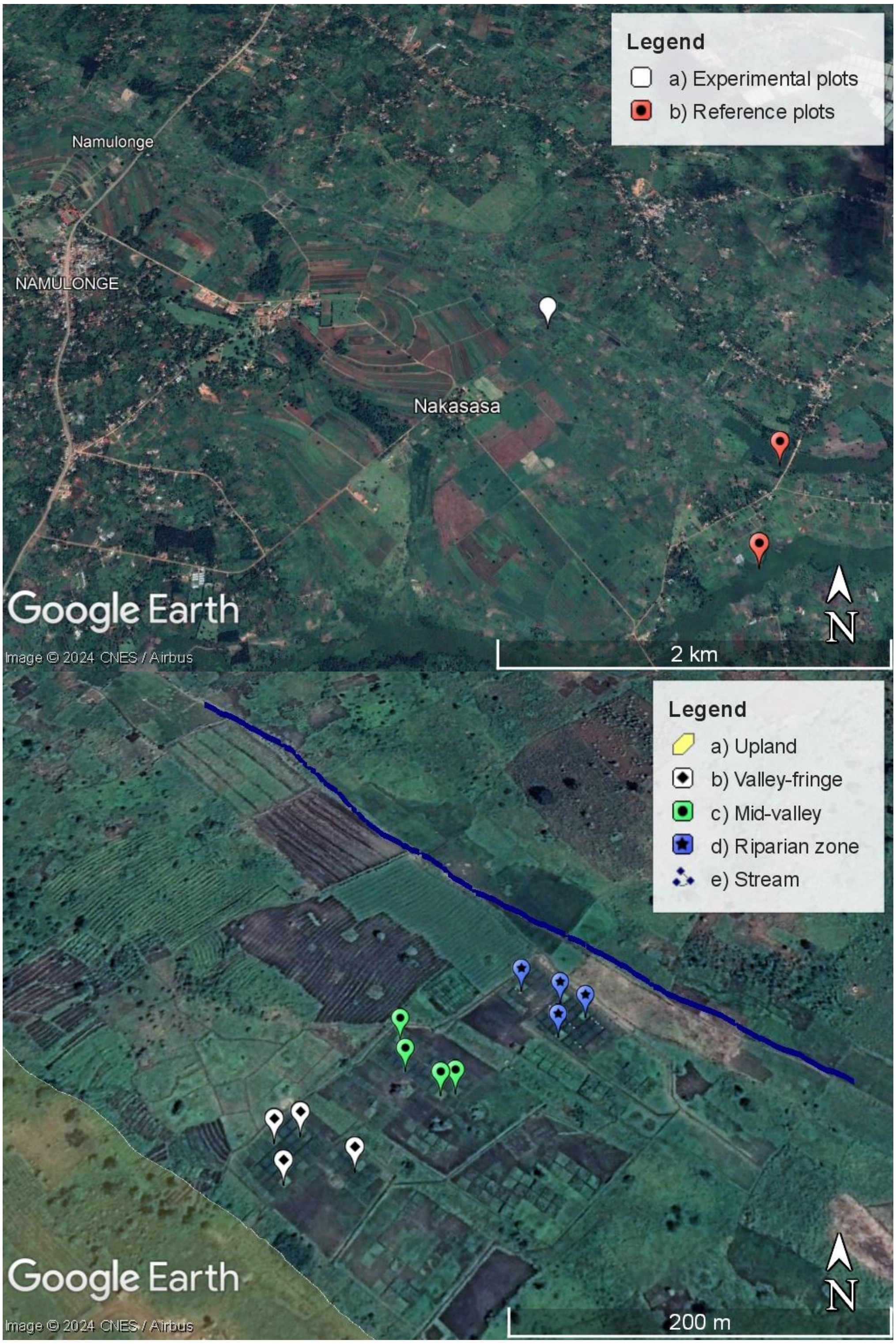

Figure 9: Location of the study sites around Namulonge, Uganda (above) and the experimental plots within the hydrological zones (below) on a satellite imagine from November 2014, shortly after the experiment was implemented. Maps created with Google Earth™, images © CNES / Airbus 2024.

cm^{-3}) and lowest in the riparian zone (1.06 ± 0.33 g cm^{-3}). On the other hand, soil organic carbon content was higher in the in the riparian zone (2.49 ± 1.7%) than in the valley fringe (1.62 ± 1.30%), with the mid-valley was in between the other positions regarding both soil attributes.

At each wetland zone, four plots (repetitions) of 4 by 4 m were designated and marked with poles and lines. In the plots, on 15 Sep 2014 all aboveground biomass was removed. Subsequently, the soil was tilled and turbated to destroy structures of perennial plants. This soil preparation resembled the common agronomic practice of seedbed preparation at the study site.

Sample and Data collection

In each plot, regular samplings of species composition and abundances (relevés; Müller-Dombois and Ellenberg 1974), and plant biomass were conducted between October 2014 and January 2017. Sampling intervals were about two weeks in the beginning and were extended to about three months at later stages of the experiment. Samplings took place in both the wet and the dry seasons.

In total, 13 sampling events for vegetation relevés were done on the following days: 07 October 2014, 23 October 2014, 25 November 2014, 14 December 2014, 9 January 2015, 21 March 2015, 22 April 2015, 24 July 2015, 17 October 2015, 6 January 2016, 14 April 2016, 6 August 2016, and 8 December 2016. Seven relevés sampled in 22 October 2015, 23 October 2015 and 24 October 2015 in a little disturbed area upstream in the Namulonge valley were used as reference plots. Vegetation community composition (vascular plant species and their estimated cover) was recorded in 2 by 2 m squares in the center of each plot. Plants were predominantly identified in the field. In few cases, specimens were collected and identified with the help of experts at the herbarium of the Makerere University in Kampala, Uganda, and at the East African Herbarium in Nairobi, Kenya, using the identification keys of Flora of Tropical East Africa (Polhill 1949-2010).

Eighteen sampling events for biomass were done on the following days: 25 October 2014, 13 November 2014, 26 November 2014, 15 December 2014, 10 January 2015, 30 March 2015, 25 June 2015, 27 October 2015, 20 November 2015, 06 January 2016, 22 April 2016, 21 May 2016, 15 June 2016, 07 July 2016, 10 August 2016, 22 November 2016, 8 December 2016, 10 January 2017. For plant biomass, all aboveground living biomass was cut at 1 cm height in 25 cm x 25 cm squares. Dead biomass was removed and not considered. Biomass was oven-dried at 90 °C when constant weight was reached. The values for dry biomass were transformed to kg m^{-2} by multiplying them with a factor of 0.016. The location of the biomass sampling was outside the central square to avoid interference with the species composition sampling. The size of only 0.125 m^2 and a rotation of biomass sampling plots around the central square were chosen to minimize the effects of destructive sampling and hence legacy effects of previous samplings.

To each plant species, life forms specifically developed for tropical wetlands were assigned following Behn et al. (2022). Data on (potential) use of plants as food, medicine or raw material were taken from the online database "useful tropical plants" (Fern, 2023) and Tolo et al. (2023), unless stated otherwise.

Visualization and statistical analysis

For the aboveground live biomass development over time, average values and standard errors were calculated from individual values of the four repetitions separately for each zone. Dominant species, number of species, and evenness were visualized in the same way. Effect of time and position on aboveground live biomass was assessed with a linear mixed effect model using the *lmer* function from *lme4* package (Bates et al., 2015) and Satterthwaite-test using *anova* from *lmerTest* package (Kuznetsova et al., 2017). Aboveground live biomass data was log transformed to meet assumption of normality. The effect of position and time on species number and evenness was assessed analogue to biomass but without log transformation.

A principal coordinate analysis (PCO) visualized changes in species composition in the course of the succession. To increase the floristic contrast between plots, cover values were reclassified into four classes, i.e., 1 (>0-25% cover), 2 (>25-50%), 3 (>50-75%), and 4 (>75-100%) (Behn et al., 2022). PCO was performed using the *cmdscale* function from the *stats* package (R Core Team, 2024), based on a distance matrix created with *vegdist* function using "Bray"-dissimilarity index. For each sampling event, coordinates of all four repetitions were averaged to create centroids for an easier visualization. Effect of time and position were analyzed with a PERMANOVA using *adonis2* function. The functions *vegdist* and *adonis2* are included in the *vegan* package (Oksanen et al., 2024).

Effect of position and time on life form proportion was assessed with a generalized linear mixed effect model with binomial distribution using *glmer* function from *lme4* package (Bates et al., 2015) and Wald-chi-square test using *Anova* function from *car* package (Fox and Weisberg, 2019).

All data visualization and analyses were done in R (R Core Team, 2024). Data storage and handling was done using *vegtable* package (Alvarez, 2023). The dataset is available as supplement S1 of the published article.

7.1.3 Results

Vegetation recovery after a disturbance event

Following the initial disturbance in October 2014, vegetation quickly regrew in all experimental plots and plots were completely covered by vegetation within two months after the initial disturbance. Aboveground live biomass reached a first peak after about 200 days and a second, higher peak at around 600 days. The peaks were followed by a decline, related to a dying-down of plants or plant parts (Figure 10).

The effect of time on biomass was statistically significant. In addition, the position in the wetland, and the interaction between position and time were significant (Table 16) despite generally similar trends across the positions. Living biomass in the riparian zone was higher than in the other positions at the time of the biomass peak, but declined thereafter, likely due to temporary accumulation of dead biomass. Photographs of exemplary plot observations are available as in appendix A4.

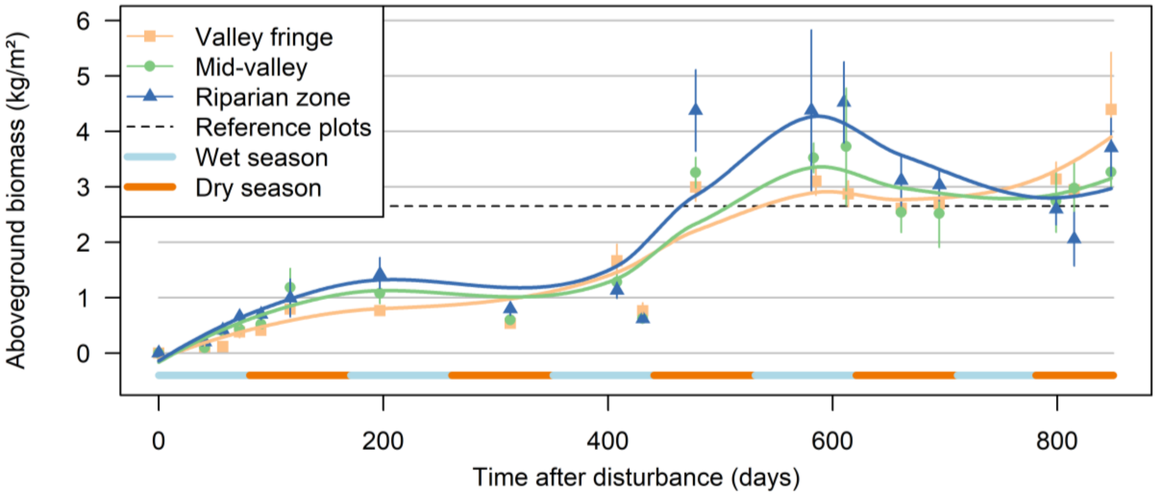

Figure 10: Aboveground live biomass (dry weight) development in a regeneration experiment after initial disturbance in different positions in the Namulonge valley, displaying the average of four repetitions and standard error from repeated samplings. The trend lines are based on local polynomial regression and are displayed for visualization purposes only. The dashed black line represents the mean value for biomass samplings at the natural reference sites.

Table 16: Effects of position and time after disturbance (days) on aboveground live biomass, number of species, and evenness in wetland vegetation in Namulonge valley, Uganda. Displayed are results of Type III Satterthwaite-anova based on a linear mixed effect model.

	Sum Sq.	Mean Sq.	DF	Den DF	F value	p-Value	Sign.
Effect of position and time on aboveground live biomass[1]							
Position	4.078	2.039	2	48.229	5.252	0.009	*
Time	155.410	155.410	1	189.000	400.322	0.000	*
Position*Time	2.937	1.469	2	189.000	3.782	0.024	*
Effect of position and time on number of species							
Position	91.029	45.514	2	16.709	2.594	0.104	ns
Time	82.903	82.903	1	141.000	4.724	0.031	*
Position*Time	9.963	4.981	2	141.000	0.284	0.753	ns
Effect of position and time on evenness							
Position	0.291	0.145	2	150	10.121	0.000	*
Time	0.034	0.034	1	150	2.339	0.128	ns
Position*time	0.078	0.039	2	150	2.719	0.069	ns

Sum Sq. = sum of squares, Mean Sq. = mean squares, DF= degrees of freedom, Den DF= denominator degrees of freedom, Sign. = significance, * <0.05, ns= not significant. [1] biomass data were log-transformed to meet assumption of normality of the residuals.

Diversity, taxonomic, and functional changes in the recovery process

The number of species per plot rose fast at all positions, reaching values above 20 species on four-m² in some plots after around 100 days after disturbance, followed by a decline to about ten species (Figure 11). Consequently, the effect of time proved to be significant, unlike the effect of position (Table 16). Conversely, species evenness remained rather constant and time effects were not significant. Position effect was significant with lower values in the riparian zone (Figure 10 and Table 16). A comparison with the reference plots showed similar median values for species richness (10/4 m² plot) but lower evenness (0.49) values due to the dominance of *Cyperus papyrus* in the reference plots, with a cover of >50%.

The dominant species changed over time and differed across the positions (Figure 12). The first phase was dominated by obligate or facultative annual species such as *Ageratum conyzoides*, an introduced forb of the Asteraceae family in the valley fringe. In the mid-valley position and riparian zone, native Cyperaceae *Cyperus distans* and *Cyperus difformis* dominated. After about a year, these species almost completely disappeared and were replaced by perennial graminoids, such as *Paspalum scrobiculatum*, *Leersia hexandra* (both Poaceae), and *Fuirena pubescens* (Cyperaceae). Their abundance reached a maximum between 300 and 500 days after the disturbance event. Later, forbs including *Ludwigia*

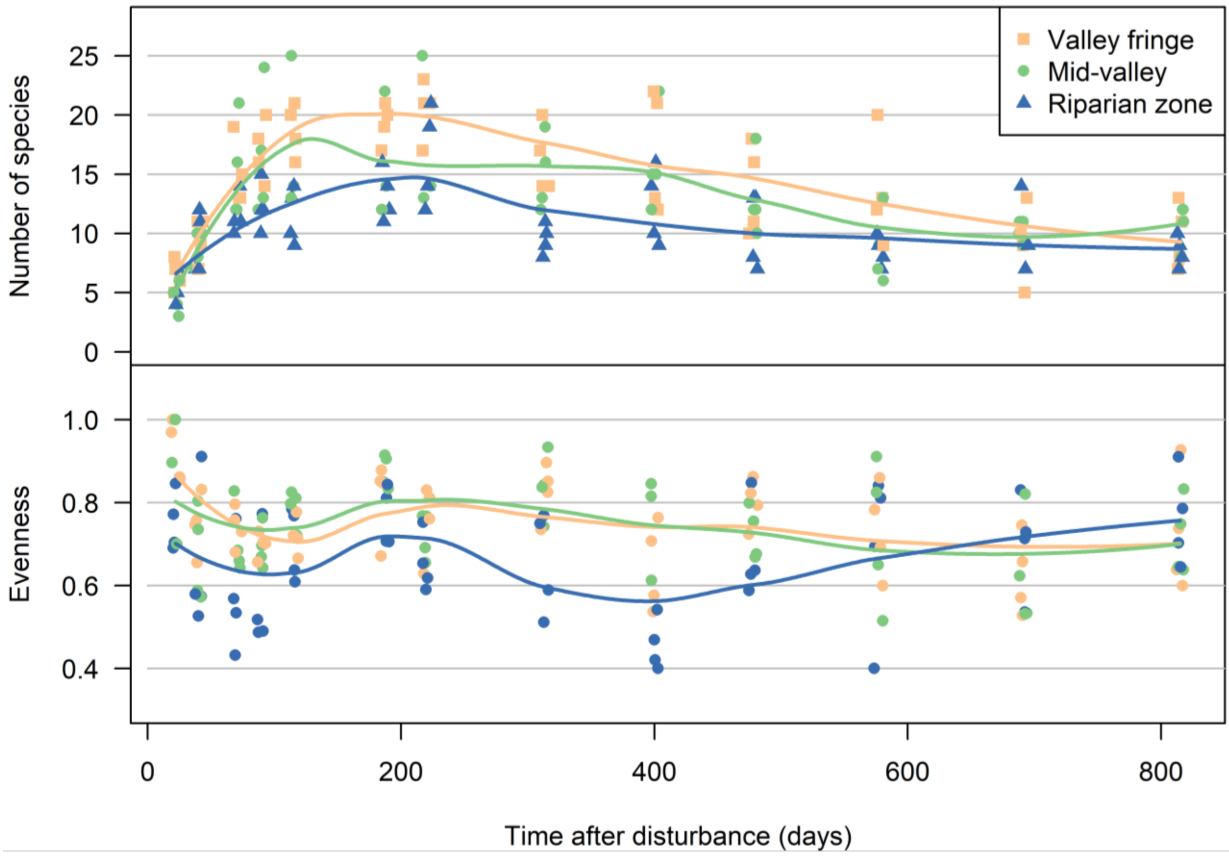

Figure 11: Number of species in 4 m² plots and Evenness during succession after an induced disturbance event in different positions of an inland valley wetland in Namulonge, Uganda; 4 replications and 13 repeated sampling dates over a period of about 2 years. The trend lines are based on local polynomial regression and for visualization only.

abyssinica (Onagraceae) and woody species increased in abundance. In this experiment, most relevant woody species were the invasive shrub *Mimosa pigra* (Fabaceae) in three out of four repetitions at the mid-valley position and *Triumfetta brachyceras* (Malvaceae) that occurred in two repetitions in the riparian zone. In two repetitions in the valley fringe, the perennial Poaceae *Panicum maximum* became the dominant species.

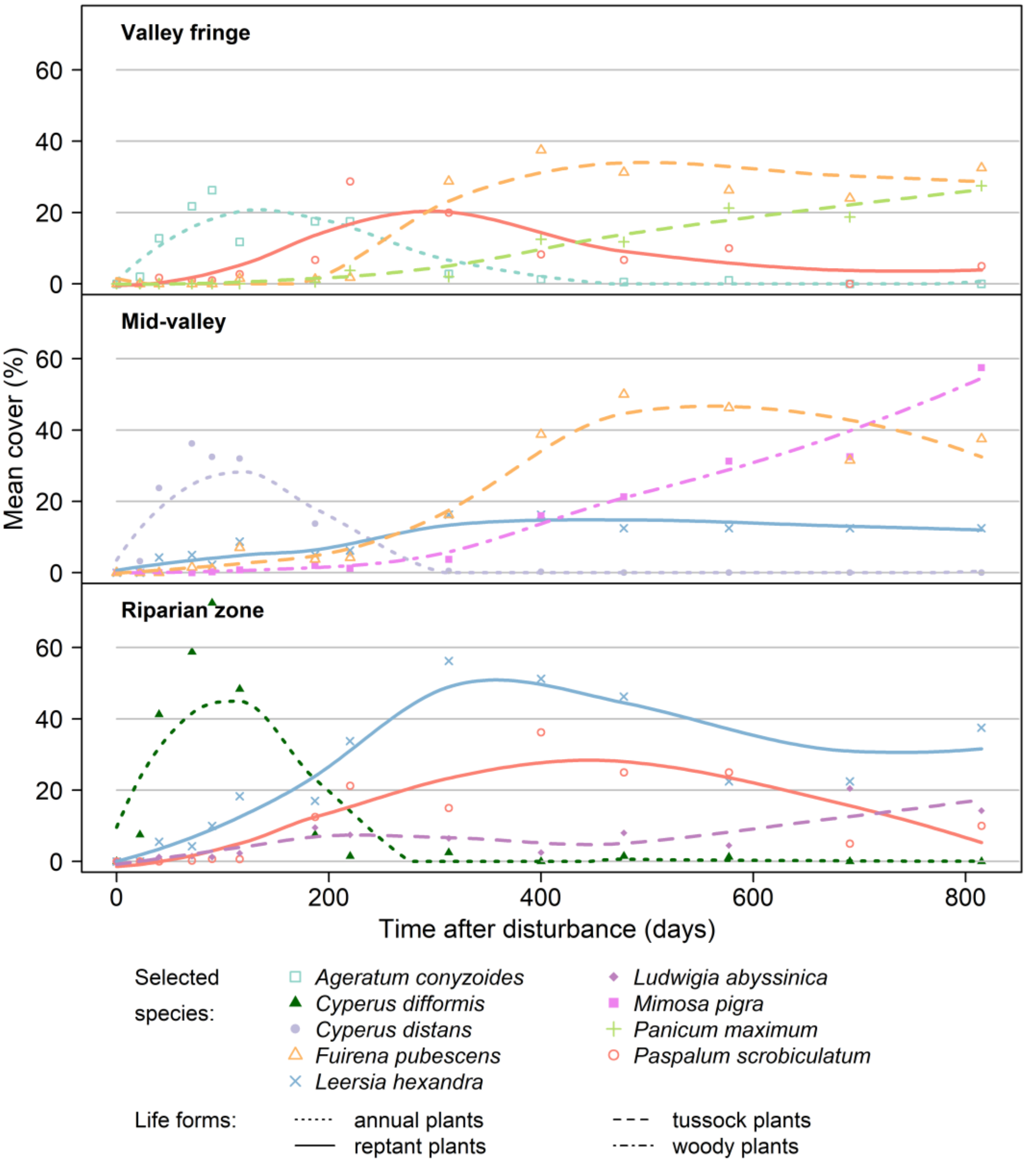

Figure 12: Changes in selected dominant species after disturbance in an experiment at different positions in the Namulonge valley, Uganda. Colors and symbols referring to individual species, the line type of the trend line indicates the life form. Note: not all species are present in all four repetitions of each 4 m². Error bars are however purposefully left out not to overload the figure. The trend lines are based on local polynomial regression are displayed for visualization purposes only. Meaningless negative values were set to 0.

Species composition showed a directional change in all positions (Figure 5). While the initial sampling (22 days after the disturbance event) was similar across positions, species composition changed, and positions subsequently developed differently. The first PCO axis (eigenvalue 11.97) explained about

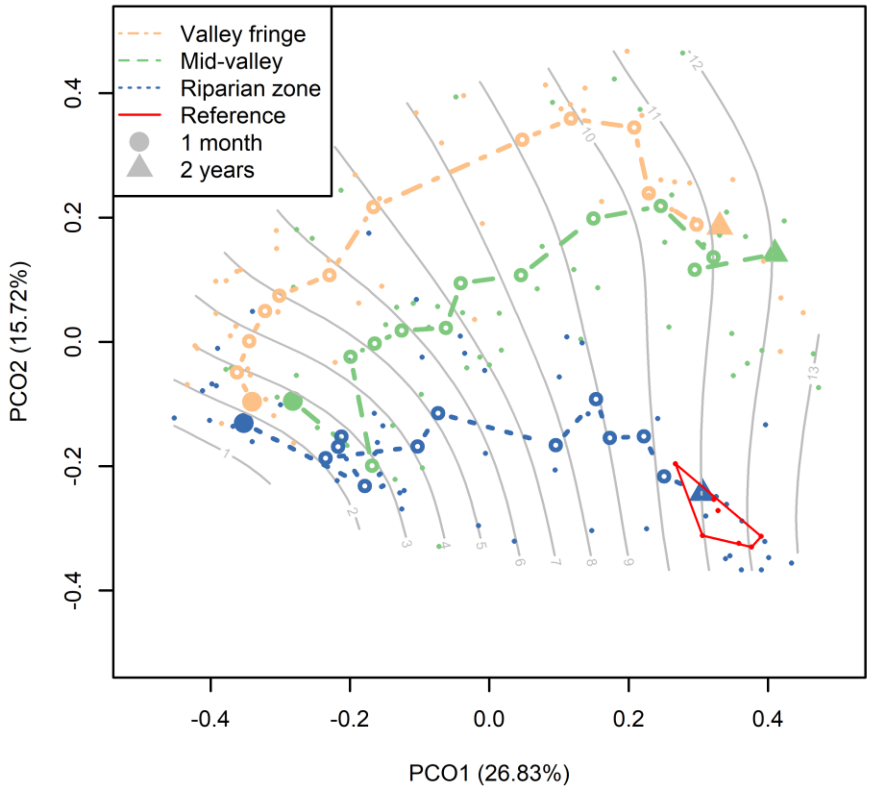

Figure 13: Ordination (Principal coordinates analysis with "bray"-dissimilarity) showing directional changes in species composition in the course of succession after disturbance in an experiment at different positions in the Namulonge valley, Uganda, with repeated sampling over a period of about 2 years. The ordination is based on all plots recorded. The line connecting the centroids for each position and sampling event are for illustrative purposes. Grey lines and numbers reflect sampling events fitted to the ordination. Numbers in brackets mean the variance explained by the first and the second axis.

27% of the variation of the species composition, and largely represents the time after the disturbance event. The second axis (eigenvalue 7.01) explained about 16% of the total variation and appeared to be correlated to the zone in the wetland and the distance from the central stream. The explained variance and the significance of time and zone are in line with the results from a PERMANOVA that indicate significant effects of the position, the sampling event, and their interaction on species composition, explaining together around 60% of the variation (Table 2).

Table 17: Effect of position and time after disturbance (repeated sampling events) on species composition in wetland vegetation in Namulonge valley, Uganda. Results are based on PERMANOVA.

	Sum Sq.	DF	Partial R^2	F value	p-Value	Sign.
Position	5.556	2	0.136	19.553	0.001	*
Sampling event	14.612	12	0.357	8.571	0.001	*
Position*Sampling Event	4.088	24	0.100	1.119	0.001	*
Residuals	16.622	117	0.407			
Total	40.878	155				

Sum Sq.= sum of squares, DF= degrees of freedom, Sing. = significance, *significant at p<0.05

The mid-valley position (located between valley fringe and riparian zone), also took an intermediate position in terms of species composition, however eventually more similar to the valley fringe than to the riparian zone. The ordination further indicates that the vegetation in the riparian zone, but not in the other positions, developed to be similar to the undisturbed reference plots (semi-natural vegetation) in terms of species composition. However, the similarity displayed in the ordination has to be seen in the context of the very different earlier succession stages. When comparing the physiognomy and the dominance of Cyperus papyrus in the reference plots, differences to the center plots in the late samplings remain very large.

Proportions of aggregated species by life forms provided similar change trends (Figure 14). Initially, annual species dominate the plots in all positions. After about 200 days after the disturbance event, emerging perennial tussock and reptant plants largely replaced the annual plants. Simultaneously, reed plants, woody plants, and climbing species emerged while remaining at low abundance until about 600 days after disturbance. These three different phases can be understood as successional stages, which is supported by the significant time effect on the proportion of these lifeforms (Table 18), even though exact delineations of these stages are not possible.

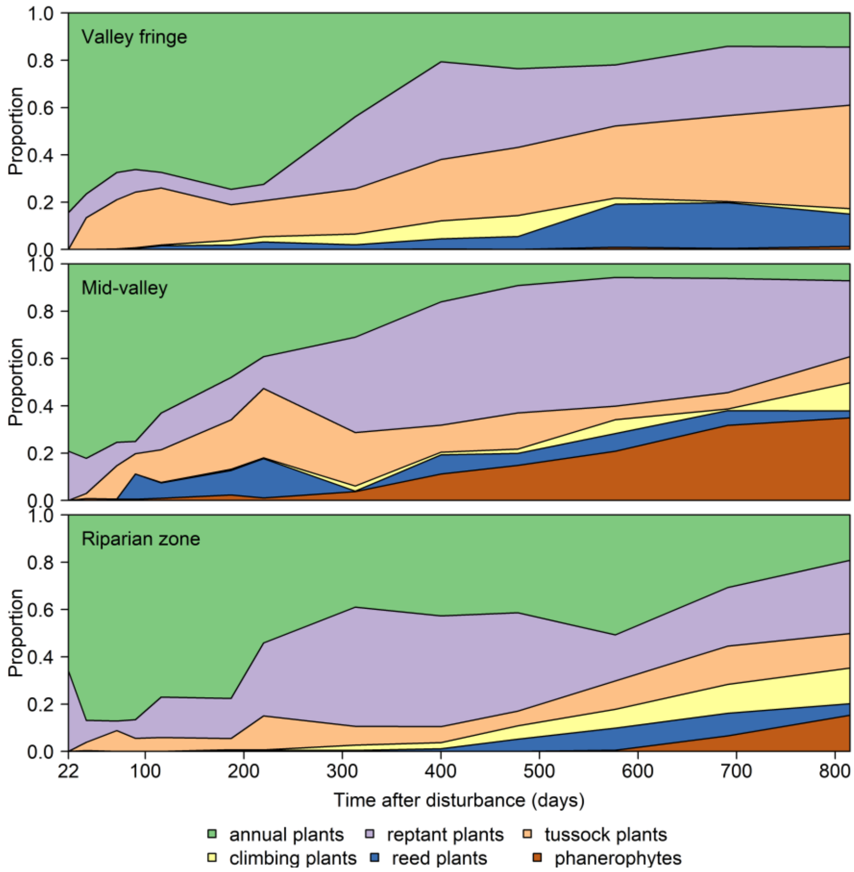

Figure 14: Average share of different lifeforms after disturbance at different positions in the Namulonge valley, Uganda (2014-2017); repeated samplings over a period of 27 months and observation plots sizes of 4m² with four repetitions in each position and sampling date.

Table 18: Effect of position and time (days) on aggregated proportions of plant life forms in wetland vegetation in Namulonge valley, Uganda. Displayed values are results of type II Wald chi-square test based on generalized linear mixed effect models.

	ChiSquare	DF	p-Value	Sign.
Effect of position and time on proportion of annual species				
Position	8.541	2	0.014	*
Time	38.860	1	0.000	*
Position*Time	1.4394	2	0.487	ns
Effect of position and time on proportion of perennial species (reptant and tussock plants)				
Position	3.930	2	0.140	ns
Time	23.131	1	0.000	*
Position*Time	1.235	2	0.539	ns
Effect of position and time on proportion of perennial species (reeds and phanerophytes)				
Position	0.009	2	0.996	ns
Time	4.4598	1	0.035	*
Position*Time	5.4533	2	0.065	ns

DF= degrees of freedom, Sign. = significance, *significant at $p<0.05$; ns=not significant.

Implications of changing plant diversity for ESS provision

Throughout the observation period, (potentially) useful plants occurred. However, corresponding with general changes in species and lifeforms, many useful plants could be found only in earlier or later stages of succession. Hence, ecosystem service provision such as medicinal plants for specific purposes varies with the fallow duration. Table 19 provides an overview on selected example species.

Table 19: *Selected species and their potential use recorded in a 27-months regeneration experiment (3 successional stages) in an inland valley wetland in Namulonge, Uganda. Stage 1 refers to vegetation dominated by annuals, stage 2 to a dominance of perennial tussock and reptant plants, and stage 3 to the emerge of reed, woody and climbing plants. The column zone indicates in which of the zones in the wetland the plant mostly occurred (VF – Valley fringe, close to the slope limiting the wetland; MV - mid-valley, RZ – riparian zone close to the central stream in the valley. The direct use is according to "useful tropical plants" (Fern 2023 and Tolo et al. (2023).*

Species	Family	Succ.stages	Zone	Direct uses	Comment
Ageratum conyzoides	Asteraceae	1-2	VF	Medicinal	Common introduced weed
Bidens pilosa	Asteraceae	1-2	VF, MV	Food, Medicinal	Common introduced weed
Cyperus distans	Cyperaceae	1-2	VF, MV, RZ	Food, Material, Medicinal	
Digitaria abyssinica	Poaceae	1-2	VF, MV, RZ	Medicinal	Often considered a problematic weed
Acmella caulirhiza	Asteraceae	2	VF, MV, RZ	Medicinal	
Paspalum scrobiculatum	Poaceae	2	VF, MV, RZ	Food	
Centella asiatica	Apiaceae	2-3	VF, MV	Medicinal	
Cyperus latifolius	Cyperaceae	2-3	VF, MV	Forage, Material, Medicinal	Commonly used for thatching, also used in waste

					water treatment
Leersia hexandra	Poaceae	2-3	MV, RZ	Forage	
Ludwigia abyssinica	Onagraceae	2-3	VF, MV, RZ	Food, Medicinal	
Cyperus papyrus	Cyperaceae	3	RZ	Material	Important for several ecosystem services, including habitat provision and water regulation
Ipomoea cairica	Convolvulaceae	3	RZ	Food, Medicinal	
Melanthera scandens	Asteraceae	3	MV, RZ	Food, Medicinal	
Mimosa pigra	Fabaceae	3	MV	Firewood Medicinal	Valuable pollen source for bees; largely considered a problematic invasive species
Panicum maximum	Poaceae	3	VF	Forage, Material	

7.1.4 Discussion

Our empirical research highlights that the vegetation biomass of a tropical inland valley wetland is able to recover fast after a disturbance event. However, biomass production, dominant species, and species composition differed between hydrological positions in the wetland.

The year-round water availability, particularly close to the central stream (riparian zone), enabled continuous plant growth. Early pioneer species, comprising mainly annual species, are commonly considered to be weeds in paddy rice cultivation (Makhoka et al., 2017), such as *Ageratum conyzoides, Cyperus difformis,* and *Cyperus distans* dominated a first succession phase. These annuals have large amounts of seeds in the seedbank, as reported for *Cyperus difformis* seeds in a wetland soil in South Sudan (Esaete et al., 2021). In a second phase, perennial species were gradually taking over. Tussock plants were the first perennials, while reptant plants, mainly graminoids such as *Leersia hexandra* and *Fuirena pubenscens*, subsequently followed in the succession. In a third phase, typical wetland plants such as *Cyperus latifolius* and *Cyperus papyrus* started to dominate, along with climbing plants and woody plants. This successional phase was also characterized by the emergence of the invasive species, such as the shrub *Mimosa pigra*. These results largely confirm observations and succession theories from the literature. For instance, Burrows (1990) described a typical progression in an abandoned garden in the temperate region of New Zealand: annuals characterized the first growing season. They were followed by perennial herbs in the second, by dense and sward-forming perennial herbs in the third and the following seasons, and eventually by trees and shrubs. The author further noted that these changes occur much faster in wet tropical regions, which is in line with our observations. In the presented study, these successional stages could be identified, however, due to the continuous growth and the gradual changes in species abundances, exact delineation of successional stages is not possible. Similarly, variation in vegetation, even between plots of the same hydrological zone, might be caused by variations in hydro-edaphic conditions or the availability of diaspores, which may complicate a clear delineation of successional stages. Besides similar trends, there were significant differences between the hydrological positions. Aboveground live biomass was significantly different and highest in the riparian zone for most of the assessed time. Prominent were also differences regarding dominant species, evenness, and species composition in general. Species numbers were highest in the beginning of the second succession stage, when annuals were replaced by perennials. While evenness remained rather constant during the succession process, there was a significant difference between positions, and the riparian zone had lowest evenness in the beginning. The valley fringe had a higher prevalence of plants that are not restricted to wetlands, such as *Ageratum conyzoides* or *Panicum maximum* (Fern, 2023). Plots near the central stream developed towards the state of undisturbed vegetation found elsewhere on hydrologically not altered sites in the valley. However, even after two years, these plots still differed from undisturbed sites. Apart from these reference sites in the riparian zone, we did not compare undisturbed to our experimental sites in the presented study, which may constitute a limitation. Besides the difficulty of identifying appropriate reference sites, the period of the study was too short to expect a regeneration of natural swamp forest.

The results may however be only partly explained by hydrological conditions. Gabiri et al. (2018) noted that overall, positions do not significantly differ regarding their hydrological regime. However, they also found that soil moisture of the mid-valley position was significantly higher than in the valley-fringe, but not different from the riparian zone. Our results on species composition showed that after two years, the mid-valley zone was more similar to the valley fringe than to the riparian zone. Other potential explanations include variation in soil conditions or cultivation history, as the valley-fringe plots are closer to the upland and therefore easier to access. Runoff water transporting diaspores of upland plants from adjacent fields to the valley-fringe, but not to the riparian zone, may also explain differences in species composition, even though this was not investigated in this work. While we studied vegetation dynamics directly after a disturbance event, in practice post-cultivation fallows dominate. We therefore expect the first succession stage to comprise mostly the weeds that are associated with crop cultivation, though less prominent due to weed control measures, and to be followed by the second stage after crop harvest.

Relevance for wetland science

The results show that vegetation development in tropical inland valley wetlands is highly dynamic after a disturbance event, such as land clearing, tillage, and weeding operations. Vegetation structure and composition can dramatically change within weeks or months after the disturbance event. Similarly, small-scale differences in hydro-edaphic conditions that and are common in wetlands (Diamond et al., 2021), were observed at the study site (Gabiri et al., 2018), and may cause variation in the vegetation development. Research on land uses in wetlands must therefore consider the diversity and dynamics of fallow land. Thus, repeated measures on the same plots, e.g. on ecosystem functions and services, may have a limited value for comparability due to constantly changing vegetation. Hence, vegetation should always be described regarding dominant and other important species, or with vegetation associations (Behn et al., 2022). Further, wetlands differ in terms of their type, their hydrology, their edaphic conditions, and in the way they are used. Consequently, also the findings of the present work can only be extrapolated to wetlands with similar properties, meaning a tropical inland valley wetland that has despite a seasonality in precipitation almost continuously favorable conditions for plant growth. Floristic classifications of wetland vegetation based on species occurrences and abundances (e.g., Behn et al., 2022) can further help to identify such wetlands with similar hydro-edaphic conditions, and in which similar dynamics as described here may be observed. Such extrapolation domains would exclude wetlands that do not provide year-round conditions for plant growth due to the occurrence of distinct dry seasons or extended periods of flooding. Yet, similar empiric studies of short-term succession in tropical wetlands are rare. Hence, it is of great interest for vegetation science, conservation and land use planning, to obtain data on species successions and recovery dynamics from a wide range of regions and from different wetland types.

Changes of land use intensity

While biodiversity conservation is often focused on natural landscapes, the majority of species can be found in “production landscapes”. However, many species are negatively affected by practices of land use intensification, including land drainage, irrigation and the use of agrochemicals (Baudron et al., 2021). On the other hand, agricultural land use can also increase biodiversity, i.e., by creating open habitats for some species that may disappear by land abandonment, extended fallow periods or strict protection measures. Farmers particularly in low-income countries rely on a wide range of ESS such as soil fertility regulation, pest and disease control, and pollination. With reference to our study, these opposing developments of land use intensity would reduce the early and intermediate succession stages that proofed to be of importance for both biodiversity and the provision of ESS. Either way would lead to a reduction of intermediate succession stages, by increasing the disturbance frequency and/or intensity, or by avoiding anthropogenic disturbance. These contrasting developments of diverging pathways of conservation and agricultural intensification at the expense of areas with moderate land use intensity are currently also observed in other ecosystems in Africa (e.g., Sandhage-Hoffmann et al., 2022). This can strongly alter distribution and abundance of various species in the respective areas. In Central Europe, for instance, anthropogenic grass- and heathlands grazed by sheep covered large areas and harbored an enormous floral and faunal diversity. However, in the 19th and 20th centuries, the extent of these sites was strongly reduced, by intensification of agriculture, afforestation, and abandonment. These land use changes are considered to be among the major reasons for biodiversity loss in Central Europe. Today, remaining sites of nutrient-poor grassland and heathland are under strict protection and require a specific management (Schellenberg and Bergmeier, 2020).

The relevance of intermediately disturbed sites

The findings of the present study are in line with studies showing a change in ESS provision during succession (e.g., Cortés-Calderón et al., 2021). They suggest a prevalence of species in each successional stage that can provide specific ecosystem services. Plants with medical properties or those used as food were found throughout the observed succession process, though not the same species in each stage. Plants used for forage and as raw materials occurred in intermediate or later stages of the succession. A mosaic of sites of different successional stages therefore provides a diversity of potentially useful and actually used plants (Tolo et al., 2023), many of which support medical needs, particularly for low-income households. Many medicinal plants, however, occur mainly during early succession stages. Other non-cultivated plants are widely used for food, feed, and other purposes by farmers in Kenya and Tanzania, but are frequently removed by weeding operations from crop fields (Makokha et al., 2017). On the other side, disturbances by agricultural land uses often provide “windows of opportunity” for the establishment of invasive (Orbán et al., 2021) and generalist species. This may have negative effects on specialist species with narrow ecological amplitude including birds nesting in papyrus marshes (Owino and Ryan, 2007). In our study, we observed the emergence of invasive *Mimosa pigra* following disturbance, which is of growing concern in African wetlands as it negatively impacts biodiversity and ESS provision (Witt et al., 2020). Interestingly, the invasive *Mimosa pigra* was found in the experimental plots almost exclusively in the middle position of the inland valley wetland in Uganda, despite being known to thrive on a variety of soil types and to tolerate soil flooding (Kato-Noguchi, 2023) and being present in some of the reference plots. Being a woody plant, it was not found in the first successional stages, but started to emerge in the second and became dominant in the third stage of succession. Consequently, extended fallow periods may presumably increase the risk of *Mimosa pigra* invasion. Short fallow periods or permanent cropping may, on the other hand, reduce the risk, as proven for *Prosopis juliflora*, another invasive woody Fabaceae in East Africa (Mbaabu et al., 2021). Also, clearing vegetation from a fallow of two or more years presumably requires far more labor force than clearing a fallow of less than a year (Choge et al., 2022; Wakie et al., 2016).

In general, wetland management in Uganda and beyond has to deal with various and often conflicting stakeholder interests between destructive use of wetlands (land for farming, mining), non or limited destructive use (source of materials and herbs), and conservation. Difficulties further arise from disputed ownership and access rights that complicate management (Kadoma et al., 2023). The presented work should neither deny the need for adequate food production nor question the need for large scale conservation. The latter is of major importance for several ecosystem functions and services that are best delivered with minimal anthropogenic disturbance (Owino and Ryan, 2007; Plumtre et al., 2019). Given that intermediate succession stages show large biodiversity while providing many services to local communities, one may advocate for a spatially and temporally restricted use of wetlands for cropping followed by fallow periods. Management must include local stakeholders to ensure its success (Barakagira and de Wit, 2019, Kadoma et al., 2023). Further, the potential spread of invasive species must be considered (Seebens et al., 2021). This may contribute to reconcile food production with environmental protection, as would allow to a certain extent smallholder crop production in otherwise protected sites. In summary, this work calls for the consideration of intermediately disturbed sites, combining production and protection, and ensuring the presence of all successional stages within the wetland landscape.

7.1.5 Conclusion

We studied short-term regeneration processes after an induced disturbance in a tropical inland valley wetland. The process of vegetation recovery was rapid and highly dynamic, involving three successional stages, considering plant biomass, species composition and the dominance of life forms. Future wetland use planning must consider these successional dynamics following anthropogenic disturbance events, and it must involve monitoring and controlling invasive species.

Electronic supplements:

Supplement S1: Dataset used in this work

https://static-content.springer.com/esm/art%3A10.1007%2Fs11273-024-10011-6/MediaObjects/11273_2024_10011_MOESM1_ESM.zip

8 Applying integrity assessment and vegetation classification to recovery studies and to other wetland sites in East Africa

Chrysopogon nigritanus (top left) and experimental fields (top right) in Kilombero floodplain, Tanzania, experimental plot (bottom left) and Taro *(Colocasia esculenta)* cultivation (bottom right) in Namulonge valley, Uganda.

Chapter 5.2 has introduced a novel method for assessing the state of a wetland using vegetation attributes, while Chapter 6.2 developed a classification of East African wetland vegetation. Chapter 7 presented a study on secondary successions in agriculturally used wetlands in the Namulonge inland valley in Uganda. This following chapter first presents a similar recovery study that was conducted in the floodplain wetland of Kilombero in Tanzania, and subsequently applies the assessment method of chapter 5.2 and the proposed classification of chapter 6.2 to these vegetation recovery studies and to other wetlands beyond.

8.1 Vegetation development after disturbance in the Kilombero floodplain

Beside the detailed study on vegetation dynamics after disturbance in the inland valley of Namulonge, Uganda (Chapter 7), a similar study was conducted in Ifakara, Tanzania. While this study was conducted at a lower intensity and with less sampling dates than in Namulonge (only five sampling events for species composition and ten for aboveground live biomass were possible as opposed to thirteen and fourteen, respectively in Namulonge), the data collection, visualization, and analysis followed the same methods as described in chapter 7. While the lower number of sampling events was not sufficient to allow for extensive statistical analyses, the results provide an interesting comparison of inland valley and flooplain wetlands.

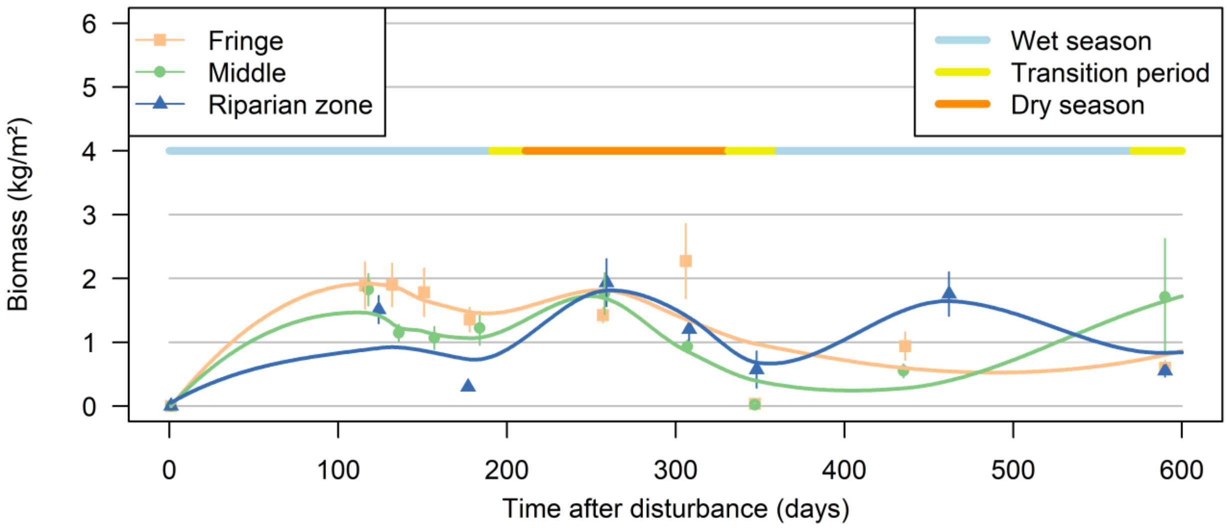

Figure 15: Biomass development in a regeneration experiment after initial disturbance in different positions in the Kilombero floodplain, Tanzania, displaying the average of four repetitions and standard error from repeated samplings. The trend lines are based on local polynomial regression and are displayed for visualization purposes only.

Unlike the inland valley wetland in Namulonge, Uganda, where the climatic and hydro-edaphic conditions provided almost continuous growing conditions (Chapter 7), the hydrological regime and the savanna macroclimate in Ifakara showed distinct wet and dry seasons, and resulted in strong seasonal and spatial variations in vegetation composition and recovery dynamics. Thus, favorable hydrological conditions occurred during the early dry and wet seasons, with a moderate soil moisture regime. However, the conditions for vegetation can be classified as adverse, with severe drought during the late dry season, especially in fringe and middle sections, and with deep soil submergence during the main wet season, particularly in the center position close to the river. During these periods of unfavorable hydrological conditions, most annual plants died, and the aboveground biomass of most perennial species was strongly reduced (Figure 14).

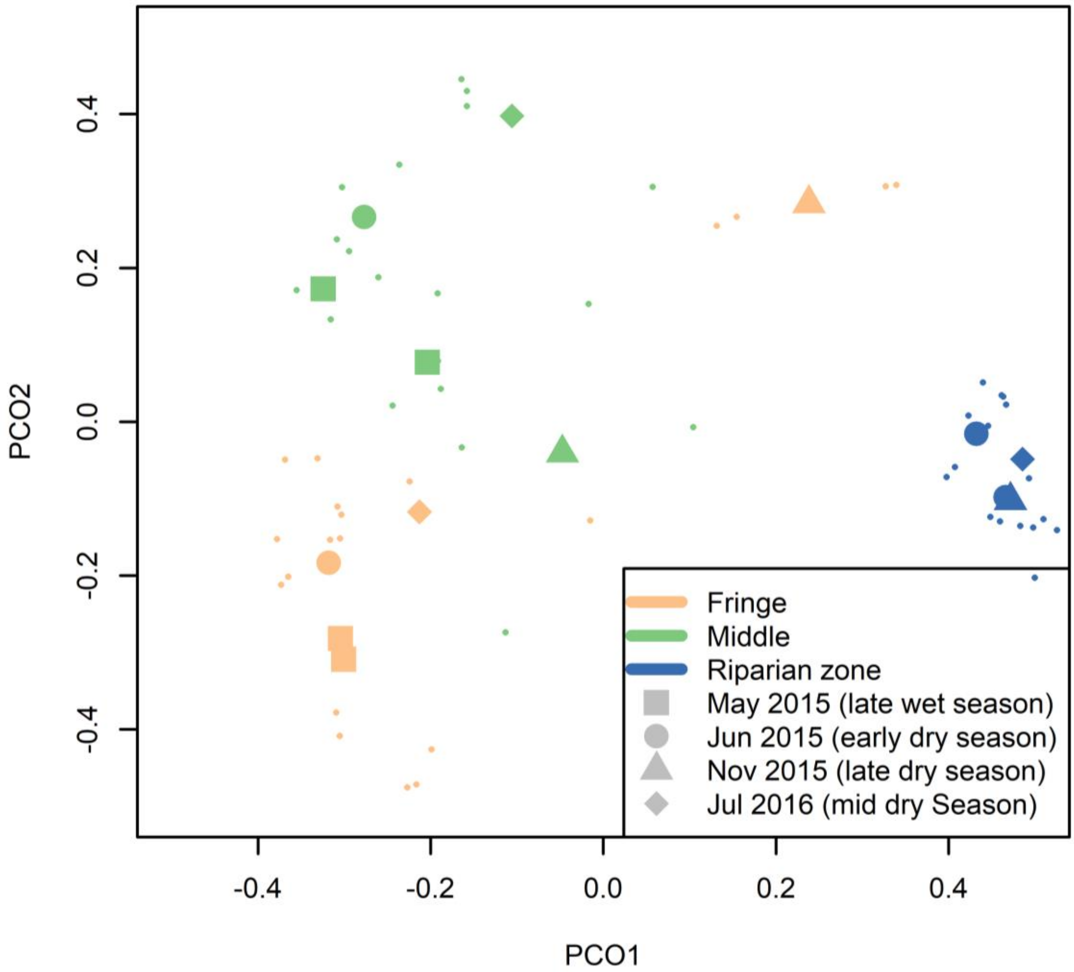

Figure 16: Ordination (Principal Coordinates Analysis with “bray”-dissimilarity) showing species composition in the course of succession after disturbance in an experiment at different positions in the Kilombero floodplain, Tanzania, with repeated sampling over a period of about 1.5 years. The ordination is based on all plots, and big symbpols represent centroids of the respective sampling dates.

Similarly, no clear shifts regarding species composition could be observed. In the fringe and middle positions, the season appeared to be much more important than the time after disturbance. Plots in the riparian zone were similar, regardless of sampling date (Figure 15). A sampling in the late rainy season (May 2015) was however not possible due to deep submerge. As for species composition, no strong changes were observed, also in the case of dominant species. Thus, the vegetation in the second year was dominated by the same annual species as in the first year (Figure 16), with the exception *Oryza longistaminata* that was mainly found in the second year. The low abundance of annual species such as *Ischaemum rugosum* in the second year may rather be attributed to different sampling dates lacking a wet season sampling event in 2016 than to their disappreance in the course of succession (Figure 16). We only exceptionally observed signs of regeneration, such as reemergence of tall perennial grasses, constituting the natural vegetation in the area (e.g., *Phragmites australis, Panicum fluviicula, Hyperarrhenia rufa*).

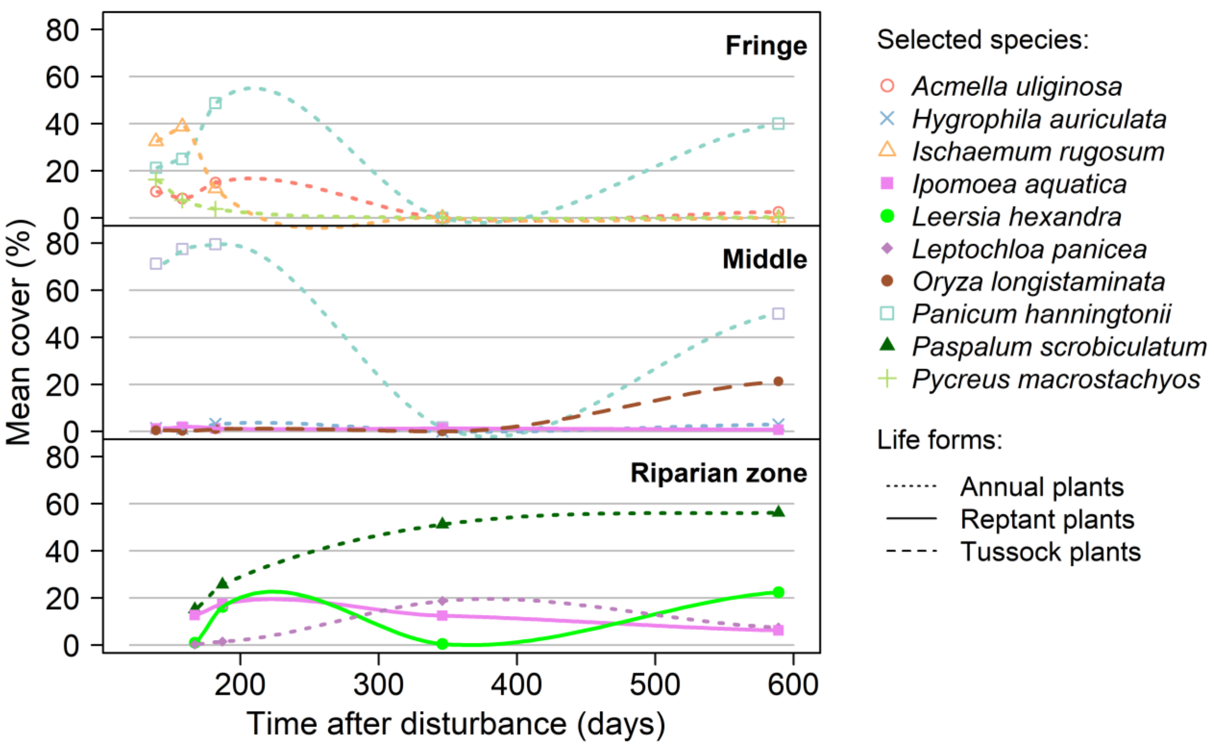

Figure 17: Changes in selected dominant species after disturbance in a field experiment conducted at different positions in the Kilombero floodplain, Tanzania. Note: not all species are present in all four repetitions of each 4 m². Error bars are however purposefully left out not to overload the figure. The trend lines are based on local polynomial regression are displayed for visualization purposes only.

The number of species and their evenness (Figure 17) were relatively constant and rather low in the riparian zone. In the other zones (fringe and middle positions), very sparse vegetation in the late dry season (around 350 days after disturbance) resulted in high evenness values, while the dominance of *Panicum hanningtonnii*, resulted in low evenness in the middle zone.

In general, the vegetation in the Kilombero floodplain with its typical seasonal savanna climate seemed to less resilient to disturbance compared to the vegetation in the inland valley wetland of Namulonge with continuous favorable hydrological conditions for plant growth.

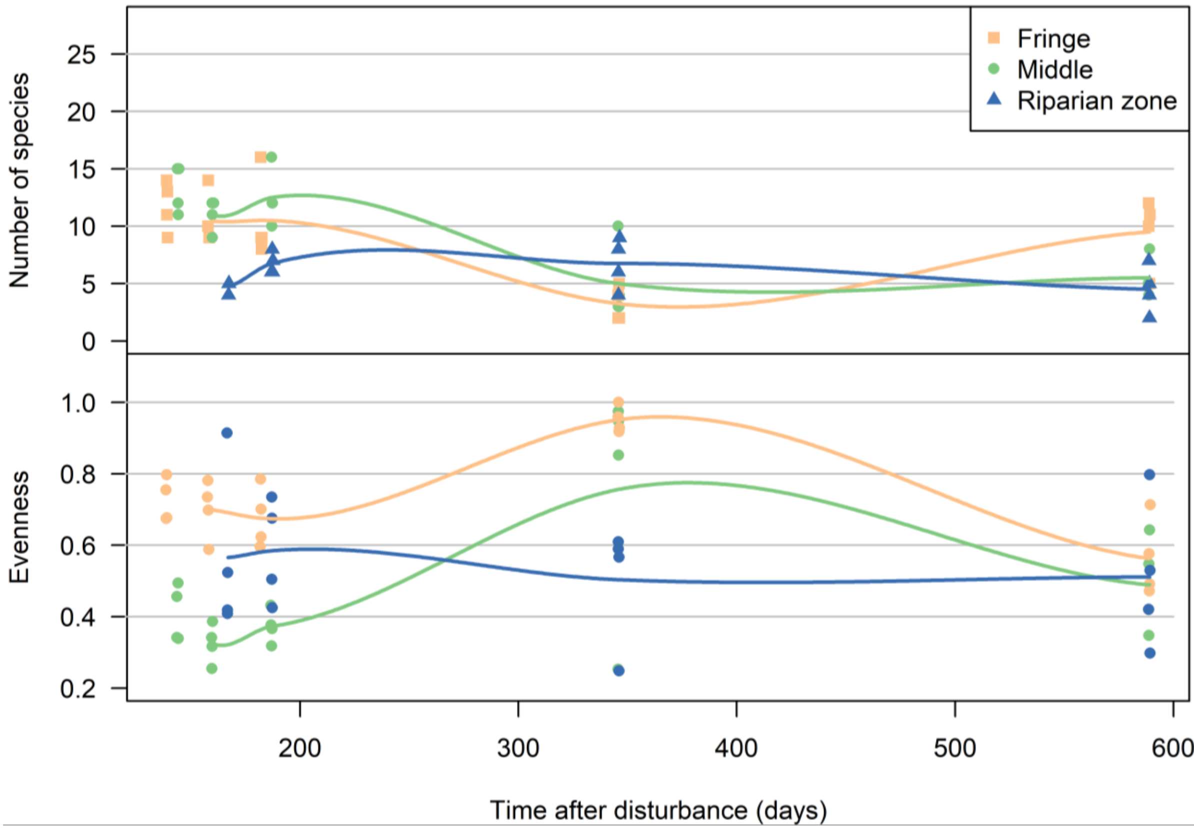

Figure 18: Number of species in 4 m² plots and Evenness during succession after an induced disturbance event in different positions of in the Kilombero floodplain, Tanzania; 4 replications and 6 repeated sampling dates over a period of about 1.5 years. The trend lines are based on local polynomial regression and for visualization only

8.2 Biotic integrity changes during the regeneration process

The Vegetation-based Index of Biotic Integrity (VIBI) predicting the vegetation module of the Wet-Health approach (Behn et al., 2018) has been applied to the different phases of vegetation recovery in the inland valley wetland of Namulonge. However, to avoid out-layers and overestimation, this assessment set the boundary for the total cover of perennial species to 100%, when the sum of individual cover data of perennial plants exceeded 100%.

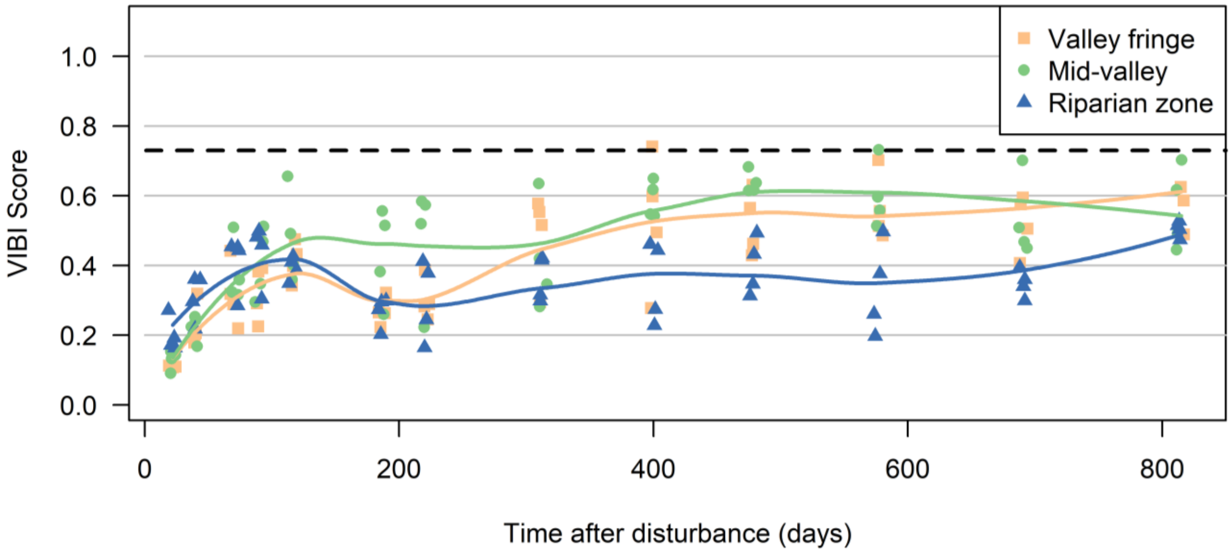

Figure 19: Application of the VIBI for Vegetation developed by Behn et al. (2018) (Chapter 5.2) on the vegetation development after disturbance at Namulonge study site. The dashed black line indicates the mean value of selected little-disturbed reference plots from the near surrounding in the same valley. The trend lines are based on local polynomial fitting are displayed for visualization purposes only.

Figure 18 shows that-the VIBI-Scores are initially very low (strong impact of soil disturbance by tillage), but increase during the duration of the recovery period. However, VIBI scores never reached those of the undisturbed reference (relatively little disturbed papyrus marsh in the areas surrounding the recovery experiment) during the 800-day observation period. Besides the relatively short experimental period, hydrological modifications that occurred in the Namulonge valley (Gabiri et al., 2018) may also have limited the recovery potential. Additionally, the papyrus marsh is mainly a reference for the riparian zone and to some extent to the mid-valley position, but it is probably unsuited for valley fringe position.

For the experiment conducted in Ifakara (see chapter 8.1), the insufficient number of data points prevented a similar visualization of the recovery dynamics, and instead the VIBI-Scores from four distinct sampling events are displayed in Table 20. Disturbances in this case comprised (in addition to the initial soil tillage) also natural disturbances by soil submergence and fires of natural origin that may have exacerbated the observed seasonal variations in plant growth. Consequently, the data should be taken with care, as they are not solely the result of an anthropogenic disturbance, as discussed in Behn et al. (2018).

Table 20: Application of the VIBI for Vegetation developed by Behn et al. (2018) (Chapter 5.2) on the vegetation development after disturbance at Ifakara study site.

Floodplain fringe				
Time after disturbance (days)	139	182	346	587
VIBI average	0.45	0.40	0.17	0.34
VIBI standard deviation	0.04	0.08	0.03	0.03
Middle position				
Time after disturbance (days)	144	187	346	587
VIBI average	0.40	0.43	0.09	0.43
VIBI standard deviation	0.03	0.03	0.03	0.07
Riparian zone				
Time after disturbance (days)	167	187	346	587
VIBI average	0.23	0.33	0.40	0.41
VIBI standard deviation	0.02	0.05	0.05	0.02

This is apparent in the zonation: in the late wet/ early dry season (first sampling in Table 20) scores are low in the riparian zone where the submerge had just ended. Towards the end of the dry season (third sampling) on the other hand, scores in the riparian zone are relatively high, whereas the seasonal drought affects the other positions. However, according to field observations, these natural disturbances seemed to have a much stronger impact on sites previously subjected to anthropogenic disturbance, whereas little-disturbed sites with tall stands of *Phragmites australis* in the riparian zone or deep-rooted grasses in the other zones were more resistant to seasonal variation of abiotic site conditions.

8.3 Plant associations according to in the recovery process after disturbance

In the Namulonge valley in Uganda, most plots were initially classified as *Cypero distantis-Cyperetum difformis*, an association dominated by annual Cyperaceae in the beginning of the succession process. With time, this association was gradually replaced by *Cypero denudati-Fuirenetum pubescentis* (valley fringe and mid-valley) or by *Melanthero scandentis-Leersietum hexandrae* (riparian zone) associations (Figure 19), both representing communities of later revovery stages that are dominated by herbaceous perennial plants. Some plot observations were not classified, as during the very early stages, shortly after disturbance, insufficient numbers of species occurred to match the classification criteria. In addition, for some observations in the center position no matching Cocktail definitions from Behn et al. (2022) were available, as their species composition was distinctly different from other plots and positions.

While during the early sampling stages all plots were classified as the same association of annual Cyperaceae, these differentiated into various other associations during later stages of recovery. Consequently, early stages are characterized by pioneer species, and appear to be less specific to microhabitat differences then later successional stages, when interspecific competition becomes more relevant. This differentiation of associations appears further to be affected by the distance to the stream, but also by small-scale variations in soil attributes (see chapter 7).

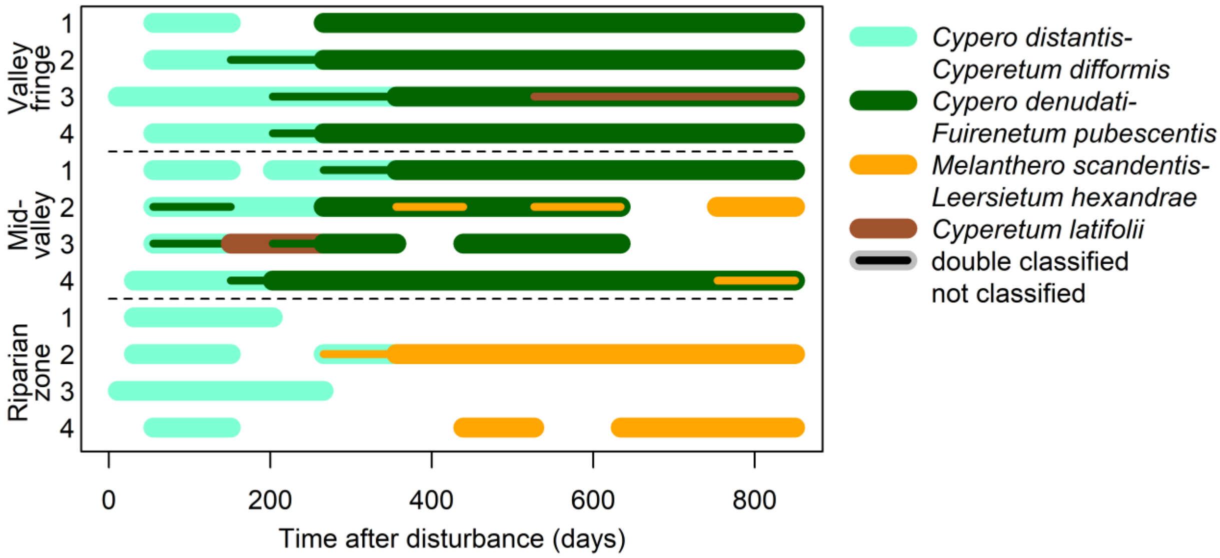

Figure 20: Vegetation associations (according to Behn et al., 2022) during recovery after disturbance in an inland Valley wetland in Namulonge, Uganda, observed over two years following an initial disturbance in September 2014.

While in the case of the floodplain, no comparable shift of associations could be observed, the differentiation between wetland positions was however stronger than in the inland valley wetland. The association in the fringe position was mainly *Pycreo macrostachyos-Ischaemetum rugosum*, in one plot this was double-classified with *Corchoro fascicularis–Panicetum hanningtonii.* Observations done in the dry season were rarely classified. In the middle position, all classified relevés were *Corchoro fascicularis–Panicetum hanningtonii.* Also, here, observations from dry season were often not classified. Vegetation in the riparian zone was variable and species poor, most plots were not classified. Only the third repetition was dominated by *Ipomoea aquatica* at all samplings and classified as *Grangeo maderaspatanae-Ipomoeetum aquaticae*.

8.4 Flora and vegetation at other study sites in East Africa

Beyond full vegetation relevés collected at Namulonge, Uganda, and Ifakara, Tanzania (chapter 6.2), plot observations containing only dominant plant species were available from the “Integrity”-field campaign. Due to time constraints, recordings of all vascular plant species were not possible in. Hence, data collected at these sites, as well as further plots from Kampala, Uganda, and the Kilombero valley, Tanzania, were only sampled in the “Integrity” activity, and could not be used for the vegetation classification presented in chapter 6.2. For differentiation, I will refer to the latter two sites in the following as “Kampala” and “Kilombero” as opposed to “Namulonge” and “Ifakara”. While these plot observations are incomplete in terms of the occurrence of vascular plant species, the available data still permit a descriptive comparison of the study sites regarding species occurrences and presumed vegetation units.

The Kilombero study site differed from the three other sites, with little overlap regarding species and vegetation units. Only *Phragmitetum mauritiani* was also encountered at the Kigali site, but communities dominated by *Phragmites australis*, are widespread across the globe (Sieben, 2019). Apart from that, only very common species such as *Bidens pilosa* and *Commelina benghalensis* are shared between Ifakara and the other study sites. The other three sites had more common species and vegetation units. The association of *Cypero papyri – Dryopteridetum gongylodes* was found beyond Namulonge at Kampala site, i.e., in the Ewaso Narok / Rumuruti study site in Kenya, and in the Nyabarongo floodplain belonging to the Kigali study site in Rwanda. It was the most common vegetation unit in the least disturbed and permanently flooded areas. At the Kigali site, *Cyclosorus interruptus* was less frequent and the relative abundance of *Cyperus papyrus* as well lower. Instead, *Persicaria setusola* was more abundant. *Cyperus latifolius*-dominated plots that were grouped with the *Cyperetum latifolii* were found in both Kigali and Rumuruti study sites. Kigali and Kampala showed many common species in croplands and fallows, including *Cyperus distans* or *Digitaria abyssinica*, but the available data do not suffice to support the occurrence of any of the associations described for the Namulonge in Kigali study sites.

Further potential vegetation units that were not described from Namulonge and Ifakara included the *Typha dominguensis*-dominated vegetation, found at Kigali and Kampala. *Cynodon dactylon*-dominated vegetation was found at all sites except Kilombero. In Kigali and Kampala, but not in Rumuruti, *Cynodon* was frequently encountered together with *Centella asiatica*. Additionally, while woody vegetation (shrubland, forest, Miombo woodland) occurred both at the wetland fringes and within the wetland of all study sites, these species were not considered in the present study that was restricted to herbaceous vegetation.

9 General discussion and conclusion

Agriculturally used wetland in Namulonge valley, Uganda (top left), African sacred ibis (*Threskiornis aethiopicus*) in Rwanda (top right), green gram (*Vigna radiata*) cultivation in Ewaso Narok, Kenya (bottom left), and Papyrus marsh with *Cyperus papyrus* and *Desmodium salicifolium* (bottom right) in Namulonge valley, Uganda.

The presented work deals with wetland vegetation in East Africa regarding aspects of "Integrity", "Diversity", and "Recovery dynamics". These topics were covered in the previous chapters with specific research questions, results, and discussions. This chapter addresses the overarching research questions of the thesis, including limitations and research recommendations. This is followed by a broader contextualization and policy perspectives.

9.1 Research questions and objectives

9.1.1 Integrity: What is the current ecological state of representative East African wetlands and how can it be assessed?

East African wetlands face threats of degradation. However, due to their vast area extent and diverse country-specific protection policies, there are still large areas of wetlands in good state (Beuel et al., 2016). A wetland´s ecological state can be assessed at different scales and with various methods. Large-scale assessments have been conducted at regional or national scale via remote sensing. Respective studies used indicators such as land cover changes and soil moisture (e.g., Munishi & Jewitt, 2019; Steinbach et al., 2023). In contrast to such remote-sensed attributes, field assessments require more effort, are often highly site- or location-specific, but can provide data at a much finer scale. There is a need for standardized and cost-effective approaches to ensure objectivity and comparability between assessments done by different experts. In chapter 4 of this thesis, the WET-Health approach (Kotze et al., 2012) and "Indices of Biotic Integrity" were presented. Beuel et al. (2016) modified the WET-Health approach and applied it in East Africa. On this basis, Behn et al. (2018) developed a "Vegetation-based index of Biotic Integrity" to predict WET-Health scores. While this approach worked well for the actual vegetation module of WET-Health, the results were not satisfactory for other modules "Geomorphology", "Hydrology" and "Water Quality". These two works result in chapter 5 of this thesis.

In all four study regions with five different wetlands (table 5 in chapter 3) we were able to identify areas of both high disturbance and areas being in relatively good ecological state. While completely degraded wetlands that neither fulfilled ecological functions nor provided food (e.g., wetlands used as dumping sites or being destroyed by mining activity) did occur, these constituted only a very small share of the observation sites and were thus excluded from the analysis. Across wetlands, the vegetation module of the WET-Health approach showed the largest impact, which is in line with studies at other sites (Kotze & Wood, 2021). Key determining factors comprised both present and recent agricultural land uses. However, even in the unused "natural vegetation" class, scores for vegetation estimates tended to be higher than those in other WET-Health modules. This was likely caused by off-site effects and by previous disturbances, leading to an increased occurrence of ruderal and/or invasive plant species. Particularly for the hydrology module, we identified large differences between study sites. Thus, the wetlands in Kampala and Kigali had moderate to high impact scores, while the wetlands in Rumuruti and Ifakara had low to very low impact scores (Beuel et al., 2016). In summary, we identified (parts of) wetlands in both good and poor ecological states, with the latter constituting mainly sites of intensive agricultural production, predominantly rice and vegetables.

However, the studies had limitations. The large extent of the wetlands and access restrictions reduced the number of samples. While we were able to collect information from representative wetlands in four countries, the data collection was restricted to one rapid assessment campaign. Thus, each study site was sampled in less than two weeks and the finding present only a snapshot. A strong seasonality limited the application of the methods and restricted the results, particularly for the vegetation module in the Kilombero floodplain in Tanzania. There, large areas were submerged towards the end of the rainy season, but sampling took place only the dry season. This effect of seasonality was less pronounced at the other study sites. Additionally, the number of variables that could be recorded during the multidisciplinary rapid assessment campaign were also limited. Collecting more vegetation attributes might have further improved the results. Lastly, the ecological state of the wetlands was determined only in 2013. As drivers for wetland degradation continued to evolve, a further deterioration of the state of the study wetlands was expected to occur, although this may not be the case for all sampling plots.

Regarding statistical analyses, the response variable (WET-Health scores) for developing the “Vegetation-based Index of Biotic Integrity” (VIBI), were not completely independent of the selected predictor variables. This is a general difficulty in the development of IBIs, as the ecological integrity is an abstract concept. Similarly, the metrics were not strictly independent from each other, resulting in some statistical redundancies, which was tolerated following Miller et al. (2006).

Future research should improve the VIBI by testing more predictor variables, such as invasive species and functional groups. The assessment would also be strengthened by including aspects of seasonality, either by using data from different seasons, by including a season-based correction coefficient, or by a season-specific choice and weighing of metrics. Finally, the calibration of the Integrity Index in other wetlands could further strengthen VIBI. Thus, repeating several assessment campaigns in the same wetlands, based on either the WET-Health approach or the derived VIBI, would provide valuable additional information regarding ongoing or progressing degradation of wetlands in East Africa.

9.1.2 Diversity: How diverse is East African wetland vegetation?

This work used the Cocktail method to classify vegetation based on plant species composition and abundances at the wetland sites in Namulonge, Uganda, and Ifakara, Tanzania. Thirteen different vegetation units were identified along gradients of land use and successional stages after disturbance events, and regarding their position along the spatial gradient from the central stream/river to the wetland fringe. For each unit, Cocktail definitions were created. If possible, vegetation units were matched with existing phytosociological associations from the literature. Remaining units were newly described. Particularly at the Namulonge site, different units could be identified at very small spatial and temporal scales. While the two sites had no common units, and only few common species, most of the units were confirmed by the literature, proving their existence beyond the study sites. However, the study centered on vegetation units at the two sites can therefore only represent a snapshot of the actual diversity in East African wetlands. The findings from wetlands that were researched in the first part of this thesis ("Integrity") highlighted the presence of many more possible vegetation units, even though data from the integrity activity could not be used for the classification, as full vegetation relevés were not conducted as part of the rapid assessment scheme. Some units could however be clearly identified, such as the Papyrus march (*Cypero papyri-Dryopteridetum gongylodes)* that was also found in the highland floodplains of Ewaso Narok in Kenya and the Akagera floodplain in Rwanda. The same is true for the *Cyperetum latifolii*. However, intensive cattle grazing in the Ewaso Narok swamp and at the two study sites in Rwanda entailed specific combinations of weed species and communities that were dominated by *Cynodon dactylon*. The associations found in the floodplain wetland in Ifakara were not found in any of the other wetlands investigated in this work. Potential units of herbaceous vegetation were excluded for having insufficient numbers of relevés. Woody wetland vegetation was present at all study sites but not considered in this work. The inclusion of data from the SWEAdataveg vegetation database (Alvarez et al., 2021) partially compensated this limitation. The works by Schmitz (1988), Alvarez (2017), and Behn et al. (2022) comprise important steps towards depicting the prevailing diversity of East African wetland vegetation. However, the use of different methods of vegetation classification and the non-transferable site-specific classifications used in the past constitute a continuing challenge. Nevertheless, the Braun-Blanquet system in combination with the Cocktail Classification are useful pillars towards improving our understanding of wetland vegetation. Particularly, the Cocktail algorithms developed by Alvarez (2017) and Behn et al. (2022) and the two-stop approach presented by Behn et al. (2022) appear highly suitable to reaching the goal of developing a more comprehensive classification of the diversity of East African wetlands. However, this classification must be extended to more study sites in the region to improve the quality of the results and to more accurately capture the prevailing diversity. Additional land use types may include intensively grazed wetlands in highland floodplains and other wetland types (beyond inland valley swamps and floodplains) that were not addressed within the GlobE-project such as peat bogs, coastal wetlands, and gallery forests. Future research should further create a better linkage of vegetation units with biophysical site conditions to promote the use of vegetation units as bio-indicators. In addition, more detailed studies on the role of different vegetation units for ecosystem functions and services provision would be of great value; including the actual contribution to the livelihoods of the local populations living around the wetlands.

9.1.3 Recovery Dynamics: How does East African wetland vegetation recover after disturbance?

Wetlands in East Africa, apart from effectively protected areas, are subject to regular disturbances, including agricultural use, biomass harvesting, grazing, mining, and fire. In addition, submergence can be considered a disturbance, particularly in the seasonally flooded central areas of floodplain wetlands. Depending on the cause of disturbance, the recovery processes after the event are different. In the present work, we studied succession in an experimental set-up in the Namulonge inland valley wetland in Uganda. The succession process was regularly monitored after initial soil tillage. In a second experiment in the Kilombero floodplain near Ifakara in Tanzania, soil submergence constituted an additional and interacting disturbance factor.

The vegetation recovered rapidly in the inland valley wetland after tillage, following three roughly distinguishable stages within two years: (1) annuals, followed by (2) herbaceous perennials with reptant or tussock-like growth forms, (3) emerge of reed and woody plants. These stages evolved gradually without interruption, due to permanently favorable (wet) conditions for vegetation growth and the pattern was similar across wetland positions. Species composition was similar during the initial successional stage, but differentiated during later stages. Despite a fast and almost uninterrupted growth, the reference state of (undisturbed) vegetation was not reached within the two-year observation period. However, the succession process highlights that occasional disturbances can create a mosaic of microhabitats that are beneficial for increasing biodiversity and stimulating occurrence of useful plants. On the other hand, disturbances may also stimulate invasive plant species, such as *Mimosa pigra*.

In the Kilombero floodplain in Ifakara, the process of species succession is very different from the vegetation dynamics in the inland valley of Namulonge. The strongly seasonal savanna climate and the associated seasonally variable flooding regimes hampered plant growth. Both extended dry periods in the fringe position during the dry season and severe submergence in the center position during the wet season interrupted the recovery process. On the other hand, in the moderately wet and dry middle section of the floodplain, vegetation was dominated by tall grasses, and recovery was possible and occurred relatively rapidly. In the fringe section, comprising the transitional zone between wet grasslands and Miombo woodlands, signs of a development towards natural Miombo woodlands could not be observed in the monitored period. In the severely submerged central parts of the floodplain, a recovery of the natural vegetation of tall, flood-tolerant grasses (*Phragmites australis* and *Panicum fluviicola*) is possible, if the rhizomes of these plants survive the disturbance. Otherwise, seasonal pioneer vegetation emerges after the submergence period, replacing the grassland.

The main limitation for these succession studies was the short available time. The work presents a short-term monitoring, while recovery processes may take many years. The second limitation were the irregular sampling intervals and lower sample numbers in the Kilombero floodplain near Ifakara.

Further studies of vegetation development would profit from longer observation periods, while maintaining short intervals of sampling, specifically during the early phases of recovery or vegetation succession. Future research should include studies on ecosystem functions and the provision of ecosystem services in relation to successional stages. The inclusion of local stakeholders and local knowledge is recommended.

9.2 Relevance and recommendations

9.2.1 Relevance for biodiversity conservation

This work contributes to biodiversity conservation through the collection and provision of baseline data and through methodological development, which were made available in international publications and presentations at scientific conferences (Table 4, Chapter 2).

A good basis of reliable data is crucial for science-based conservation. While numerous scientists have studied vegetation in East Africa for a long time, data on vegetation integrity, diversity and dynamics is often difficult to access, outdated, and patchy. Available data focus either on protected areas or on weeds in cultivated fields. Few studies consider different successional stages or patches of natural vegetation within an agricultural landscape, which was the focus of the present work. Hence, the data presented here contribute to filling data gaps and provides records regarding a status quo at the time of the fieldwork that may no longer exist at some of the sites.

In addition, tool and methods to assess ecological conditions were adapted and applied in East Africa. These are the collaborative WET-Health assessment that has been applied only in Southern Africa, and the IBI-approach for which only few similar studies in East Africa exist. The application of the Cocktail Classification with an adaptation for data-scarce regions (Behn et al., 2022) is unprecedented in East Africa. Their publication in international journals may have contributed to a broader awareness of these methods in East Africa and they have a potential to support conservation efforts in the region. Lastly, the results from the three main topics of this thesis can be used in conservation, land use management, and to promote further research. In the nexus of agriculture and biodiversity, I recommend more studies of biodiversity responses to different intensification strategies and pathways of wetland systems changes.

9.2.2 Relevance for agriculture and land use management

As stated in chapter 1, several political, socioeconomic, and biophysical factors drive the agricultural use of wetlands, which offers the potential to increase domestic food production. As these drivers continue to exert pressure on wetland resources, agricultural expansion and land use intensification in wetlands are foreseen to continue and to even increase in East Africa. Such system shifts will cause trade-offs with biodiversity and various other ecosystem functions and services provided by wetlands. To optimize resource allocation and to minimize these trade-offs, stakeholders and decision makers require data for taking informed decisions about which wetlands can be used and to what extent, and which wetlands need to be protected. Decision support tools guiding the process of land conversion and aiming at a wise use of wetlands have been developed recently (e.g., Langensiepen et al., 2023). Findings from the present work can be used to further improve these tools by adding information on diversity and dynamics of wetland vegetation. The informative value of species and vegetation units may thus improve the estimation of potentials and risks associated with agricultural production and to delineate areas of value for conservation and with high production risks such as the central parts of floodplain wetlands (Kwesiga, 2021).

There is an ongoing debate on how to allocate land for conservation and agricultural use, and how to reconcile the need for increased food production with concerns for protection, which has led to the introduction of the “land sparing – land sharing” framework (Green et al., 2005). This concept refers to the dichotomy between intensification and protection on the one side (“land sparing”) and wildlife- or conservation-friendly farming (“land sharing”) on the other side. This model and the related strategies g have been intensively discussed, criticized, and often misunderstood (Phalan, 2018). Conservationists often favor the land sparing approach. They note that - based on empirical evidence - producing food on as little area as possible while setting aside the remaining area for protection purposes may be preferable, particularly for species with small ranges (e.g., Phalan et al., 2011). In response to criticism, Phalan (2018) agreed that the “land sparing - land sharing” model results need to be interpreted the social, political, and economic context of the concerned region. Baudron et al. (2021) stressed the need for agronomic perspectives in the debate. They argue that “production landscapes” play a significant role as habitats for most species, and that synergies between agriculture and biodiversity are often overlooked. Lele et al. (2010) rejected conservation by exclusion as “unfair and undemocratic” towards local people despite occasional provision of biodiversity gains. Thus, a case study in the wetlands around Nyabarongo River in Rwanda evidenced financial losses for local people associated with restricting wetland uses for subsistence purposes, and a lack of understanding among local people if at the same time large-scale commercial farming was permitted (Nsengimana et al., 2017).

It is apparent that both conservation and intensification strategies are required, but that their apparently contradictory aims need to be reconciled. Thus, wetlands need to be used for intensive agriculture to produce the food and other goods needed to meet the needs of the rapidly growing urban centers. On the other hand, large land areas, including wetlands, must be protected for conserving wildlife, to ensure vital ecosystem functions, including carbon storage and water regulation, and to offer opportunities for economic gains from domestic and international tourism. Between these extremes of competing land use strategies, there are millions of small-scale farmers using wetlands in less intensive ways and balance often contradictory needs in a highly diverse household portfolio.

9.2.3 Policy considerations for reconciling food production with environmental protection

We need to acknowledge that each wetland has its specific biophysical conditions, socio-economic and social-cultural attributes, and diverse policy settings. Policy needs to balance conflicting interests of various stakeholders as well as including them in decision-making processes. Consequently, it appears impossible to formulate specific but generalizable policy recommendations based on this work. Nevertheless, the following aspects need attention when formulating wetland policies regarding land use and resource management:

(1) Integrative and segregating approaches for conservation and agricultural use should not be considered as competing, but rather as two endpoints of a range of possibilities or land use options that are context-specific. Thus, extensive and seasonal cultivation with spatial and temporal restrictions may be an option for small wetlands or edge areas of protected large wetlands. Intensive production may be suitable for segments of larger wetlands. with specific spatial restrictions exclusion of buffer zones that prevent or regulate fluxes of material (e.g., agrochemicals) between the land system components. Other wetlands with high importance for rare species need to be protected completely.

(2) In the submergence prone central positions of floodplain wetlands and the drought-prone fringe areas of inland valley wetlands, crop production can be risky, and such sites may be preferentially earmarked for conservation (Kwesiga, 2021). On the other hand, a comprehensive biodiversity conservation requires protected sites all along the hydrological gradient, as each set of site conditions supports different species. In any event, protection must include local people to ensure its acceptance and success.

(3) Besides annual crops such as rice and vegetables, agricultural policy should further promote a sustainable use of wild perennial plants such as *Cyperus papyrus, Cyperus latifolius,* and *Phragmites australis* for biomass, biofuel (Jones et al., 2018) as animal feed or for construction purposes. In addition, several wild wetland plants play important roles as medicinal plants. Biodiversity needs versatile landscapes and gradients of disturbance, and therefore, biodiversity and agricultural production can benefit each other. The diversity and the social and economic benefits of such provisioning ecosystem services requires more research.

9.3 Conclusion

Wetlands in East Africa are undergoing dramatic changes, as they are used increasingly for agricultural production. Such wetland uses alter their functioning and may reduce the provision of ecosystem services. At the same time, protection and sustainable use of wetlands are gaining importance. Scientifically backed, informed decision-making on use or protection of specific wetlands or of segments within those requires data and indices about the wetland status and the provision of assessment tools. This work provides such information. This comprises an index for wetlands' integrity based on easily assessable vegetation attributes, a classification of wetland plant communities in contrasting wetland types, a modified Cocktail Classification method to classify vegetation suitable for data scarce regions, and vegetation succession studies after disturbance events is unpreceded for tropical wetlands. The presented findings and proposed methods may stimulate future research and can guide wetland users, land managers and policy makers in East Africa and beyond.

10 References

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11 Appendix

A1 – Photographs of plant associations described in Chapter 6.2

A2 – Photographs of common wetland plant species ordered by plant associations

A3 –List of all vascular plant species recorded in the studied wetlands

A4 – Photographs of different recovery stages in Namulonge inland valley, Uganda

A5 – Photographs of different recovery stages in Kilombero floodplain, Tanzania

A6 – List of published articles in international journals and books

A7 – List of conference presentations

A1 – Photographs of plant associations described in Chapter 6.2

	Plate 1: *Pycreo macrostachyos-Ischaemetum rugosum* established in a fallow land after rice cultivation, Ifakara, Tanzania. 26.05.2015
	Plate 2: Stand of the *Fuireno ciliari-Ammannietum senegalensis* at the edge of a rice field during the rainy season, Ifakara, Tanzania. 19.05.2015
	Plate 3: Stand of the *Corchoro fascicularis-Panicetum hanningtonii* surrounded by rice fields during the early dry season, Ifakara, Tanzania. 14.06.2015
	Plate 4: *Grangeo madaraspatanae-Ipomoetum aquaticae* established on fallow land. Soil is just drying after seasonal floods, Ifakara, Tanzania. 02.08.2016

https://doi.org/10.5281/zenodo.5111455

A1 – Photographs of plant associations described in Chapter 6.2

Plate 5:

Early terrestrial ecophase at a stand of *Centostachyo aquaticae-Persiarietum senegalensis* in Kwasunga, Tanzania. The place has been used for fishing during the floods.

17.10.2012

Plate 6:

Weed vegetation of the *Cypero distantis-Cyperetum difformis* growing in a vegetables crop field, Namulonge, Uganda.

03.12.2014

Plate 7:

Cypero denudati-Fuirenetum pubescentis established in a fallow land without any cultivation in the last two years, Namulonge, Uganda.

06.08.2016

Plate 8:

Stand of the *Melanthero scandentis-Leersietum hexandrae* in a two years old fallow land, Namulonge, Uganda.

08.08.2016

A1 – Photographs of plant associations described in Chapter 6.2

Plate 9:

Less disturbed patch in a cultivated wetland colonized by *Cyperetum latifolii* close to Gayaza, Uganda.

04.11.2014

Plate 10:

Cypero papyri-Dryopteridetum gongylodes on a permanently submerged soil without major disturbances in Namulonge, Uganda.

22.10.2015

Plate 11:

Riverine stand of *Phragmitetum mauritiani* along the Kilombero River, Tanzania. Deep floods occur here once a year.

26.06.2015

Plate 12:

Stand of the *Vigno vexillatae-Panicetum fluviicolae* in an undistrubed area within the Kilombero floodplain, Tanzania. Shallow floods occur once a year.

05.11.2013

A2 – Photographs of common wetland plant species ordered by plant associations

Pycreo macrostachyos-Ischaemetum rugosum
Temporary pioneer community of recently disturbed sites and rice field
Recorded in Ifakara, Tanzania

Courtoisina cyperoides (Cyperaceae)
LF: obligate annual
SSA: native

Ischaemum rugosum (Poaceae)
LF: obligate annual
SSA: native

Pycreus macrostachyos (Cyperaceae)
LF: obligate annual
SSA: native

Fuireno ciliari-Ammannietum senegalensis
Rice fields and recently disturbed wetland sites
Recorded in Ifakara, Tanzania

Fuirena ciliaris (Cyperaceae)
LF: obligate annual
SSA: native

Ammannia senegalensis (Lythraceae)
LF: obligate annual
SSA: native

Fimbristylis quinquangularis (Cyperaceae)
LF: obligate annual
SSA: native

 LF (Life form) and SSA (Status in Sub-Saharan Africa), taxonomy, and syntaxonomy according to Behn et al., 2022)

A2 – Photographs of common wetland plant species ordered by plant associations

Corchoro fascicularis–Panicetum hanningtonii
Post-cultivation fallow,
Recorded in Ifakara, Tanzania

Panicum hanningtonii (Poaceae)
LF: obligate annual
SSA: native

Corchorus fascicularis (Malvaceae)
LF: obligate annual
SSA: native

Melochia chorchorifolia (Malvaceae)
LF: obligate annual
SSA: native

Grangeo maderaspatanae-Ipomoeetum aquaticae
On fallow or recently disturbed land after seasonal submerge; Recorded in Ifakara, Tanzania

Grangea maderaspatana (Asteraceae)
LF: obligate annual
SSA: native

Ipomoea aquatica (Convolvulaceae)
LF: obligate annual
SSA: native

Paspalum scrobiculatum (Poaceae)
LF: facultative annual
SSA: native

All pictures © Kai Behn; LF (Life form) and SSA (Status in Sub-Saharan Africa), taxonomy, and syntaxonomy according to Behn et al., 2022)

A2 – Photographs of common wetland plant species ordered by plant associations

Centrostachyo aquaticae-Persicarietum senegalensis
Plant community on disturbed grounds at the edge of the river, recorded in Ifakara, Tanzania

Persicaria senegalensis (Polygonaceae)
LF: tussock plant
SSA: native

Neptunia oleracea (Fabaceae)
LF: reptant plant
SSA: native

Glinus oppositifolius (left) *and G. lotoides* (right) with potential hybride (middle) (Molluginaceae)
LF: obligate annual; SSA: native

Cypero distantis-Cyperetum difformis
Temporal community on wet soils after disturbance
Recorded in Namulonge, Uganda

Cyperus distans (Cyperaceae)
LF: facultative annual
SSA: native

Cyperus difformis (Cyperaceae)
LF: obligate annual
SSA: native

Kyllinga odorata (Cyperaceae)
LF: tussock plant
SSA: native

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A2 – Photographs of common wetland plant species ordered by plant associations

Cypero denudati-Fuirenetum pubescentis

Second year fallow community in wetland fringe,
Recorded in Namulonge, Uganda

Cyperus denudatus (Cyperaceae)
LF: tussock plant
SSA: native

Fuirena pubescens (Cyperaceae)
LF: reptant plant
SSA: native

Torrenia thouarsii (Linderniaceae)
LF: tussock plant
SA: native

Melanthero scandentis-Leersietum hexandrae

Second-year fallow community in wetlands,
Recorded in Namulonge, Uganda

Melanthera scandens (Asteraceae)
LF: climbing plant
SSA: native

Triumfetta brachyceras (Malvaceae)
LF: phanerophyte
SSA: native

Ipomoea cairica (Convolvulaceae)
LF: climbing plant
SSA: native

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A2 – Photographs of common wetland plant species ordered by plant associations

Cyperetum latifolii

Long-term fallows and lesser disturbed wetland vegetation; Widespread in Africa

Cyperus latifolius (Cyperaceae)
LF: reed plant
SSA: native

*Leersia hexandra (*Poaceae*)*
LF: reptant plant
SSA: native

Ludwigia abyssinica (Onagraceae)
LF: facultative annual
SSA: native

Cypero papyri-Dryopteridetum gongylodes

Common pristine and recovered stage of wetland vegetation under permanently flooded conditions Widespread in Africa

Cyperus papyrus (Cyperaceae)
LF: reed plant
SSA: native

Cyclosorus interruptus (Thelypteridaceae)
LF: reptant plant
SSA: native

Pilogyne minutiflora (Cucurbitaceae)
LF: climbing plant
SSA: native

All pictures © Kai Behn; LF (Life form) and SSA (Status in Sub-Saharan Africa), taxonomy, and syntaxonomy according to Behn et al., 2022)

A2 – Photographs of common wetland plant species ordered by plant associations

Phragmitetum mauritiani

Tall reed community bordering rivers and lakes, Widespread in Africa

Phragmites australis (Poaceae)
LF: reed plant
SSA: native

Ludwigia adcendens var. *diffusa* (Onagraceae)
LF: reptant plant
SSA: native

Pistia stratiotes (Araceae)
LF: acropleustophyte
SSA: native

Vigno vexillatae-Panicetum fluviicolae

Tall grass community in under seasonally flooded soils; Recorded in Ifakara, Tanzania

Panicum fluviicola (Poaceae)
LF: reed plant
SSA: native

Chrysopogon nigritanus (Poaceae)
LF: reed plant
SSA: native

Vigna vexillata (Fabaceae)
LF: climbing plant
SSA: native

All pictures © Kai Behn; LF (Life form) and SSA (Status in Sub-Saharan Africa), taxonomy, and syntaxonomy according to Behn et al., 2022)

A2 – Photographs of common wetland plant species ordered by plant associations

Major invasive alien plant species recorded in the study area in Kenya, Rwanda, Tanzania, and Uganda.

Ageratum conyzoides (Asteraceae)
LF: obligate annual
Origin: Mexico

Eichhornia crassipes (Pontederiaceae)
LF: acropleustophyte
Origin: Tropical and Subtropical America

Lantana camara (Verbenaceae)
LF: phanerophyte
Origin: Mexico and Tropical America

Mimosa pigra (Fabaceae)
LF: phanerophyte
Origin: South America

Mimosa pudica (Fabaceae)
LF: tussock plant
Origin: South America

Psidium guajava (Myrtaceae)
LF: phanerophyte
Origin: South America

All pictures © Kai Behn; LF (Life form) and SSA (Status in Sub-Saharan Africa), taxonomy, and syntaxonomy according to Behn et al., 2022)

A3 –List of all vascular plant species recorded in the studied wetlands

ACANTHACEAE	*Acanthus polystachyus* Delile
	Asystasia gangetica (L.) T. Anderson
	Asystasia mysorensis (Roth) T.Anderson
	Dyschoriste nagchana (Nees) Bennet
	Hygrophila auriculata (Schumach.) Heine
	Hygrophila uliginosa S.Moore
	Thunbergia alata Bojer ex Sims
AMARANTHACEAE	*Alternanthera sessilis* (L.) R. Br. ex DC.
	Amaranthus hybridus L.
	Chenopodium carinatum R.Br.
	Gomphrena celosioides Mart.
	Justicia anselliana (Nees) T.Anderson
	Justicia exigua S.Moore
	Nelsonia canescens (Lam.) Spreng.
ANACARDIACEAE	*Mangifera indica* L.
	Searsia natalensis (Bernh. ex C.Krauss) F.A.Barkley
	Spondias mombin L.
APIACEAE	*Centella asiatica* (L.) Urb.
	Oenanthe palustris (Chiov.) C. Norman
APOCYNACEAE	*Carissa spinarum* L.
	Pentarrhinum insipidum E. Mey.
ARACEAE	*Colocasia esculenta* (L.) Schott
	Pistia stratiotes L.
ARALIACEAE	*Hydrocotyle mannii* Hook. f.
	Hydrocotyle ranunculoides L. f.
	Hydrocotyle sibthorpioides Lam.
ARECACEAE	*Hyphaene compressa* H.Wendl.
	Phoenix reclinata Jacq.
ASTERACEAE	*Acmella caulirhiza* Delile
	Acmella uliginosa (Sw.) Cass.
	Adenostemma caffrum DC.
	Adenostemma viscosum J.R. Forst. & G. Forst.
	Ageratum conyzoides L.
	Aspilia africana (Pers.) C. D. Adams
	Bidens pilosa L.
	Blumea axillaris (Lam.) DC.
	Conyza bonariensis (L.) Cronquist
	Crassocephalum crepidioides (Benth.) S. Moore
	Crassocephalum vitellinum (Benth.) S. Moore
	Eclipta prostrata (L.) L.
	Emilia discifolia (Oliv.) C.Jeffrey
	Ethulia conyzoides L. f.
	Ethulia paucifructa M. G. Gilbert
	Galinsoga parviflora Cav.
	Galinsoga quadriradiata Ruiz & Pav.

	Grangea maderaspatana (L.) Desf.
	Launaea cornuta (Hochst. ex Oliv. & Hiern) C.Jeffrey
	Melanthera scandens (Schumach. & Thonn.) Roberty
	Mikania sagittifera B. L. Rob.
	Pseudognaphalium luteoalbum (L.) Hilliard & B.L. Burtt
	Schkuhria pinnata (Lam.) Thell.
	Senecio picridifolius DC.
	Sphaeranthus africanus L.
	Sphaeranthus suaveolens (Forssk.) DC.
	Sonchus oleraceus L.
	Synedrella nodiflora Gaertn.
	Tagetes minuta L.
	Tridax procumbens L.
	Vernonia amygdalina Delile
	Vernonia cinerea (L.) Less.
	Xanthium strumarium L.
BIGNONIACEAE	*Kigelia africana* (Lam.) Benth.
	Spathodea campanulata P.Beauv.
BORAGINACEAE	*Coldenia procumbens* L.
	Euploca baclei (DC.) Diane & Hilger
	Euploca ovalifolia (Forssk.) Diane & Hilger
	Heliotropium indicum L.
	Heliotropium steudneri Vatke
	Trichodesma zeylanicum (Burm.f.) R.Br.
BRASSICACEAE	*Cardamine hirsuta* L.
CAMPANULACEAE	*Gunillaea emirnensis* (A. DC.) Thulin
CARYOPHYLLACEAE	*Ceratophyllum demersum* L.
	Pollichia campestris Aiton
CLEOMACEAE	*Cleome schimperi* Pax
COMMELINACEAE	*Aneilema spekei* C.B.Clarke
	Commelina africana L.
	Commelina benghalensis L.
	Commelina diffusa Burm. f.
	Floscopa confusa Brenan
COMBRETACEAE	*Terminalia superba* Engl. & Diels
CONVOLVULACEAE	*Hewittia malabarica* (L.) Suresh
	Ipomoea aquatica Forssk.
	Ipomoea batatas (L.) Lam.
	Ipomoea cairica (L.) Sweet
	Ipomoea eriocarpa R.Br.
	Ipomoea sinensis (Desr.) Choisy
	Ipomoea wightii (Wall.) Choisy
	Lepistemon owariense (P.Beauv.) Hallier f.
	Merremia hederacea (Burm. f.) Hallier f.
	Merremia pterygocaulos (Choisy) Hallier f.
CUCURBITACEAE	*Cucumis maderaspatanus* L.

	Momordica foetida Schumach.
	Pilogyne minutiflora (Cogn.) W.J.de Wilde & Duyfjes
	Zehneria capillacea (Schumach.) C.Jeffrey
CYPERACEAE	*Abildgaardia ovata* (Burm.f.) Kral
	Bulbostylis hispidula (Vahl) R.W. Haines
	Bulbostylis striatella C.B.Clarke
	Cladium jamaicense Crantz
	Courtoisina assimilis (Steud.) Maquet
	Courtoisina cyperoides (Roxb.) Soják
	Cyperus denudatus L. f.
	Cyperus dichrostachyus Hochst. ex A.Rich.
	Cyperus difformis L.
	Cyperus distans L. f.
	Cyperus dives Delile
	Cyperus foliaceus C.B. Clarke
	Cyperus imbricatus Retz.
	Cyperus latifolius Poir.
	Cyperus papyrus L.
	Cyperus rigidifolius Steud.
	Cyperus rotundus L.
	Fimbristylis bisumbellata (Forssk.) Bubani
	Fimbristylis dichotoma (L.) Vahl
	Fimbristylis quinquangularis (Vahl) Kunth
	Fuirena ciliaris (L.) Roxb.
	Fuirena pubescens (Poir.) Kunth
	Fuirena umbellata Rottb.
	Kyllinga bulbosa P. Beauv.
	Kyllinga brevifolia Rottb.
	Kyllinga crassipes Boeckeler
	Kyllinga polyphylla (Kunth) Kük.
	Kyllinga odorata Vahl
	Kyllinga pumila Michx.
	Mariscus sumatrensis (Retz.) J.Raynal
	Pycreus flavescens (L.) P. Beauv. ex Rchb.
	Pycreus macrostachyos (Lam.) J. Raynal
	Pycreus pumilus (L.) Nees
	Schoenoplectiella articulata (L.) Lye
	Schoenoplectiella juncea (Willd.) Lye
	Scleria melanomphala Kunth
	Scleria nyasensis C.B. Clarke
EUPHORBIACEAE	*Alchornea cordifolia* (Schumach. & Thonn.) Müll. Arg.
	Croton dichogamus Pax
	Euphorbia heterophylla L.
	Euphorbia hirta L.
	Manihot esculenta Crantz
	Ricinus communis L.

FABACEAE	*Abrus canescens* W
	Acacia nilotica (L.) Willd. ex Delile
	Acacia polyacantha Willd.
	Acacia seyal Delile
	Acacia xanthophloea Benth.
	Aeschynomene afraspera J. Léonard
	Aeschynomene cristata Vatke
	Aeschynomene indica L.
	Aeschynomene schimperi Hochst. ex A.Rich.
	Aeschynomene sensitiva Sw.
	Aeschynomene uniflora E.Mey.
	Cassia kirkii Oliv.
	Centrosema pubescens Benth.
	Chamaecrista mimosoides (L.) Greene
	Crotalaria bernieri Baill.
	Crotalaria incana L.
	Crotalaria lanceolata E.Mey.
	Crotalaria ochroleuca G.Don
	Desmodium adscendens (Sw.) DC.
	Desmodium incanum (Sw.) DC.
	Desmodium salicifolium (Poir.) DC.
	Desmodium setigerum (E. Mey.) Benth. ex Harv.
	Desmodium tortuosum (Sw.) DC.
	Desmodium triflorum (L.) DC.
	Desmodium uncinatum (Jacq.) DC.
	Eriosema montanum Baker f.
	Indigofera arrecta Hochst. ex A.Rich.
	Indigofera hirsuta L.
	Indigofera schimperi Jaub. & Spach
	Indigofera secundiflora Poir.
	Indigofera spicata Forssk.
	Mimosa pigra L.
	Mimosa pudica L.
	Neptunia oleracea Lour.
	Pseudarthria hookeri Wight & Arn.
	Rhynchosia minima (L.) DC.
	Sesbania hirtistyla J. B. Gillett
	Sesbania sesban (L.) Merr.
	Stylosanthes guianensis (Aubl.) Sw.
	Tephrosia linearis (Willd.) Pers.
	Tephrosia nana Kotschy ex Schweinf.
	Teramnus labialis (L.f.) Spreng.
	Teramnus uncinatus (L.) Sw.
	Vigna heterophylla A.Rich.
	Vigna kirkii (Baker) J. B. Gillett
	Vigna luteola (Jacq.) Benth.

	Vigna parkeri Baker
	Vigna reticulata Hook. f.
	Vigna unguiculata (L.) Walp.
	Vigna vexillata (L.) A. Rich.
GENTIANACEAE	*Anthocleista grandiflora* Gilg
LAMIACEAE	*Basilicum polystachyon* (L.) Moench
	Hyptis lanceolata Poir.
	Hyptis spicigera Lam.
	Leonotis martinicensis (Jacq.) J. C. Manning & Goldblatt
	Leonotis nepetifolia (L.) R.Br.
LEMNACEAE	*Lemna aequinoctialis* Welw.
LENTIBULARIACEAE	*Utricularia stellaris* L.f.
LINDERNIACEAE	*Lindernia parviflora* (Roxb.) Haines
	Torenia thouarsii (Cham. & Schltdl.) Kuntze
LYTHRACEAE	*Ammannia auriculata* Willd.
	Ammannia baccifera L.
	Ammannia senegalensis Lam.
MALVACEAE	*Corchorus fascicularis* Lam.
	Corchorus olitorius L.
	Hibiscus cannabinus L.
	Hibiscus diversifolius Jacq.
	Hibiscus flavifolius Ulbr.
	Hibiscus surattensis L.
	Malvastrum coromandelianum (L.) Garcke
	Melochia corchorifolia L.
	Melochia melissifolia Benth.
	Sida ovata Forssk.
	Sida rhombifolia L.
	Sida schimperiana Hochst. ex A.Rich.
	Triumfetta annua L.
	Triumfetta brachyceras K. Schum.
	Triumfetta pentandra A.Rich.
	Triumfetta rhomboidea Jacq.
	Urena lobata L.
MARSILEACEAE	*Marsilea minuta* L.
MELASTOMATACEAE	*Antherotoma debilis* (Sond.) Jacq.-Fél.
	Tristemma mauritianum J.F.Gmel.
MENISPERMACEAE	*Cissampelos mucronata* A. Rich.
	Stephania abyssinica (Quart. -Dill. & A. Rich.) Walp.
MOLLUGINACEAE	*Glinus lotoides* L.
	Glinus oppositifolius (L.) Aug.DC.
	Paramollugo nudicaulis (Lam.) Thulin
MORACEAE	*Ficus thonningii* Blume
MYRTACEAE	*Psidium guajava* L.
	Syzygium staudtii (Engl.) Mildbr.
NYCTAGINACEAE	*Boerhavia diffusa* L.

NYMPHAEACEAE	*Nymphaea nouchali* Burm. f.
ONAGRACEAE	*Ludwigia abyssinica* A. Rich.
	Ludwigia adscendens (L.) H. Hara
	Ludwigia erecta (L.) H.Hara
	Ludwigia leptocarpa (Nutt.) H.Hara
	Ludwigia octovalvis (Jacq.) P.H. Raven
OROBANCHACEAE	*Striga forbesii* Benth.
OXALIDACEAE	*Biophytum umbraculum* Welw.
	Oxalis corniculata L.
	Oxalis latifolia Kunth
PEDALIACEAE	*Sesamum angustifolium* (Oliv.) Engl.
PHYLLANTHACEAE	*Flueggea virosa* (Roxb. ex Willd.) Royle
	Phyllanthus amarus Schumach. & Thonn.
	Phyllanthus nummulariifolius Poir.
PLANTAGINACEAE	*Limnophila indica* (L.) Druce
	Veronica abyssinica Fresen.
POACEAE	*Alloteropsis paniculata* (Benth.) Stapf
	Aristida adoensis Hochst.
	Bothriochloa insculpta (Hochst. ex A.Rich.) A.Camus
	Brachiaria decumbens Stapf
	Cenchrus clandestinus (Hochst. ex Chiov.) Morrone
	Cenchrus mezianus (Leeke) Morrone
	Chloris gayana Kunth
	Chloris pycnothrix Trin.
	Chrysopogon nigritanus (Benth.) Veldkamp
	Cleistachne sorghoides Benth.
	Coix lacryma-jobi L.
	Cynodon dactylon (L.) Pers.
	Dactyloctenium aegyptium (L.) Willd.
	Digitaria abyssinica (Hochst. ex A. Rich.) Stapf
	Digitaria ciliaris (Retz.) Koeler
	Digitaria horizontalis Willd.
	Digitaria ternata (A. Rich.) Stapf
	Digitaria thouarsiana (Flüggé) A. Camus
	Digitaria velutina (Forssk.) P. Beauv.
	Diplachne caudata K.Schum.
	Echinochloa colona (L.) Link
	Echinochloa crus-pavonis (Kunth) Schult.
	Echinochloa haploclada (Stapf) Stapf
	Echinochloa pyramidalis (Lam.) Hitchc. & Chase
	Echinochloa stagnina (Retz.) P.Beauv.
	Echinochloa ugandensis Snowden & C.E.Hubb.
	Eleusine indica (L.) Gaertn.
	Eragrostis aspera (Jacq.) Nees
	Eragrostis ciliaris (L.) R. Br.
	Eragrostis japonica (Thunb.) Trin.

Eragrostis lappula Nees
Eragrostis mildbraedii Pilg.
Eragrostis paniciformis (A.Braun) Steud.
Eragrostis tenuifolia (A. Rich.) Steud.
Eriochloa fatmensis (Hochst. & Steud.) Clayton
Hackelochloa granularis (L.) Kuntze
Hemarthria altissima (Poir.) Stapf & C.E.Hubb.
Hyparrhenia filipendula (Hochst.) Stapf
Hyparrhenia rufa (Nees) Stapf
Imperata cylindrica (L.) Raeusch.
Ischaemum rugosum Salisb.
Leersia hexandra Sw.
Leptochloa panicea (Retz.) Ohwi
Melinis repens (Willd.) Zizka
Oryza longistaminata A. Chev. & Roehr.
Oryza sativa L.
Panicum coloratum L.
Panicum fluviicola Steud.
Panicum hanningtonii Stapf
Panicum hygrocharis Steud.
Panicum hymeniochilum Nees
Panicum maximum Jacq.
Panicum monticola Hook.f.
Panicum subalbidum Kunth
Panicum trichocladum Hack. ex K. Schum.
Paspalum conjugatum P. J. Bergius
Paspalum notatum Alain ex Flüggé
Paspalum scrobiculatum L.
Pennisetum purpureum Schumach.
Perotis patens Gand.
Phragmites australis (Cav.) Trin. ex Steud.
Rottboellia cochinchinensis (Lour.) Clayton
Sacciolepis africana C.E. Hubb. & Snowden
Sacciolepis indica (L.) Chase
Saccharum officinarum L.
Schizachyrium brevifolium (Sw.) Nees ex Büse
Setaria homonyma (Steud.) Chiov.
Setaria kagerensis Mez
Setaria longiseta P.Beauv.
Setaria sphacelata (Schumach.) Stapf & C.E. Hubb.
Setaria verticillata (L.) P. Beauv.
Sorghastrum stipoides (Kunth) Nash
Sorghum arundinaceum (Desv.) Stapf
Sporobolus africanus (Poir.) Robyns & Tournay
Sporobolus agrostoides Chiov.
Sporobolus pyramidalis P.Beauv.

	Themeda triandra Forssk.
	Urochloa comata (Hochst. ex A.Rich.) Sosef
	Urochloa setigera (Retz.) Stapf
	Vossia cuspidata (Roxb.) Griff.
	Zea mays L.
POLYGALACEAE	*Polygala sphenoptera* Fresen.
POLYGONACEAE	*Oxygonum sinuatum* (Hochst. & Steud. ex Meisn.) Dammer
	Persicaria decipiens (R. Br.) K. L. Wilson
	Persicaria senegalensis (Meisn.) Soják
	Persicaria setosula (A. Rich.) K. L. Wilson
	Persicaria strigosa (R. Br.) Nakai
	Polygonum pulchrum Blume
PONTEDERIACEAE	*Eichhornia crassipes* (Mart.) Solms
PORTULACACEAE	*Portulaca oleracea* L.
PRIMULACEAE	*Lysimachia ruhmeriana* Vatke
RUBIACEAE	*Mitracarpus hirtus* (L.) DC.
	Oldenlandia corymbosa L.
	Oldenlandia fastigiata Bremek.
	Pentodon pentandrus (Schumach. & Thonn.) Vatke
	Richardia brasiliensis Gomes
	Spermacoce princeae (K. Schum.) Verdc.
	Spermacoce ruelliae DC.
SALVINIACEAE	*Azolla pinnata* R. Br.
SAPINDACEAE	*Dodonaea viscosa* Jacq.
	Paullinia pinnata L.
SCROPHULARIACEAE	*Alectra sessiliflora* (Vahl) Kuntze
	Scoparia dulcis L.
	Stemodia serrata Benth.
SOLANACEAE	*Lycopersicon esculentum* Mill.
	Physalis lagascae Roem. & Schult.
	Solanum aethiopicum L.
	Solanum incanum L.
	Solanum nigrum L.
SPHENOCLEACEAE	*Sphenoclea zeylanica* Gaertn.
THELYPTERIDACEAE	*Cyclosorus interruptus* (Willd.) H. Itô
TYPHACEAE	*Typha domingensis* Pers.
	Typha latifolia L.
URTICACEAE	*Pouzolzia parasitica* (Forssk.) Schweinf.
VERBENACEAE	*Lantana camara* L.
	Stachytarpheta jamaicensis (L.) Vahl
	Verbena bonariensis L.
VITACEAE	*Cissus petiolata* Hook.f.
	Cyphostemma adenocaule (Steud. ex A. Rich.) Desc. ex Wild & R. B. Drumm.
ZINGIBERACEAE	*Aframomum alboviolaceum* (Ridl.) K.Schum.
	Aframomum angustifolium (Sonn.) K. Schum.

A4 – Photographs of different recovery stages in Namulonge inland valley, Uganda

Wetland fringe (4th repetition)

25.11.2014
71 days after disturbance
Dominance of annual species

Main species	Life form	Cover (%)
Cyperus difformis	OA	30
Ageratum conyzoides	OA	25
Cyperus distans	FA	15
Kyllinga odorata	TP	10
Ludwigia abyssinica	FA	5

22.04.2015
220 days after disturbance
Increase of perennial grasses

Main species	Life form	Cover (%)
Ageratum conyzoides	OA	25
Cyperus denudatus	RP	20
Panicum maximum	TP	15
Centella asiatica	RP	10
Sacciolepis indica	OA	10

20.10.2015
400 days after disturbance
Dominance of perennial grasses and sedges

Main species	Life form	Cover (%)
Panicum maximum	TP	50
Fuirena pubescens	TP	15
Ludwigia octovalvis	TP	10
Leersia hexandra	RP	10
Chamaecrista mimosoides	FA	8

06.08.2016
691 days after disturbance
Increase of reeds and woody plants

Main species	Life form	Cover (%)
Panicum maximum	TP	60
Ludwigia abyssinica	FA	25
Cyperus latifolius	RD	5
Leersia hexandra	RP	5
Desmodium salicifolium var. *densiflorum*	PP	2

Life forms (Behn et al. 2022): OA = Obligate annual, FA = Facultative annual, RP = Reptant plants, TP = Tussock plants, RD = Reed plant, CP = Climbing plant, PP = Phanerophyte

A4 – Photographs of different recovery stages in Namulonge inland valley, Uganda

Pictures from the mid-valley zone (3rd repetition)

25.11.2014
71 days after disturbance
Dominance of annual species

Main species	Life form	Cover (%)
Cyperus difformis	OA	20
Cyperus distans	FA	10
Leersia hexandra	RP	10
Ludwigia abyssinica	FA	8
Fuirena pubescens	TP	5

22.04.2015
220 days after disturbance
Dominance of perennial grasses and reeds

Main species	Life form	Cover (%)
Cyperus latifolius	RD	55
Digitaria abyssinica	RP	10
Leersia hexandra	RP	10
Paspalum scrobiculatum	FA	10
Ludwigia abyssinica	FA	5

20.10.2015
400 days after disturbance
Increase of shrubs

Main species	Life form	Cover (%)
Leersia hexandra	RP	30
Fuirena pubescens	TP	15
Cyperus latifolius	RD	15
Ludwigia abyssinica	FA	15
Mimosa pigra	PP	10

06.08.2016
691 days after disturbance
Dominance of shrubs

Main species	Life form	Cover (%)
Mimosa pigra	PP	30
Leersia hexandra	RP	20
Digitaria abyssinica	RP	20
Fuirena pubescens	TP	15
Aspilia africana	PP	10

Life forms (Behn et al. 2022): OA = Obligate annual, FA = Facultative annual, RP = Reptant plants, TP = Tussock plants, RD = Reed plant, CP = Climbing plant, PP = Phanerophyte

A4 – Photographs of different recovery stages in Namulonge inland valley, Uganda

Pictures from the riparian zone (4th repetition) – Namulonge inland valley wetland, Uganda

25.11.2014
71 days after disturbance
Dominance of annual species

Main species	Life form	Cover (%)
Cyperus difformis	OA	95
Leersia hexandra	RP	10
Panicum subalbidum	FA	5
Commelina diffusa	OA	3
Ludwigia abyssinica	FA	3

22.04.2015
220 days after disturbance
Dominance of perennial grasses

Main species	Life form	Cover (%)
Leersia hexandra	RP	55
Ludwigia abyssinica	FA	25
Sacciolepis africana	TP	15
Commelina diffusa	OA	6
Cyperus papyrus	RD	2

20.10.2015
400 days after disturbance
Dominance of perennial grasses

Main species	Life form	Cover (%)
Leersia hexandra	RP	85
Hyptis lanceolata	FA	5
Persicaria decipiens	TP	5
Polygonum pulchrum	TP	4
Cyperus papyrus	RD	3

06.08.2016
691 days after disturbance
Increase of reeds and perennial forbs

Main species	Life form	Cover (%)
Ludwigia abyssinica	FA	40
Polygonum pulchrum	TP	25
Persicaria decipiens	TP	10
Melanthera scandens	CP	5
Cyperus papyrus	RD	5

Life forms (Behn et al. 2022): OA = Obligate annual, FA = Facultative annual, RP = Reptant plants, TP = Tussock plants, RD = Reed plant, CP = Climbing plant, PP = Phanerophyte

A5 - Photographs of different recovery stages in Kilombero floodplain, Tanzania

Pictures from the wetland fringe (1st repetition)

07.05.2015
139 days after disturbance / wet season
Exclusively annual species

Main species	Life form	Cover (%)
Panicum hanningtonii	OA	30
Ischaemum rugosum	OA	20
Acmella uliginosa	OA	15
Schizachyrium brevifolium	OA	15
Hibiscus cannabinus	OA	10

19.06.2015
182 days after disturbance / early dry season
Exclusively annual species

Main species	Life form	Cover (%)
Panicum hanningtonii	OA	65
Acmella uliginosa	OA	20
Ischaemum rugosum	OA	10
Hibuscus cannabinus	OA	10
Schizachyrium brevifolium	OA	10

30.11.2015
346 days after disturbance / late dry season
Large amounts of dead biomass, few living plants

Main species	Life form	Cover (%)
Oryza longistaminata	RD	3
Cyperus spec.	OA	2
Ipomoea aquatica	OA	1
Paspalum scrobiculatum	FA	1

30.07.2016
589 days after disturbance / dry season
Exclusively annual species

Main species	Life form	Cover (%)
Panicum hanningtonii	OA	45
Ipomoea eriocarpa	OA	15
Vernonia cinerea	OA	5
Physalis lagascae	OA	2
Schizachyrium brevifolium	OA	2

Life forms (Behn et al., 2022): OA = Obligate annual, FA = Facultative annual, RP = Reptant plants, TP = Tussock plants, RD = Reed plant, CP = Climbing plant, PP = Phanerophyte, All pictures © Kai Behn

A5 - Photographs of different recovery stages in Kilombero floodplain, Tanzania

Pictures from the middle zone (1st repetition)

12.05.2015
144 days after disturbance / wet season
Exclusively annual species

Main species	Life form	Cover (%)
Panicum hanningtonii	OA	70
Melochia corchorifolia	OA	10
Ipomoea eriocarpa	OA	5
Corchorus fascicularis	OA	2
Hibiscus cannabinus	OA	2

24.06.2015
187 days after disturbance / early dry season
Exclusively annual species

Main species	Life form	Cover (%)
Panicum hanningtonii	OA	87
Hygrophila auriculata	OA	3
Melochia corchorifolia	OA	3
Hibiscus cannabinus	OA	3
Corchurus fascicularis	OA	2

30.11.2015
346 days after disturbance / late dry season
Dead biomass burnt, few living plants

Main species	Life form	Cover (%)
Panicum haningtonii	OA	3
Melochia corchorifolia	OA	1
Physalis lagascae	OA	1

30.07.2016
589 days after disturbance / dry season
Dominance of annual species

Main species	Life form	Cover (%)
Panicum hanningtonii	OA	70
Oryza longistaminata	RD	20
Hygrophila auriculata	OA	5
Ipomoea aquatic	OA	1

Life forms (Behn et al., 2022): OA = Obligate annual, FA = Facultative annual, RP = Reptant plants, TP = Tussock plants, RD = Reed plant, CP = Climbing plant, PP = Phanerophyte

A5 - Photographs of different recovery stages in Kilombero floodplain, Tanzania

Pictures from the riparian zone (3rd repetition)

04.06.2015
167 days after disturbance / early dry season, after flooding
Dominance of semiaquatic annual species

Main species	Life form	Cover (%)
Ipomoea aquatica	OA	50
Utricularia stellaris	AC	10
Meremmia hederacea	OA	1
Paspalum scrobiculatum	FA	1
Leptochloa panicea	OA	1

24.06.2015
187 days after disturbance / dry season
Dominance of semiaquatic annual species

Main species	Life form	Cover (%)
Ipomoea aquatica	OA	70
Meremmia hederacea	OA	10
Leptochloa panicea	OA	3
Paspalum scrobiculatum	FA	3
Neptunia oleracea	RP	1

30.11.2015
346 days after disturbance / late dry season
Dominance of semiaquatic annual species

Main species	Life form	Cover (%)
Ipomoea aquatica	OA	50
Paspalum scrobiculatum	FA	15
Leptochloa panicea	OA	10
Leersia hexandra	RP	2
Aeschynomene cristata	PP	2

30.07.2016
589 days after disturbance / dry season
Grass-dominated vegetation

Main species	Life form	Cover (%)
Paspalum scrobiculatum	FA	45
Ipomoea aquatica	OA	20
Indigofera spec.	TP	20
Leersia hexandra	RP	15
Leptochloa panicea	OA	10

Life forms (Behn et al., 2022): OA = Obligate annual, FA = Facultative annual, RP = Reptant plants, TP = Tussock plants, RD = Reed plant, CP = Climbing plant, PP = Phanerophyte, AC = Acropleustophyte

A6 – List of published articles in international journals and books

Journal articles

Botha, D., Barnard, S., Du Plessis, M., Allam, M., **Behn, K.,** Ismail, A., ... & Siebert, F. (2024). Application of a dual-locus metabarcoding approach for a more comprehensive account of cattle dietary items in a semi-arid African savanna with special reference to forbs. *MBMG Metabarcoding and Metagenomics*, *8*, 1.

Behn, K., Alvarez, M., Mutebi, S., & Becker, M. (2024). Recovery dynamics of wetland vegetation along a hydrological gradient in an agriculturally used inland valley in Uganda. *Wetlands Ecology and Management*, *32*(6), 959–974.

Smith, M. D., Wilkins, K. D., Holdrege, M. C., Wilfahrt, P., Collins, S. L., Knapp, A. K., Linstädter, A., **Behn, K.**, (...) & Sun, W. (2024). Extreme drought impacts have been underestimated in grasslands and shrublands globally. *Proceedings of the National Academy of Sciences*, *121*(4), e2309881120.

Wirth, S. B., Poyda, A., Taube, F., Tietjen, B., Müller, C., Thonicke, K., Linstädter, A., **Behn, K.,** Schaphof, S., von Bloh, W. & Rolinski, S. (2024). Connecting competitor, stress-tolerator and ruderal (CSR) theory and Lund Potsdam Jena managed Land 5 (LPJmL 5) to assess the role of environmental conditions, management and functional diversity for grassland ecosystem functions. *Biogeosciences*, 21(2), 381-410.

Behn K., Alvarez M., Mutebi S., Becker M. (2022). Vegetation diversity in East African wetlands: Cocktail algorithms supported by a vegetation-plot database. *Phytocoenologia* 392

Roetter, R. P., Scheiter, S., Hoffmann, M. P., Pfeiffer, M., Nelson, W. C. D., Ayisi, K., Taylor, P., Feil, J.-H., Bakhsh, S. Y., Isselstein, J., Lindstaedter, A., **Behn, K**., Westphal, C., Odhiambo, J., Twine, W., Grass, I., Merante, P., Bracho-Mujica, G., Bringhenti, T., (…) Erasmus, B. (2021). Modeling the multi-functionality of African savanna landscapes under global change. Land Degradation & Development, 32(6), 2077–2081.

Munjonji L., Ayisi K.K., Mudongo E. I., Mafeo T. P., **Behn K.,** Mokoka M.V., Linstädter A. (2020) Disentangling drought and grazing effects on soil carbon stocks and CO2 fluxes in a semi-arid African savanna. *Frontiers in Environmental Science*, 8, 207.

Behn K., Becker M., Burghof S., Möseler B.M., Willy D.K., Alvarez M. (2018). Using vegetation attributes to rapidly assess degradation of East African wetlands. *Ecological Indicators*, 89, 250-259.

Beuel, S., Alvarez, M., Amler, E., **Behn, K**., Kotze, D., Kreye, C., Leemhuis, C., Wagner, K., Kyalo Willy, D., Ziegler, S., Becker, M. (2016). A rapid assessment of anthropogenic disturbances in East African wetlands. *Ecological Indicators* 67, 684–692.

Books and book chapters

Scheiter, S., Pfeiffer, M., **Behn, K**., Ayisi, K., Siebert, F., & Linstädter, A. (2024). Managing Southern African Rangeland Systems in the Face of Drought: A Synthesis of Observation, Experimentation and Modeling for Policy and Decision Support. In *Sustainability of Southern African Ecosystems under Global Change: Science for Management and Policy Interventions* (pp. 439-470). Cham: Springer International Publishing.

Becker M., Alvarez M., **Behn K**., Möseler B.M., Handa C., Oyieke H., Misana S., Mogha N. (2014) Small wetlands in East Africa: A field guide to the representative flora. Selbstverlag, Bonn. Germany. 202 pp. ISBN 978-3-00-047349-4.

A7 - Selected presentations at international conferences

Tropentag 2024: **Behn, K.,** Kamiri, H., Mutuku, D., Ndikumwenayo, M., Sainepo, B, Becker, M.: Invasive plant species drive land use changes in East Africa, Tropentag 2024, Vienna, Austria, 11 -13 September 2024 (Oral presentation)

Tropentag 2023: **Behn, K.,** Greyvenstein, B., Siebert, F., van den Berg, J., Mokoka, V., Westphal, C., Yazdan-Bakhsh, S., Feil, J.-H., Foord, S., 7, Graß, I., Rötter, R. P., Taylor, P., Linstädter, A.: Land-use effects on plant and arthropod diversity in South African savannahs. Tropentag 2023, Berlin, Germany, 20-22 September 2023 (Oral presentation)

Tropentag 2022: **Behn, K**., Pfeiffer, M., Mokoka, V., Mudongo, E., Ruppert, J., Scheiter, S, Ayisi, K., Linstädter, A.: Assessing the relevance of drought duration on dryland rangelands: an experimental and modelling study. Tropentag 2022, Prague, Czech Republic, 14-16 September 2022 (Poster)

IGC-IRC 2021: **Behn, K.,** Mokoka, V., Mudongo, E., Ruppert, J., Ayisi, K., Linstädter, A.: Which role play grazing and drought duration for desertification? Insights from a tipping point experiment in southern Africa. International Grassland/Rangeland Congress 2021, 25-29 October 2021, Kenya (virtual). (Poster).

GFÖ 2021: **Behn, K.,** Pfeiffer, M., Mokoka, V., Mudongo, E., Ruppert, J., Scheiter, S, Ayisi, K., Linstädter, A. Drought length matters for vegetation resistance and resilience in a South African savanna grassland. Virtuelle 50. Jahrestagung der GfÖ – 30. August – 1. September 2021 (Oral presentation)

Tropentag 2017: **Behn, K.**, Mutebi, S., Alvarez, M.: Diversity of East African wetland vegetation: A classification based on current and historic Surveys 20-22 September 2017, Bonn, Germany (Oral presentation)

16th Meeting on Vegetation Databases 2017: **Behn, K.**, Mutebi, S., Alvarez, M.: Combining current and historical surveys for classification of wetland vegetation in East Africa 9-10 March 2017 Freiburg, Germany (Oral presentation)

Tropentag 2016: **Behn, K.,** Alvarez, M., Becker, M., Möseler, B.M.: Flora and vegetation in East African wetlands in the context of land use changes 18-21 September 2016, Vienna, Austria Poster (Poster)

Tropentag 2015: **Behn, K.**, Alvarez, M., Becker, M., Mutebi, S.: Monitoring wetland vegetation regeneration in an inland valley in Uganda. 16-18 September 2015, Berlin, Germany (Poster)
14th Meeting on Vegetation Databases 2015: **Behn, K.,** Alvarez, M., Amler, E., Beuel, S., Wagner, K., Willy, D.K., Ziegler, S. A vegetation-based index of biotic integrity applied to riparian vegetation in East Africa 4 -6 March 2015. Oldenburg, Germany (Oral presentation)

13th Meeting on Vegetation Databases 2014: **Behn, K**., Alvarez, M.1, Amler, E., Beuel, S., Gabiri, G., Koko, I., Macharia, J., Umuhumuza, G., Wagner, K., Willy, D.K., Ziegler, S.: Assessment of floristic and structural variables of vegetation: the impact of agricultural use in East African wetland ecosystems, 24-26 February 2014, Koblenz, Germany (Poster)