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

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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.

Nomenclature: Haines & Lye (1983); CJBG & SANBI (2012); The Plant List (2013); TNRS (2018).

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

Abbreviations: DCA = Detrended Correspondence Analysis; DRC = Democratic Republic of the Congo; MRPP = Multiple Response Permutation Procedure.

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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 (van Dam et al. 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

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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 & Wiser 2012; de Cáceres et al. 2018). 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.

Material and methods

Study sites

The data were collected at two study sites, Namulonge in Uganda and Ifakara in Tanzania (Fig. 1), representing an inland valley and a floodplain, the dominant wetland types in East Africa (Leemhuis et al. 2016).

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 (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 WRB 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. 2018a), 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. 2018b). 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).

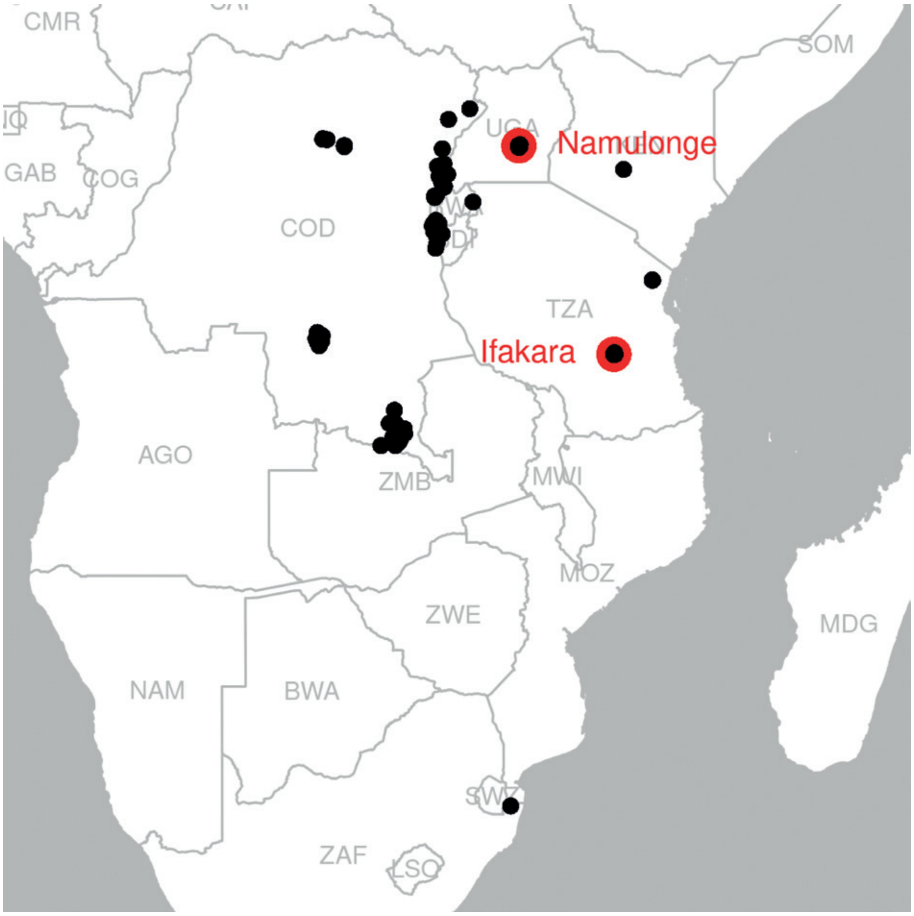

Fig. 1. Location of assessed plot observations in Sub-Saharan Africa. In gray color are oceans, borderlines and the abbreviation of the respective countries. Red circles and labels indicate the location and name of field surveys in Uganda and Tanzania. Black dots indicate the location of plot observations used in the database assessment.

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), and Plants of the World Online (POWO 2021). Based on these data and considering the Raunkiær system (Müller-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 1). 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 1. 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 (Lebrun 1947; Germain 1951; Mullenders 1954; Taton & Risopoulos 1955; Schmitz 1971; Furness & Breen 1980; Nyakabwa 1981; Szafranski & Apema 1983, Alvarez 2017). The localities of these works are shown in Figure 1. The relevés were imported to R (R Core Team 2020) 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 (Fig. 2). 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). 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 where 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.

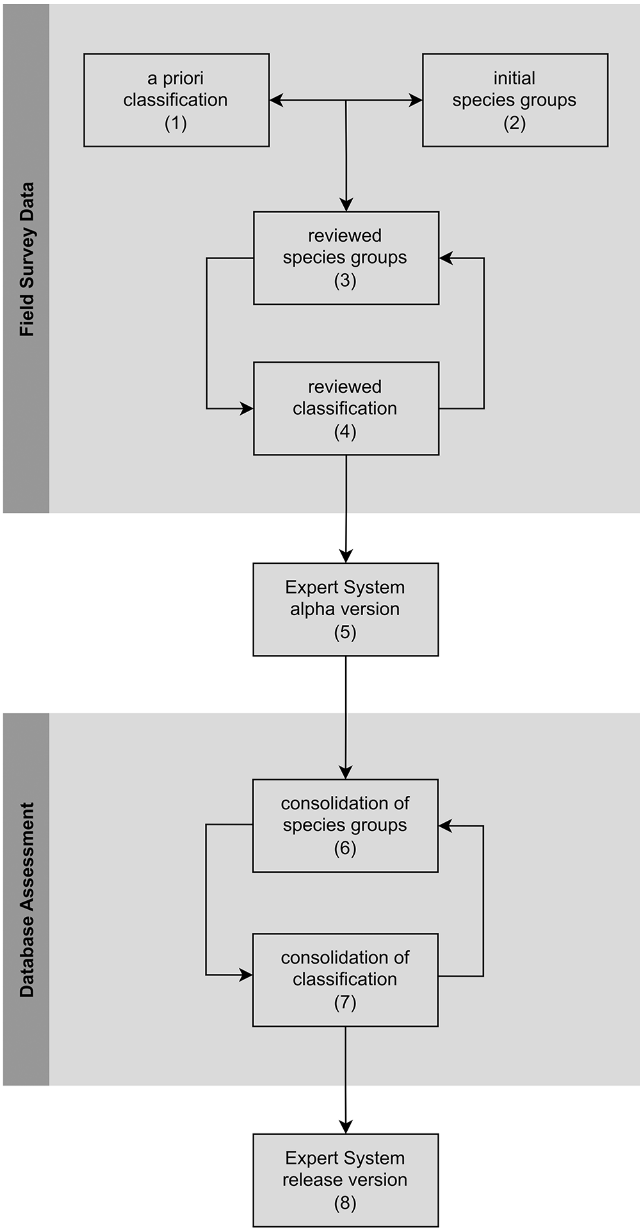

Fig. 2. Workflow for the design of classification algorithms and their compilation in an expert system for wetland vegetation in East Africa. The classification is restricted to a field survey in the first stage and in a second stage expanded to data stored in a vegetation-plot database. After digitizing data, a table will be 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.

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 2020). For a pairwise comparison we used the Kruskal pairwise test (function "kruskal()" from the package "agricolae") (de Mendiburu 2020). We further calculated the proportion of dominant families weighed on cover for each association.

Results

Assessed data set

In total we pre-selected 1,566 plot observations, which were used for fine-tuning the classification. 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 2) and formal definitions for 13 vegetation units corresponding to phytosociological associations (Table 3). These groups are related to both the wetlands hydrology types (floodplain vs. inland valley) and to the type and level of anthropogenic disturbances.

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

Holotypus: column 1 in Table 4; relevé ID 3467 in AF-00-006

Iconography: Supplement S3, 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 Compositae *Acmella uliginosa* is consumed as a wild vegetable and used in traditional medicine (Fern 2021).

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

Holotypus: column 2 in Table 4; relevé ID 3532 in AF-00-006

Iconography: Supplement S3, 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 to be 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.

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

Holotypus: column 3 in Table 4, relevé ID 3488 in AF-00-006

Iconography: Supplement S3, Plate 3

Diagnostic species (phi-value x 100): *Corchorus fascicularis* (64), *Hyptis spicigera* (55), *Ipomoea eriocarpa* (54),

Table 2. 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	*Centrostachys aquatica*	Amaranthaceae	obligate annual
Group	*Coldenia procumbens*	Boraginaceae	obligate annual
	Glinus lotoides	Molluginaceae	obligate annual
	Heliotropium indicum	Boraginaceae	obligate annual
	Pycreus polystachyos	Cyperaceae	obligate annual
Corchorus fascicularis	*Corchorus fascicularis*	Malvaceae	obligate annual
Group	*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	*Cyperus difformis*	Cyperaceae	obligate annual
Group	*Cyperus distans*	Cyperaceae	facultative annual
	Echinochloa haploclada	Poaceae	tussock plant
	Kyllinga odorata	Cyperaceae	tussock plant
	Panicum subalbidum	Poaceae	facultative annual
Cyperus papyrus	*Cyclosorus interruptus*	Thelypteridaceae	tussock plant
Group	*Cyperus papyrus*	Cyperaceae	reed plant
	Desmodium salicifolium	Leguminosae	climbing plant
Fuirena ciliaris	*Ammannia senegalensis*	Lythraceae	obligate annual
Group	*Fimbristylis bisumbellata*	Cyperaceae	obligate annual
	Fimbristylis quinquangularis	Cyperaceae	obligate annual
	Fuirena ciliaris	Cyperaceae	obligate annual
	Pycreus pumilus	Cyperaceae	obligate annual
Fuirena pubescens	*Cyperus denudatus*	Cyperaceae	reptant plant
Group	*Fuirena pubescens*	Cyperaceae	tussock plant
	Torenia thouarsii	Linderniaceae	tussock plant
Ischaemum rugosum	*Acmella uliginosa*	Compositae	obligate annual
Group	*Courtoisina cyperoides*	Cyperaceae	obligate annual
	Schizachyrium brevifolium	Poaceae	obligate annual
	Ischaemum rugosum	Poaceae	obligate annual
	Pycreus macrostachyos	Cyperaceae	obligate annual
Melanthera scandens	*Hyptis lanceolata*	Lamiaceae	facultative annual
Group	*Ipomoea cairica*	Convolvulaceae	climbing plant
	Melanthera scandens	Compositae	climbing plant

Table 3. 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 4. 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 number	1	2	3	4	6	7	8	13
Relevé number	3467	3532	3488	3596	3664	3692	3733	3576
Country	Tanzania	Tanzania	Tanzania	Tanzania	Uganda	Uganda	Uganda	Tanzania
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 (degrees)	36.712	36.701	36.690	36.690	32.642	32.641	32.642	36.696
Latitude (degrees)	-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**	.	.	.	.	.	.

Table 4. cont.

Column number	1	2	3	4	5	6	7	8
Association number	1	2	3	4	6	7	8	13
Relevé number	3467	3532	3488	3596	3664	3692	3733	3576
Country	Tanzania	Tanzania	Tanzania	Tanzania	Uganda	Uganda	Uganda	Tanzania
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 (degrees)	36.712	36.701	36.690	36.690	32.642	32.641	32.642	36.696
Latitude (degrees)	-8.128	-8.155	-8.172	-8.173	0.521	0.520	0.521	-8.176
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**	.	.

Table 4. cont.

Column number	1	2	3	4	5	6	7	8
Association number	1	2	3	4	6	7	8	13
Relevé number	3467	3532	3488	3596	3664	3692	3733	3576
Country	Tanzania	Tanzania	Tanzania	Tanzania	Uganda	Uganda	Uganda	Tanzania
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 (degrees)	36.712	36.701	36.690	36.690	32.642	32.641	32.642	36.696
Latitude (degrees)	-8.128	-8.155	-8.172	-8.173	0.521	0.520	0.521	-8.176
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**

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).

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

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

Iconography: Supplement S3, 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.

5. *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, 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.

6. *Cypero distantis-Cyperetum difformis* ass. nova hoc loco
Holotypus: column 5 in Table 4, relevé ID 3664 in AF-00-006
Iconography: Supplement S3, 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 (Fig. 3). 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 Compositae (0.14). Many plants occurring in this association are reported to have medicinal properties or are used in other ways (Makokha et al. 2017).

7. *Cypero denudati-Fuirenetum pubescentis* ass. nova hoc loco
Holotypus: column 6 in Table 4, relevé ID 3692 in AF-00-006

Iconography: Supplement S3, 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 Compositae (0.10). In some plots of this association, invasive *Mimosa pigra* (Witt et al. 2020) and consequently Leguminosae (0.12) are dominant. Although most species are common in the region, we did not find similar vegetation described in the consulted literature.

8. *Melanthero scandentis-Leersietum hexandrae* ass. nova hoc loco
Holotypus: column 7 in Table 4; relevé ID 3733 in AF-00-006
Iconography: Supplement S3, 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.

9. *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, 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, 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 *Cy-*

perus 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 raw material for thatching material, 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 Fig. 3). 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, 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. (1997), 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. 1997) 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 4, 3576 in AF-00-006
Iconography: Supplement S3, 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 field work 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. Also, 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 used for medicinal purposes.

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 river banks as well as the *Phragmitetum mauritiani*. Table 5 gives an overview of the complete syntaxonomy of the associations described in this work.

Ordination and classification goodness

The ordination by DCA supports the classification of communities in two classes, namely *Phragmito-Magno-Caricetea* and *Oryzetea sativae* (Fig. 3). 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

Table 5. 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 given.

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-Dryopterideturn gongylodes (Germain 1951) Schmitz 1963	**[10]**

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 was available on that for a proper analysis with all plots, it is known from literature (e. g. Lind et al. 1974) that the *Cypero papyri-Dryopteridetum gongylodes* needs at least 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).

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 Fig. 3 for selected and Supplement S5 for all 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*. 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 (Fig. 4). 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, 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

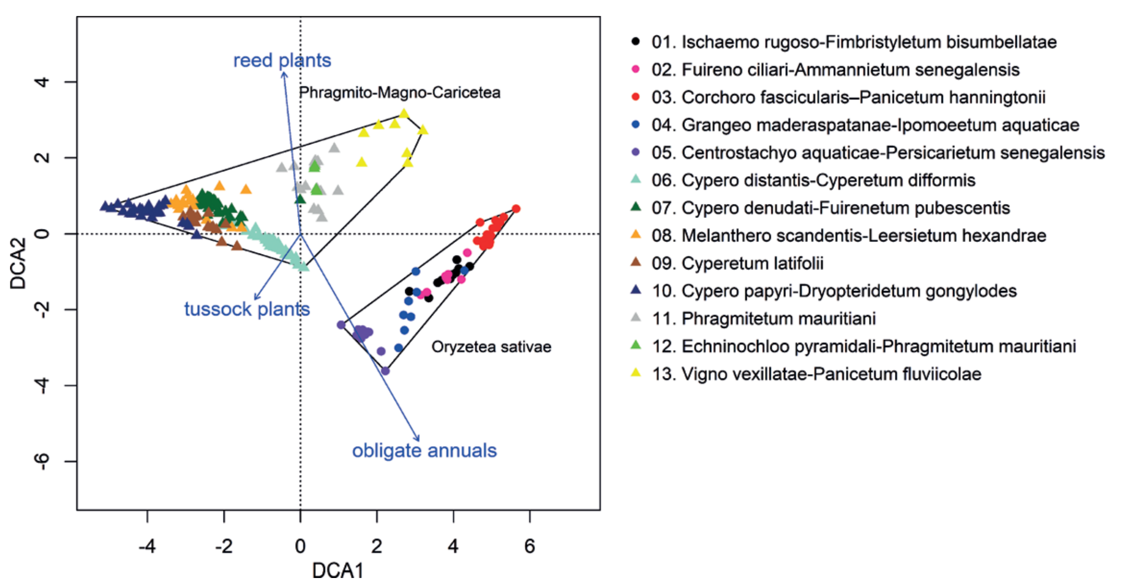

Fig. 3. Detrended correspondence analysis (DCA) of all classified plots in this work based on an inland valley swamp of Uganda and a floodplain wetland in Tanzania (2014–2016) and secondary data sources using the diagnostic species of one or more vegetation units. Hulls connect all plots belonging to the phytosociological classes of Phragmito-Magno-Caricetea and *Oryzetea sativae*.

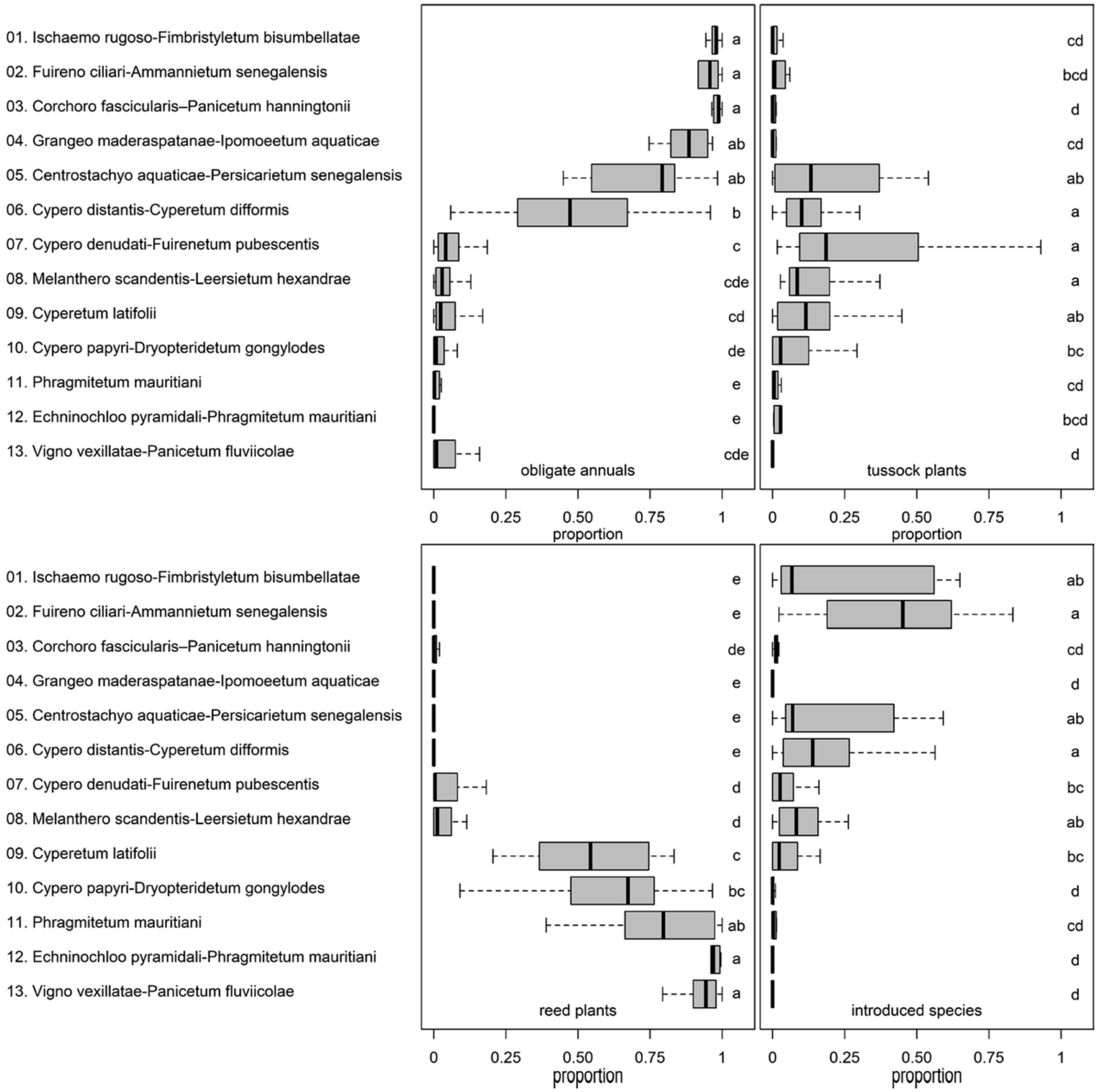

Fig. 4. Proportion of obligate annuals, tussock plants, reed plants and introduced species for each association in this work based on wetlands of East Africa (inland valley swamp in Uganda and floodplain in Tanzania, 2014–2016 and secondary data sources). Letters on the right indicate significant (p>0.05) differences between the associations.

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).

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 (e.g. 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 that justifies 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 as a result 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 (Hood et al. 2002; Alvarez et al. 2012) 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.

Author contributions

MA, MB and KB planned the research, KB and SM conducted the field sampling, KB performed the statistical analyses and led the writing with support of MA. MA built the database used in this work with support of KB. All authors critically reviewed the manuscript.

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Conflict of interests

The authors declare no conflict of interests.

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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).

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