From meadow to shallow lake: Monitoring secondary succession in a coastal fen after rewetting by flooding based on aerial imagery and plot data

M. Koch[1], F. Koebsch[2], J. Hahn[1] and G. Jurasinski[1]

[1]Faculty of Agriculture and Environmental Sciences, University of Rostock, Germany
[2] Department of Forest Ecology and Management, Swedish University of Agricultural Sciences, Umeå, Sweden

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SUMMARY

Year-round flooding can be a cost-effective measure for rewetting highly degraded fens, and is gaining popularity for lowland fen restoration in Europe. We investigated the short-term effects of such permanent inundation on species composition and spatial distribution of the vegetation of a formerly drained coastal fen, and addressed the question of whether re-establishment of peat-forming reed vegetation is foreseeable. For vegetation mapping and monitoring we combined permanent plot data acquired during four years following shallow flooding, high-resolution aerial imagery and an elevation model. Five vegetation types were distinguished, and we analysed their spatial distribution and succession patterns throughout the years. Pre-existing vegetation, its spatial arrangement and the water level played major roles in secondary succession. Existing patches of _Phragmites australis_ showed high stability, but their growth was not consistent through the years and at all inundation depths. Existing stands of _Bolboschoenus maritimus_ were outcompeted by _Schoenoplectus tabernaemontani_ or vanished and formed relatively stable ponds of open water with hydrophytic species. We concluded that the expansion of reed as peat-forming vegetation is likely to proceed slowly, but fluctuations in water level and edge effects will probably maintain a persistent mosaic of vegetation and open water in the near future.

KEY WORDS: fen restoration, image classification, _Phragmites australis_, vegetation mapping

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INTRODUCTION

Restoration of drained and disturbed fens is aimed at both abiotic (physico-chemical) and biotic objectives (Pfadenhauer & Grootjans 1999). Abiotic objectives include the curtailment of peat mineralisation to reduce CO_2 emissions, which are typically high in drained fen peatlands, and the retention or reinforcement of water retention capacity. The paramount biotic objectives are to restore habitats for specialised plant and animal species and to promote their re-establishment after intensive land use. Locally, the desired biotic developments can differ significantly from site to site depending on restoration potential, intended management effort and socio-economic considerations. In Europe, a common aim in fen restoration is to re-establish former species-rich target communities (Patzelt _et al_. 2001, Rosenthal 2003, Klimkowska _et al_. 2007, Schrautzer _et al_. 2013). However, several constraints make this difficult to achieve. After decades of drainage and intensified use, the hydraulic properties of the decomposing peat may have changed irreversibly. In particular, the reduced hydraulic conductivity and reduced water retention capacity of the upper peat layers may impair successful rewetting (Richert _et al_. 2000, Holden _et al_. 2004). Spatially heterogeneous peat shrinkage can make it difficult to set a desirable water level for a target area as a whole (Succow & Joosten 2001, Hoogland _et al_. 2012). Peat mineralisation and fertiliser application can cause eutrophication, and the soil seed bank may be depleted in propagules of the desired target species (van Dijk _et al_. 2007). Finally, the development and stability of plant communities after an initial intervention to effect restoration remain unclear, and unpredicted and unwanted developments can occur (Klötzli & Grootjans 2001).

Under these constraints, various concepts of fen rewetting and vegetation re-establishment have been discussed and applied in the past, including topsoil removal and sowing of the target species (Roth _et al_. 1999, Patzelt _et al_. 2001, Succow & Joosten 2001). The ambitious objective of recreating a near-pristine state makes large investments necessary and success is not guaranteed (Klötzli & Grootjans 2001, Klimkowska _et al_. 2010). Thus, individual rewetting aims need to be reconsidered in terms of cost and benefit. Where cost-intensive measures like topsoil removal are not realisable, changed physical

properties of the peat often make temporal or permanent inundation essential to avoid its further aeration and mineralisation. Moreover, when peat shrinkage has caused the fen surface to sink below the level of adjacent water sources, the cessation of artificial drainage measures alone can result in permanent flooding (Timmermann *et al.* 2006).

In north-eastern Germany, where this case study is located, rewetting of drained fens aims primarily to reduce ongoing peat decomposition and nutrient leaching under extensified use (MLUV 2009). Natural development without further management is desired on 10 % of the restored sites. Here, the aim of rewetting is to recreate self-regulating ecosystems with peat-accumulating vegetation (Timmermann *et al.* 2006). This restoration paradigm focuses on the restoration or protection of ecosystem functions and processes rather than on target species (Ehrenfeld 2000).

Under the constraints mentioned above, the approach of choice for these fens is often year-round flooding. Inundation after decades of drainage is heavily destabilising for the fen ecosystem and is supposed to cause a rapid shift to vegetation types dominated by helophytes (Richert *et al.* 2000, Timmermann *et al.* 2006, Toogood & Joyce 2009). However, the patterns and processes controlling short-term vegetation development after flooding of species-poor rich fens are not fully understood. Therefore, monitoring is important for success control and to improve our knowledge of early secondary succession patterns (Klimkowska *et al.* 2010, Zerbe *et al.* 2013).

Approaches for monitoring the success of restoration include pure floristic assessment, analysis of permanent plot data and vegetation mapping. Regular recording of permanent plots is a valuable tool for detecting vegetation changes over time (Bakker *et al.* 1996), and has been applied widely to study succession in wetlands under restoration (Klötzli & Grootjans 2001, Van Geest *et al.* 2005, Rosenthal 2006). However, spatial features of plant distribution are important factors controlling succession (Augustin *et al.* 2001). This is especially true for species-poor fen ecosystems in which plant species mainly propagate rhizomatously. Therefore, to detect spatial patterns and small-scale changes over short timescales it is desirable to complement plot data with annual vegetation maps. Since species-poor rich fens are often characterised by stands dominated by certain species with relatively sharp boundaries, categorical maps of vegetation types offer a good representation of such ecosystems.

Vegetation mapping based on the classification of aerial and satellite imagery is quite well developed (see Xie *et al.* 2008 for a review). Typically, multi-or hyper-spectral satellite imagery is used as the data source, offering good and reliable results at larger scales. However, high spectral resolution satellite imagery is still limited in spatial resolution, whereas airborne high spectral resolution imagery is still costly. Recently, unmanned aerial vehicle (UAV) based aerial photography has gained more and more attention (Colomina & Molina 2014), and low spectral but high spatial resolution sensors make these systems an affordable alternative for various applications. They may be especially interesting and valuable for monitoring ecosystem-scale vegetation development, although few studies are yet available.

Here, we used annual RGB aerial images with a 20 cm pixel width on the ground in combination with plot-based vegetation data and a digital elevation model for object-based vegetation mapping to monitor small-scale vegetation dynamics after rewetting and abandonment of a coastal paludification fen. We analysed both floristic changes and spatial patterns of vegetation development. Under the changed water regime we expected water level to remain an important factor controlling species distribution, and a rapid extinction of non-helophytic species. Since the remaining helophytes primarily propagate vegetatively, we furthermore expected that spatial properties of vegetation patches (primarily shape and distance to neighbours) may act as important controls for species distribution. On the basis of our short-term observations, we strive to deduce developments for the future, and address the question of whether the objective of establishing extensive peat-forming vegetation is likely to be achieved.

METHODS

Study site

The study was conducted at the "Rodewiese" (54° 12.7′ N, 12° 10.8′ E), a coastal paludification fen in the nature reserve "Heiligensee und Hütelmoor" located near the city of Rostock, Germany (Figure 1). The fen extends up to 1.6 km from north to south and up to 1.4 km from east to west. A small raised bog of a few hectares has grown on top of the fen in the southern part of the site. The site was episodically flooded with Baltic Sea water until a dune dyke was built in 1963. Since then, the fen has been almost completely hydrologically isolated from the sea, leading to an increase of freshwater influence (Scheller & Voigtländer 1996, Koebsch *et al.* 2013). The site had been actively drained and intensively used as grassland since 1960 with water levels down to 1.6 m below the surface, resulting in rapid peat
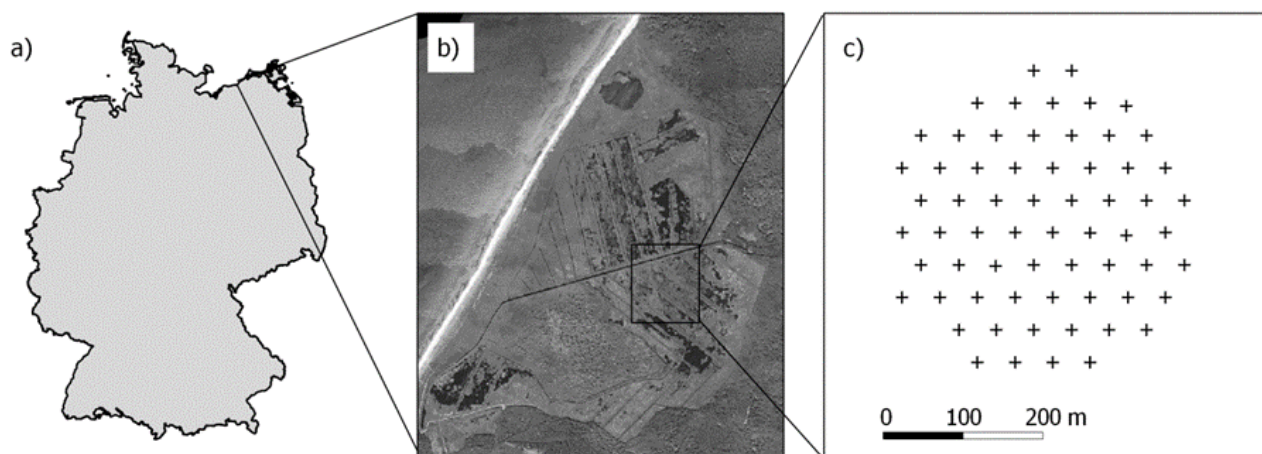
Figure 1. a) Location of the study site within Germany; b) aerial image of the nature reserve "Heiligensee und Hütelmoor" showing the study area; c) positioning of sampling points within the study area.

decomposition. The soil was identified as a sapric Histosol in 2010.

Changed economic conditions and rising awareness for nature conservation led to a change in fen use policy in former Eastern Germany. Thus, active dewatering of the study site had ceased by 1990, resulting in water levels near or above the ground surface in winter. However, water levels still dropped to 70 cm below the surface in summer, allowing ongoing peat mineralisation. Eventually, to keep water in the catchment, a loose-rock check dam (low-grade weir) was installed at the catchment outlet in winter 2009/2010. The main goals of this measure were to stop peat decomposition, to recreate a self-regulating ecosystem with peat-forming vegetation and without the need for management, and to create a hydrological protection zone (Succow & Joosten 2001) for the raised bog. It was planned as a low-cost experimental action with low follow-up expenses. The initial plan did not specify any target species, although expansion of *Phragmites australis* as the dominant species was expected for the fen area. Likewise, no adaptive further steps were planned.

The outflow limitation resulted in year-round shallow flooding of most parts of the study area with varying mean annual water levels of 0.51 m, 0.27 m and 0.32 m above ground level in 2011, 2012 and 2013, respectively, with a spatial deviation of around ±0.5 m. In 2009, before permanent inundation, the vegetation was already dominated by helophytic species, i.e. *Phragmites australis*, *Bolboschoenus maritimus*, *Schoenoplectus tabernaemontani* and *Carex acutiformis*, together with abundant remnants of grassland use.

Field sampling
We recorded vegetation annually in late June from 2011 to 2014. Plant species were recorded at 64 circular plots of 1 m radius arranged in an equidistant grid covering an area of 13 ha (Figure 1). The plots were positioned and relocated every year with an RTK-DGPS device allowing for centimetre accuracy of relocation without permanent marking. We estimated species cover and total plant cover values on a percentage scale. The area covered with open water or bare soil was recorded as well. In addition to these data, we used records of two unpublished vegetation surveys of the area from 2010. However, since their research focus was different and the sampling effort in our target area was lower, these data could be used to get an insight into diversity developments but not for mapping.

Aerial imagery and elevation model
Aerial RGB images of the site were acquired annually in late June from 2011. For logistic reasons, the camera platform changed over time. The 2011, 2012 and 2014 images were taken by an aeroplane-based camera system yielding a ground resolution of at least 20 cm. In 2013, a UAV-based camera was used yielding a ground resolution of 3 cm. We used a digital elevation model (DEM) of the site with ground resolution 1 m and vertical precision 1 dm or better, generated from airborne laser scanning data acquired by the surveying authorities in 2007, before the site was rewetted. This allowed us to derive water level information for the whole study area based on measurements from an automated water level logger that was installed at the centre of the site in 2011.

Vegetation classification and map generation
We classified vegetation data using complete-linkage hierarchical clustering based on Bray-Curtis dissimilarity (Legendre & Legendre 1998). The final number of classes was determined by identifying the first break in the explained variance *versus* number of clusters ("elbow method"). Class labels were then specified according to species with highest fidelity (diagnostic species) based on their respective φ-coefficients (Chytrý *et al*. 2002). Each plot was thus assigned to a vegetation class and served as a point for aerial image classification. In more detail, we followed the following procedure for map generation:

1. Image preparation and texture extraction: All images were re-sampled to 20 cm ground resolution for comparability. For each band, we calculated pixel-wise textural measures based on the grey level co-occurrence matrix (GLCM) of a local neighbourhood of 1m. The measures calculated were mean, energy, entropy, correlation, inverse difference moment, inertia (Haralick *et al*. 1973), cluster Shade, cluster Prominence (Conners *et al*. 1984). All resulting layers including the DEM were combined into a single multiband image.

2. Image segmentation. A problem of pixel based image classification approaches is the salt-and-pepper-effect (Yu *et al*. 2006) - neighbouring pixels are classified differently despite belonging to the same classification target due to effects of shadow, varying reflection, leaf senescence etc. The effect increases with increasing image resolution, because single pixels no longer represent the whole spectrum of the classification targets. Such classification results are useless for analysis of patch metrics. To overcome this, groups of connected pixels can be analysed. From the plethora of image segmentation algorithms (Dey *et al*. 2010) we applied the relatively recent mean shift algorithm (Comaniciu & Meer 2002) as proposed for vegetation mapping by Ponti (2013) with a minimum region size of the size of the bounding square around our ground truthing plots (4m²). This is likely to produce an over-segmentation since the vegetation stands in our ecosystem are typically much larger. However, subsequent classification should merge over-segmented areas back together. For the resulting segments, mean, range and standard deviation of all bands were calculated.

3. Classification. Features of image segments intersecting with classified vegetation sampling points were used as training instances for an svm-classifier with a 3rd degree polynomial kernel. Sampling points very close to a segment border were manually removed from the training dataset.

All image processing steps including texture calculations and segmentation were performed with the open source image processing libraries *scikit-image* (van der Walt *et al*. 2014) and *Orfeo toolbox* (Inglada & Christophe 2009) with their python interfaces. For all other statistical analyses we used R (R Core Team 2011) with various additional packages.

Analysis of vegetation development
Vegetation development was analysed on the basis of the pure plot data as well as spatially using the maps produced by the method described above. We applied non-metric multidimensional scaling (NMDS, Shepard 1962) based on Bray-Curtis distances (Faith *et al*. 1987) of vegetation composition between plots to visualise overall changes. Furthermore, we calculated alpha-, gamma-, and beta diversity in terms of effective species numbers at plot scale (Hill 1973, Jost 2007, Tuomisto 2010). These were calculated with the weighting exponent $q = 0$ (species weighted equally) and $q = 1$ (species weighted according to their proportional abundances). To enable comparison of our data with the results of the 2010 studies, we also calculated these measures as averages of 100 subsamples selected randomly from the 2011–2014 datasets ($n = 64$ each) with the same sample size ($n = 28$) as in the 2010 studies. To characterise the changed abiotic conditions we calculated site means of Ellenberg indicator values and the significance of their change, assuming them to be metrically scaled (Diekmann 2003).

From the generated vegetation maps we calculated area proportions of the respective vegetation compartments as well as patch metrics to characterise spatial developments. From the plethora of available landscape and patch metrics that are regularly applied in ecological research (McGarigal & McComb 2011, Walz 2011) we calculated indices representing different aspects of landscape structure (Riitters *et al*. 1995, McGarigal 2006), namely: aggregation index, edge density, patch core area index, mean shape index, and number of patches.

Factors controlling short-term succession
To understand what controls the short-term succession trajectories we modelled vegetation changes from year to year at ecosystem scale using a spatially explicit multinomial logit regression model (Franklin 1995, Augustin *et al*. 2001) based on the vegetation maps. Predictor variables are the vegetation type at a certain pixel in the previous year,

mean water level at that position the previous year, the distance to the nearest edge of the vegetation patch that that includes the pixel (centrality), and the respective interaction terms. Response is the vegetation type found at the same point in space in the current year. Logit regression coefficients are given with respect to symmetric side constraints (Zahid & Tutz 2009), i.e. coefficients are presented with respect not to a certain reference level, but to a median outcome. The calculation is based on 5000 randomly sampled pixels taken from the respective maps. For validation, 5000 other randomly sampled pixels were used.

RESULTS

Vegetation development at plot scale

Within the coastal fen studied, overall plant species (gamma-) richness declined drastically after flooding, with the most rapid developments taking place in the first two years. During the two studies performed in 2010, 46 species were found. In the course of our study with higher sampling effort (64 plots) species richness declined from 37 to 27 between 2011 and 2012, then increased slightly to 29 in 2013 and 33 in 2014. When sub-sampled to the effort level of the 2010 studies (28 plots), total richness was even lower, at 24.8, 19.7, 18.7 and 22.1 in the successive years from 2011 to 2014. We found a similar development at plot (alpha-) scale, with richness declining continuously from 6 to 4.4 species over the period 2010–2014. Gamma decline was more pronounced until 2012, resulting also in a decline of beta richness, but it slightly increased again in 2013 and 2014 (Table 1).

We found a similar development taking species proportional abundances into account ($q = 1$,

Table 1). From 2010 to 2014 abundance weighted gamma diversity declined from 14.4 to 5.6. Alpha diversity was low in all five years, ranging between 2.2 and 3.2 (in 2011). High contrast between richness and diversity of order $q = 1$ indicates low evenness of species distribution throughout the time after inundation, i.e. plots were mostly dominated by one or two species.

To allow direct comparison of permanent plots, in the following we consider only data from our own study covering the years 2011 to 2014 (Figure 2), accepting that the first year after flooding is omitted. Grassland species that are sensitive to high water levels (e.g. *Holcus lanatus*, *Potentilla anserina*, *Trifolium repens*) died back immediately, persisting only at a few locations that are exposed during the course of the year due to higher ground elevation. Species tolerating seasonal inundation that were formerly widely distributed across the area, namely *Agrostis stolonifera* and *Alopecurus geniculatus*, were present until 2011 but then rapidly declined and vanished from most plots. On the other hand, hydrophytic species depending on permanent inundation quickly emerged. *Lemna* spp. appeared within the first year, whereas the appearance of *Ceratophyllum submersum* was delayed until 2012. All submerged and floating helophytes are now present in almost all plots that are permanently inundated (Figure 3). The general successional trajectory towards helophytic/hydrophytic species composition becomes obvious in the NMDS ordination diagram (Figure 4).

Among the dominant emergent macrophytes some consistent patterns turn up. *Phragmites australis* did not expand significantly in frequency from 2011 to 2014. *Schoenoplectus tabernaemontani* and *Bolboschoenus maritimus* had grown in co-occurrence in many plots in 2011 with higher

Table 1. Development of alpha-, gamma- and beta diversity (Hill numbers) with respect to sampling data from 2010 to 2014. The weighting factor q determines how species abundances are taken into account (q = 0 yielding species richness). Note that the 2010 data were not acquired within this study. Numbers in brackets represent results after averaging 100 random subsamples of the 2011–2014 datasets to the number of plots in the 2010 studies.

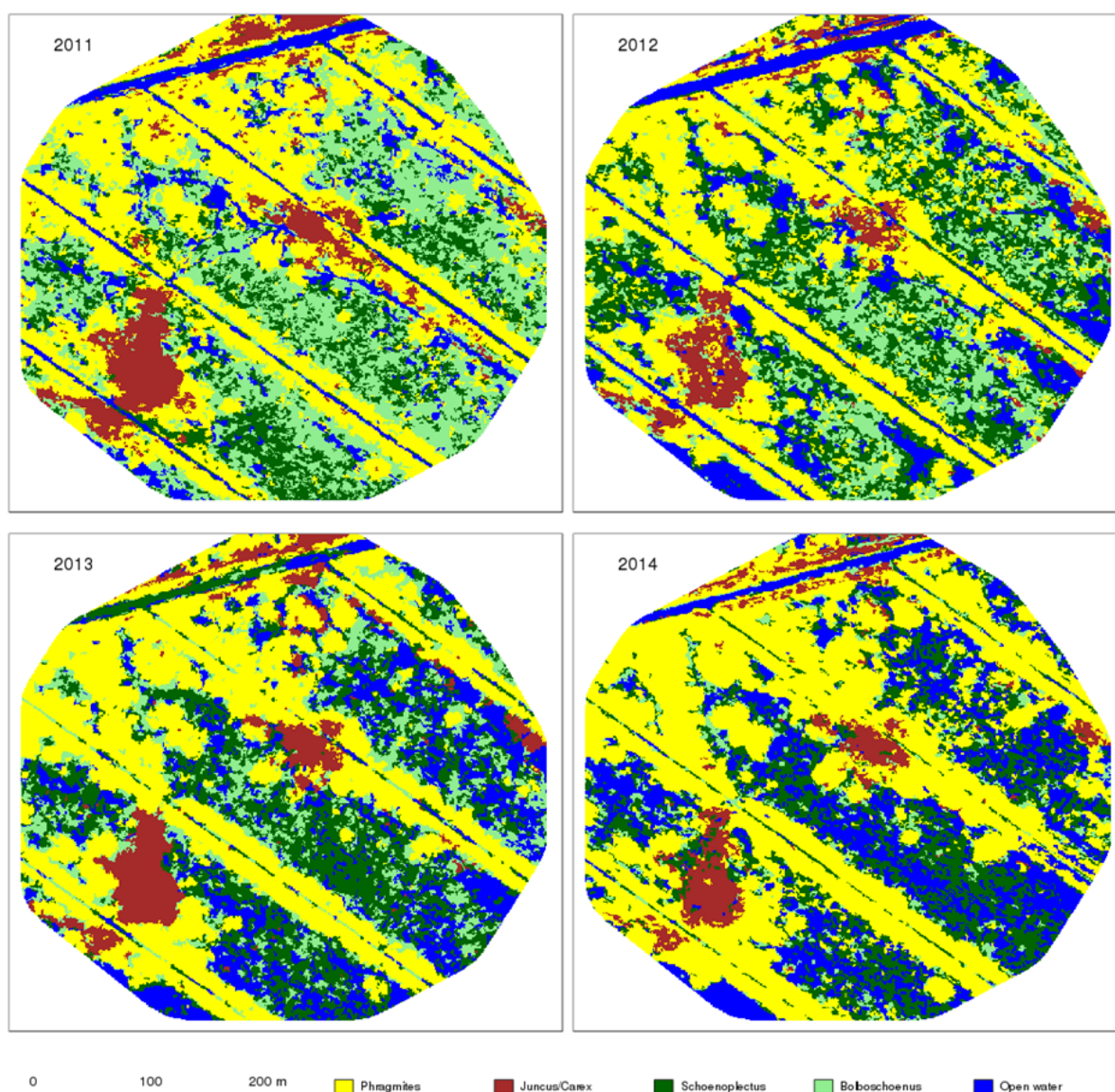|	q = 0			q = 1		
	α	γ	β	α	γ	β
2010 (n=28)	*6.0*	*46*	*7.7*	*2.9*	*14.4*	*5.0*
2011 (n=64)	5.0 (5.0)	37 (24.8)	7.3 (4.8)	3.2 (3.2)	8.0 (7.9)	2.5 (2.5)
2012 (n=64)	4.7 (4.7)	27 (19.7)	5.7 (4.1)	2.5 (2.5)	5.5 (5.2)	2.2 (2.1)
2013 (n=64)	4.4 (4.4)	29 (18.7)	6.6 (4.2)	2.7 (2.7)	5.9 (5.6)	2.2 (2.1)
2014 (n=64)	4.8 (4.7)	33 (22.1)	6.9 (4.6)	2.2 (2.2)	5.6 (5.3)	2.5 (2.4)

Figure 2. Vegetation maps of the study area generated from aerial images and plot-based vegetation data.

abundances of *Bolboschoenus tabernaemontani*. In the following years *Schoenoplectus tabernaemontani* increased in both frequency and abundance whereas *Bolboschoenus maritimus* declined both in frequency and abundance and did not dominate plots anymore.

Mean Ellenberg indicator values (Table 2) generally indicate very wet conditions (F value), marked salt influence (S), sub-oceanic climate (K) and openness of the canopy (L). The changed hydrological conditions are reflected in an increase of the F value from 8.2 in 2010 to almost 11 in later years. The N value tended to increase after 2010, possibly due to the lack of export and decomposing biomass, but this change was not significant.

Vegetation types and their succession patterns
Hierarchical clustering of plot vegetation data revealed five distinctive classes explaining 40.1 % of variance in the dataset. These clusters feature high fidelity and average cover values (Table 3) of one dominant emergent macrophyte in four cases and open water, optionally vegetated by hydrophytes, in the fifth case. Whereas *Phragmites australis* most often dominates plots where it occurs, co-occurrence of *Bolboschoenus maritimus* and *Schoenoplectus tabernaemontani* is quite common, and the cluster assignment is thus controlled by their respective abundance. In the following, we refer to the clusters by the following names: *Phragmites*, *Schoenoplectus*,
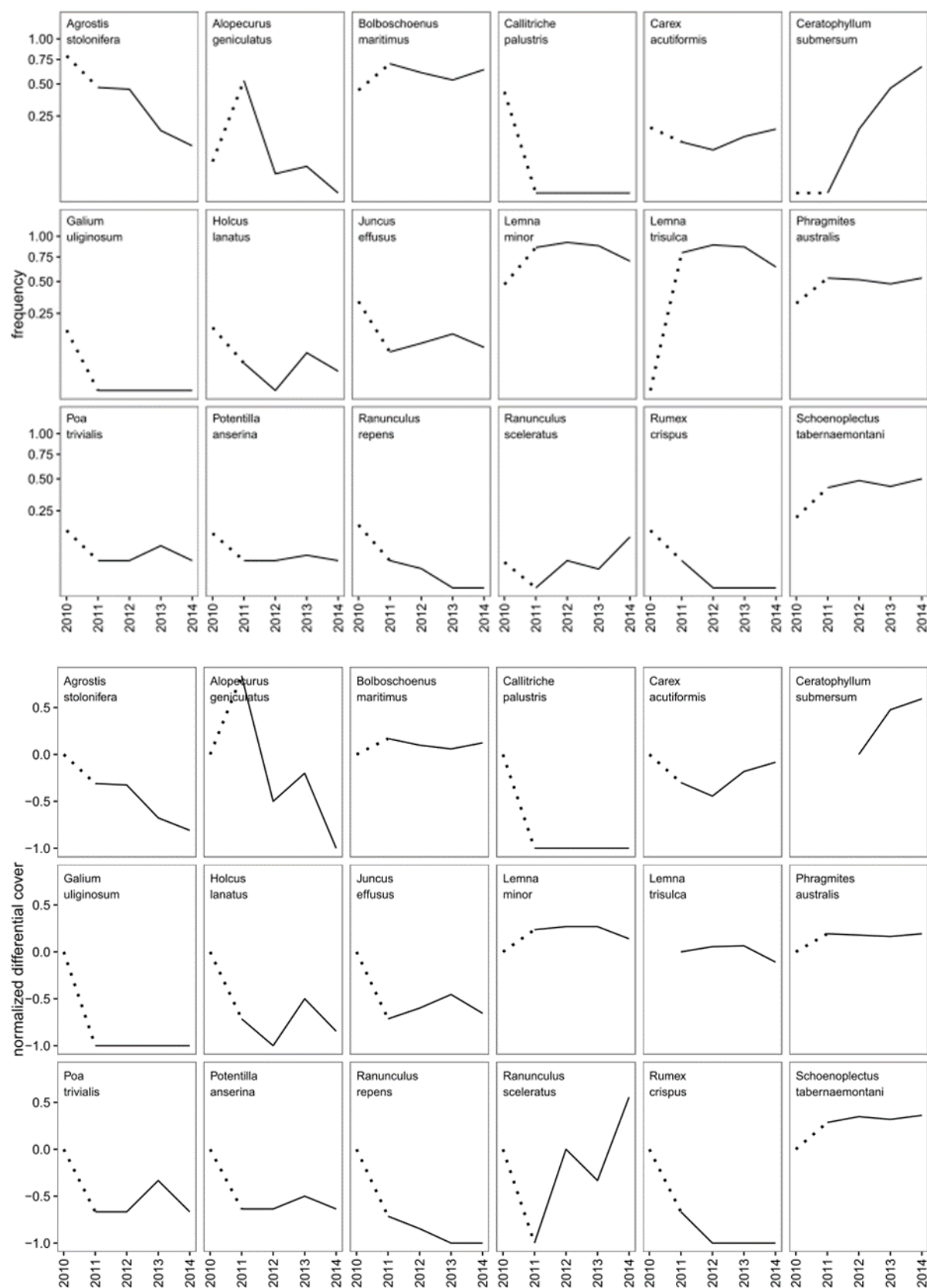
Figure 3. Development of species frequencies (a) and abundances (b) from 2011 to 2014 (normalised to the value in the year of first occurrence). Only the twelve species that underwent the greatest changes are shown.
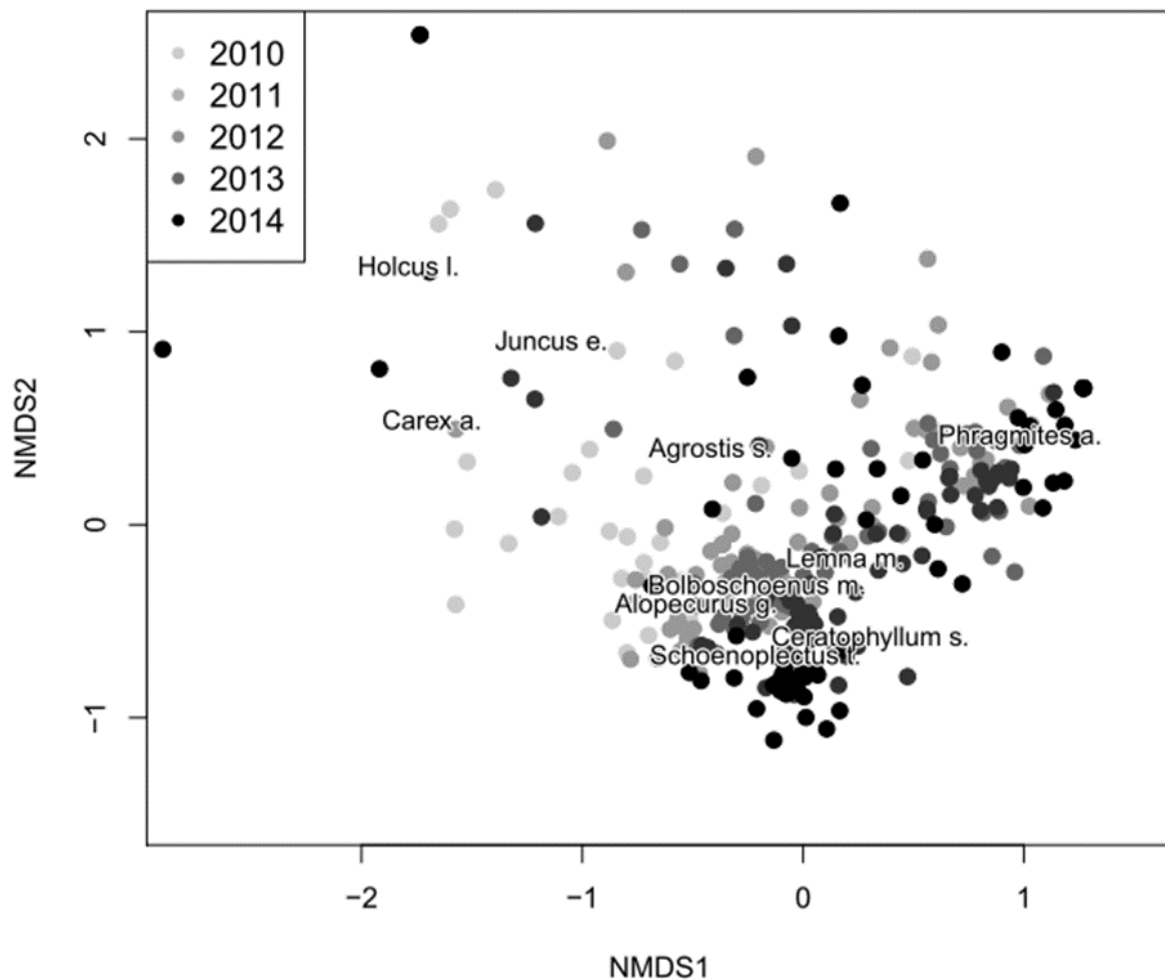
Figure 4. NMDS-ordination (stress 0.17) based on Bray-Curtis dissimilarities of vegetation records from 2010 to 2014.

Table 2. Community weighted mean Ellenberg indicator values throughout the site (standard deviation in brackets) in the course of the years. Significance of differences tested with t-test. Both imply the assumption of the indicator values being metrically scaled.

year	Indicator value						
	N	F	L	R	T	K	S
2010	5.5 (0.7)[a]	8.2 (1.8)[a]	7.5 (0.4)[a]	6.5 (1.8)[a]	5.5 (0.5)[a]	4.1 (0.9)[a]	0.6 (0.6)[a]
2011	6.1 (0.6)[ab]	9.9 (1.0)[ab]	7.6 (0.5)[a]	7.1 (1.0)[a]	5.7 (0.5)[a]	3.6 (0.7)[a]	1.1 (0.7)[a]
2012	5.8 (0.7)[a]	10.7 (0.9)[b]	7.2 (0.3)[ab]	7.2 (0.9)[a]	5.7 (0.4)[a]	3.4 (0.6)[a]	0.8 (0.5)[a]
2013	6.0 (0.8)[ab]	10.9 (0.9)[b]	7.0 (0.3)[b]	7.3 (0.9)[a]	5.9 (0.5)[a]	3.4 (0.6)[a]	0.8 (0.6)[a]
2014	6.8 (0.9)[b]	10.5 (1.0)[c]	6.9 (0.4)[b]	7.5 (1.0)[a]	6.0 (0.8)[a]	4.1 (1.1)[a]	0.5 (0.7)[a]

Table 3. Diagnostic species derived from vegetation clustering with fidelity (a) and cover values (b) for each vegetation type. The number of plots classified to each vegetation type throughout the years is given in (c).

	Vegetation type				
	Phragmites	*Schoeno-plectus*	Open water	*Juncus/ Carex*	*Bolbo-schoenus*
a) Fidelity (φ coefficient)					
Phragmites australis	**0.8**	-0.4	-0.3	-0.1	-0.3
Schoenoplectus tabernaemontani	-0.6	**0.6**	0	-0.2	0.2
Open water	-0.5	0.4	**0.2**	-0.2	0.3
Juncus effusus	-0.1	-0.1	0	**0.6**	-0.1
Poa trivialis	-0.1	-0.1	-0.1	**0.6**	-0.1
Potentilla anserina	-0.2	-0.1	-0.1	**0.6**	-0.1
Holcus lanatus	-0.1	-0.1	-0.1	**0.5**	-0.1
Carex hirta	-0.1	-0.1	0	**0.4**	-0.1
Bolboschoenus maritimus	-0.4	0.2	0.1	-0.3	**0.4**
b) Average cover (%)					
Phragmites australis	**76.3**	0.9	0.2	4	1.9
Schoenoplectus tabernaemontani	0.6	**34**	1.3	2.1	5
Open water	16	56.2	**88.8**	13	63.3
Juncus effusus	0.5	0	0.2	**18.5**	0
Poa trivialis	0	0	0	**1.9**	0
Potentilla anserina	0	0	0	**0.6**	0
Holcus lanatus	0	0	0	**2.2**	0
Carex hirta	0	0	0	**0.3**	0
Bolboschoenus maritimus	1.9	6.5	1.9	0.1	**26.5**
c) Number of plots					
2011	25	11	4	5	19
2012	26	11	9	5	13
2013	27	18	5	7	10
2014	29	17	8	6	4
Complete dataset	107	57	26	23	46

Bolboschoenus, *Juncus*/*Carex,* and "open water". Aerial images were classified (as described in Methods) according to these clusters (Figure 2). The following analyses and the reported results refer to the maps thus generated.

The five vegetation types distinguished were unevenly distributed along the altitude gradient (Figure 5). At altitudes below 0.2 m a.s.l. open water covered 46 % of the total area in 2011, whereas its cover ranged only between 5 % and 20 % at higher altitudes. *Phragmites* stands had their largest relative cover at 0.4–0.6 m a.s.l. but still contributed reasonable cover at higher and lower altitudes. *Bolboschoenus* and *Schoenoplectus* stands had noteworthy relative cover only at altitudes below 0.6 m a.s.l., whereas *Juncus*/*Carex* stands occupied only areas above 0.4 m a.s.l. The latter play a minor role at our site because the fraction of the study area at these altitudes is relatively small.

During the period of study, *Bolboschoenus* stands showed a strong spatial decline whereas open water areas increased continuously (Figure 6). This contrasts with the unclassified plot data, which do not indicate a rapid decrease of *Bolboschoenus*.
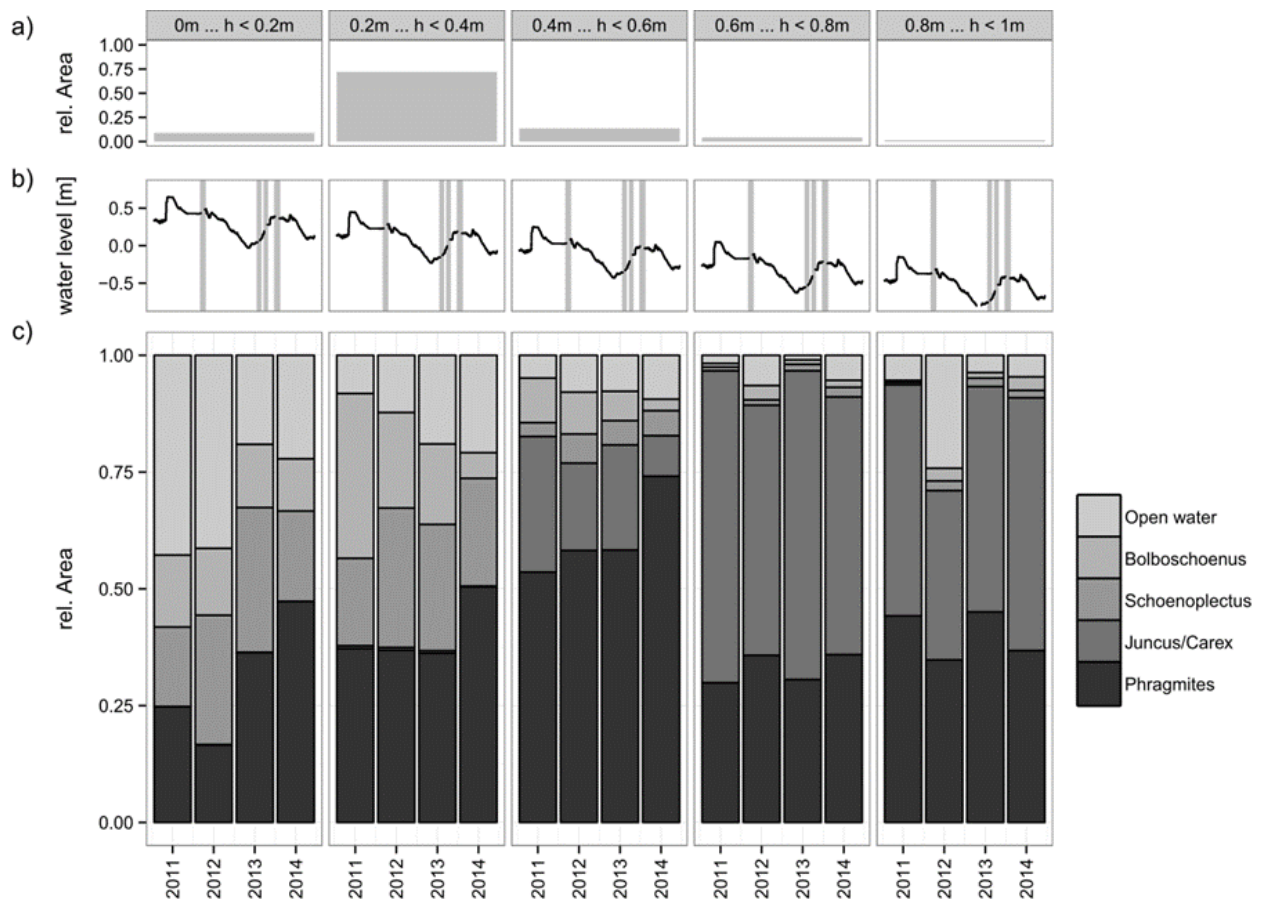
Figure 5. a) Distribution of surface altitude classes (metres above sea level; m a.s.l.) on the site. Altitudes above 1 m a.s.l. are not shown because they account for less than 1 % of the total area. b) Development of mean water levels within altitude classes. The vertical grey lines or rectangles indicate periods of ice cover. c) Development of the area proportions of vegetation types with respect to altitude above sea level.
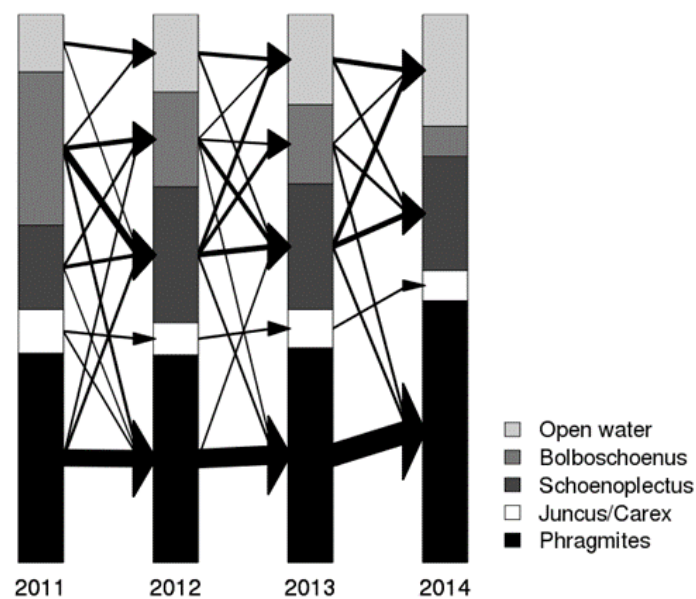

Figure 6. Succession trajectories for the five vegetation classes in the second to fifth years after rewetting. Arrows are scaled according to the area proportions of the respective paths. Only arrows representing more than 5 % of the total area are drawn.

However, its relative abundance compared to other species, especially *Schoenoplectus,* decreased. In other words, despite still being present where it was before, it was no longer dominant in later years (Table 3). The other classes distinguished changed only a little, with both *Schoenoplectus* and *Phragmites* stands increasing slightly and *Juncus/Carex* stands remaining little changed.

Looking at the specific succession trajectories it is notable that both *Phragmites* and *Juncus*/*Carex* stands, as well as areas of open water, are relatively stable (Figure 6). Relative conversion rates between the *Bolboschoenus* and the *Schoenoplectus* type are high. The increase of open water can be mostly attributed to conversions of *Schoenoplectus* and *Bolboschoenus* stands, caused by dieback or very low shoot abundance in these two species. On the other hand, areas of open water were more likely to be recolonised by these species than by *Phragmites australis*.

There was no consistent temporal trend in the selected geometrical properties for any of the vegetation types (Figure 7). *Phragmites* patches showed a tendency to merge into bigger contiguous and compact areas, expressed by increasing aggregation and core area indices and decreasing patch number and edge density from 2011 to 2014. In contrast, *Bolboschoenus* patches got smaller and disaggregated resulting in lower edge density and aggregation index.

Consistent for all patch classes is the reduction of shape index (expressing the relationship between actual patch perimeter and the perimeter of a same-sized patch of maximum compactness) from 2011 to 2012 followed by a recovery from 2012 to 2013. The decline in 2012 can be linked to an exceptionally high water level late in the 2011 growing season, caused by a heavy rainfall event. In contrast, 2012 was an exceptionally dry year.

Spatially explicit succession models of the year-to-year development had relatively high Pseudo-R² values *sensu* McFadden of more than 0.35 for each year. They show some consistent general trends accompanied by effects that change during the years

(Table 4). According to the model coefficients, there is a high probability that pixels assigned to the *Phragmites*, *Juncus/Carex* or open water classes will remain in one of these (coefficient positive), as already suggested by Figure 5. Centrality of a pixel within patches of these classes (d_0), i.e. its position in the core area of a patch, made it more likely to remain in these classes. Higher water levels made it more likely for a pixel to end up in patches of *Bolboschoenus* or *Schoenoplectus*. If the influence of water level is removed, however, we find much less significant and less important coefficients for the odds ratios involving these two classes, suggesting that there is a high uncertainty about the development within patches of these types.

Examples of inconsistencies between periods can also be found; the effects of the predictors on the odds ratios of *Phragmites* varied throughout the years. For example, colonisation of core areas of other vegetation types by *Phragmites* was less likely from 2012 to 2013 than in other periods (coefficients for interaction terms with d_0 negative). Accordingly, deep water areas ($V_{0\_Open\_water} \times W_0$) were likely to remain in the 2011–2012 and 2013–2014 periods, but not in 2012–2013. More generally, significant effects were found for year-to-year development of several predictors incorporating water level, but not for the others. Again, this coincides with the general water level trend, as seasonal water levels varied remarkably and were lowest in 2012.

DISCUSSION

Vegetation development
Typically, restoration projects in peatlands accomplish rewetting in one single step. In contrast to this the water levels in the site were increased moderately in 1990 and, thus, had been relatively high for 18 years before complete inundation, with partial inundation in winter months. Thus, vegetation prior to this rewetting project was not a typical meadow community, but already comprised helophytic species like *Bolboschoenus maritimus*,
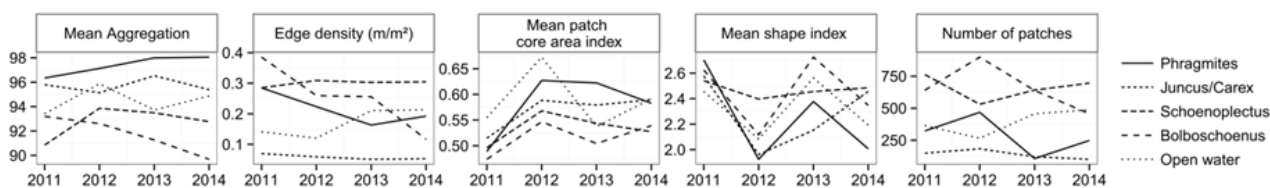

Figure 7. Development of geometrical properties of vegetation patches in the study area by class measure from 2011 to 2014.

Schoenoplectus tabernaemontani and *Phragmites australis.* Thus, even in 2010, average Ellenberg moisture (F) values of the species present were high (8.2). Furthermore, many of these species are salt-tolerant and indicate legacies of marine influence.

The F value increased to almost 11 in later years, indicating permanent inundation. The flooding led to rapid change in vegetation composition associated with a dramatic decline of plant species diversity. Remnants of grassland communities and species that are not adapted to year-round flooding vanished within two vegetation periods on almost all plots, among them *Holcus lanatus*, *Trifolium repens*, *Ranunculus repens* and *Potentilla anserina*. No new species appeared in the area besides the hydrophyte *Ceratophyllum submersum*. This dieback and the cessation of mowing might have caused in increase in nutrient availability for the remaining species. Indeed, there was a minor increase in the mean Ellenberg N value, but this change was not significant (Table 2). Likewise, there was no marked change in the other indicator values.

The initial stage of secondary succession was a mosaic of water with floating macrophytes and reed-like vegetation. The latter may serve as starting point for clonal expansion, so that a faster development of closed-canopy reed-like vegetation after flooding than known from other rewetting projects (Zerbe *et al.* 2013) could have been expected.

On the one hand, water is an important dispersal pathway for diaspores of many temperate wetland species. But even if adult individuals are adapted to frequent or permanent flooding, most of these species require exposed conditions or at least shallow water conditions for seed germination and establishment of saplings (Coops & Van der Velde 1995, Coops *et al.* 2004). This also holds for the dominant species in this study: *Bolboschoenus maritimus*, *Schoenoplectus tabernaemontani* (Clevering 1995, Clevering & Hundscheid 1998) and *Phragmites australis* (Engloner 2009). Therefore, clonal dispersal is the predominating process in the establishment of reed vegetation under flooded conditions. Thus, the seedbank in the area is unlikely to be a controlling

Table 4. Logit regression coefficients for multinomial succession models for year-to-year vegetation change. Coefficients are shown with respect to symmetric side constraints (Zahid & Tutz 2009). Significant positive values (white background) indicate a positive effect of the respective predictors on the odds ratio, negative values (dark grey) indicate a negative effect. V_0: Vegetation at sample point in previous season, d_0: distance to nearest different vegetation unit in previous season, W_0: Water level in previous vegetation period. Validation accuracies are 56 %, 57 %, 65 %; McFadden's pseudo R^2 values are 0.32, 0.37, 0.46 for the respective models. P-values: ***: $p < 0.001$; **: $p < 0.01$; *: $p < 0.05$; ': $p < 0.1$.

	Phragmites			Juncus/Carex			Schoenoplectus			Bolboschoenus			Open water		
	2011/ 2012	2012/ 2013	2013/ 2014	2011/ 2012	2012/ 2013	2013/ 2014	2011/ 2012	2012/ 2013	2013/ 2014	2011/ 2012	2012/ 2013	2013/ 2014	2011/ 2012	2012/ 2013	2013/ 2014
$V_{0\_Phragmites}$	1.3***	1.6***	2.6***			-0.6'	-0.4*			-0.4*				-1.0**	-1.2***
$V_{0\_Juncus/Carex}$	1.0***	1.1***	1.3***	0.9***	0.6*					-0.6*	-1.0*	-0.8*	-1.0*		-0.7*
$V_{0\_Schoenoplectus}$			0.6**			-1.6**		0.3'	1.1***	0.8**		-0.6*	-1.2**	0.4**	0.4*
$V_{0\_Bolboschoenus}$			1.1***	0.6'					0.7*			-1.0**		-0.4'	
$V_{0\_Open\_water}$		0.8**		-2.7*	-0.9*	-1.2*	1.0**	-0.7**	0.8***			-0.8*	1.0**	0.7***	0.8***
$V_{0\_Phragmites} \times d_0$	0.6***	0.8***	0.4***					-0.2'	-0.3'			-0.7'	-0.7***	-0.5*	0.5***
$V_{0\_Juncus/Carex} \times d_0$	0.5'	-0.7**	-0.3**	0.6'	0.4'	0.1**			0.1**		0.7*				
$V_{0\_Schoenoplectus} \times d_0$	0.3*	-0.4**	-0.6***								0.3*			0.3*	0.2*
$V_{0\_Bolboschoenus} \times d_0$		-0.7***					0.5***				0.3*		-0.2*	0.3*	
$V_{0\_Open\_water} \times d_0$		-1.2***					0.3***						0.7*	0.4***	0.5**
$V_{0\_Phragmites} \times W_0$	-2.3***	-2.4***	1.3'	-7.8***	-11.5***	-8.2***	4.5***	5.5***	4.5***	3.4***	2.4*		2.1*	5.9***	
$V_{0\_Juncus/Carex} \times W_0$	3.1**	-5.4***	-2.3'		-8.2***	-5.9***	6.7**			5.4*					6.3*
$V_{0\_Schoenoplectus} \times W_0$	2.8'	5.2***	4.6***	-14.3***	-11.3***	-14.7***	4.0**	3.8***	1.9'		2.5*	4.0**	6.1***		4.1***
$V_{0\_Bolboschoenus} \times W_0$	3.2**	3.3**		-13.2***	-10.7***	-19.5***	5.4***	3.7***	4.3***	3.0**		8.6***		2.8*	4.3**
$V_{0\_Open\_water} \times W_0$				-7.3**	-7.2**	-10.3***	2.1*	5.4***	2.8**		2.2**	6.4***	2.0*		2.3*

factor for species distribution. Since the mentioned species have differing optimum water levels and vary in their tolerance to water level fluctuations (Clevering 1995, Clevering & Hundscheid 1998, Pagter *et al.* 2005), long-term succession in the site is likely to be controlled mainly by water level, both spatially as a result of the uneven surface and temporally as a result of year-to-year changes in water supply.

A notable effect was the strong relative decline in *Bolboschoenus maritimus*. Although its frequency across the plots did not change substantially (Figure 3), its relative abundance decreased, resulting in a decreasing number of plots classified as the *Bolboschoenus* type (Table 3). Accordingly, the spatial extent of this vegetation type decreased. This demonstrates that classification approaches can reveal developments that would remain undetected otherwise. Despite being a shoreline helophyte, permanent inundation above 30 cm seems to hamper vegetative expansion of *Bolboschoenus maritimus* (Clevering & Hundscheid 1998). The high water level in 2011 promoted this development, as shown in the respective significant positive model coefficients. The core area of *Bolboschoenus* stands, expressed in the predictor $V_{0\_Bolboschoenus} \times d_0$, had no pronounced positive effect on their persistence, nor on the formation of other patches, indicating that the plants in these patches either died back because of the inundation or that *Bolboschoenus* was outcompeted by other species. Another important effect that plays a role in the spatial instability of *Bolboschoenus* and *Schoenoplectus* stands is their tendency to form Plavs (Pallis 1916), floating islands of emergent macrophytes that are not spatially fixed.

Phragmites australis showed high tolerance of varying water table levels and thus spread during the course of the study. This tolerance has been extensively observed both *in situ* and in experiments (Coops & Van der Velde 1995, Blanch *et al.* 1999, Shay *et al.* 1999, Pagter *et al.* 2005). Mechanical disturbance such as grazing and trampling by heavy animals, to which *Phragmites* shows high sensitivity (Sweers *et al.* 2013), rarely occurs in the site. Thus, existing formations of *Phragmites* display high stability and changes in the spatial extent of reed belts happen mainly at their edges, either as expansion or as dieback and thus replacement by open water. Intrusion of other emergent macrophytes seems to be impeded by competitive exclusion.

Generally, the spatial development of *Phragmites* and open water stands was more consistent throughout the years and was more precisely predictable than that of the *Bolboschoenus* and *Schoenoplectus* types. This might be partially attributable to the less-clear separation of these two classes resulting in uncertainties in assignments on the maps and in subsequent analyses.

The interplay of clonal dispersal and decline, possibly due to mechanical effects of turbulence and surface waves, ice cover, herbivory, or lack of regeneration, are those seen on shorelines of lakes and rivers especially under fluctuating water levels (Spence 1982, Coops & Van der Velde 1996). Varying water levels are known to promote the persistence of a mosaic of different vegetation types (Keddy & Reznicek 1986) and thus floral and faunal diversity. Indeed, we found pronounced compaction of vegetation patches expressed in their geometrical properties from 2011 to 2012 (high water level, causing partial dieback and low shoot abundance in *Bolboschoenus maritimus* and *Schoenoplectus tabernaemontani*), but an increase in the irregularity of patches phasing out again from 2012 to 2013 (low water level, allowing for clonal expansion).

Developments with respect to restoration targets
The main goal of the rewetting measure implemented was to restore major ecosystem functions and processes, in particular retention of carbon and nutrients due to peat formation. Peat formation as the result of a long-term excess of productivity over decomposition requires permanently anaerobic conditions and the presence of plant species with peat-forming potential (Moore 1989). The first requirement was directly met with permanent inundation, which was achievable at low cost under the prevalent polder-like topographic conditions. Our results indicate that the second requirement might be met as well in the long term, since *Phragmites australis*, as a species with high productivity and peat-forming potential (Zerbe *et al.* 2013), showed high stability and slight increase.

With all necessary precaution in view of the short observation period of four years in the initial stage of succession after inundation, we can anticipate various developments in the near future. First, *Phragmites australis* and *Schoenoplectus tabernae-montani* are likely to remain as the major emergent macrophytes. Common reed patches are likely to expand further, although relatively slowly. Open water areas with floating and submerged macrophytes will probably persist and increase in years with higher water supply. Intrusion of other species (e.g. *Typha* spp. or *Glyceria* spp.) will happen, if at all, mainly by clonal dispersal from the margins of the study site and is likely, therefore, to occur relatively slowly. As these species have lower peat-forming potential than *Phragmites australis* (Succow & Joosten 2001), this can be regarded

positively in relation to the target of restoring carbon retention.

The patterns of succession we observed in this early stage after rewetting of a coastal brackish fen are similar to those observed in the initial phases of other rewetting projects in freshwater ecosystems (Timmermann *et al*. 2006, Zerbe *et al*. 2013).

The results indicate that the reinstatement of major ecosystem functions in degraded fens is a realistic goal that can be reached at low cost in certain situations, although some follow-up interventions may be necessary. To promote faster development of peat-forming vegetation and ongoing peat accumulation, it would be necessary to ensure long-term shallow inundation without prolonged water table drawdown (allowing peat decomposition) or high-water periods, with gradual readjustment following the onset of paludification.

Conversely, the development of later successional stages with higher species diversity and the typical flora of undisturbed fens is likely to take decades. Generally, approaches focusing on particular target species or community types would require expensive ongoing adaptive interventions and manipulations, such as topsoil removal and seed transfer (Klimkowska *et al*. 2010). With regard to the highly degraded nature of our site and many of the fens in the region, it is doubtful that the re-establishment of typical fen flora would ever be a realistic goal.

Methodological aspects

The approach of using low spectral but high spatial resolution aerial images in combination with permanent plot data proved to be suitable for mapping a species-poor wetland. Our approach of vegetation classification and image processing delivered reasonable results with average classification accuracies of around 70 % (data not shown). This is lower than accuracies achievable with multispectral images (Frick *et al*. 2011) but still offers usable results. We have to admit that accuracy may have benefited from the small number of vegetation types in the study area. Lower class accuracies were associated with low occurrence of these classes and, thus, the small amounts of training area. The high ground resolution of 20 cm is a clear advantage of airborne images over satellite data, promoting both classification quality and usability in short-term vegetation monitoring. Spatial developments like the ones reported here could hardly be addressed with plot-based data only.

Thus, if the task is monitoring of vegetation that is mostly dominated by patches of a few mono- or co-dominant species, a spatially explicit year-to-year analysis based on low spectral/high spatial resolution aerial imagery can yield valuable insights about short-term and small-scale processes following restoration measures that could not be generated from monitoring plots alone.

REFERENCES

Augustin, N.H., Cummins, R.P. & French, D.D. (2001) Exploring spatial vegetation dynamics using logistic regression and a multinomial logit model. *Journal of Applied Ecology*, 38, 991–1006.

Bakker, J.P., Olff, H., Willems, J.H. & Zobel, M. (1996) Why do we need permanent plots in the study of long-term vegetation dynamics? *Journal of Vegetation Science*, 7, 147–156.

Blanch, S.J., Ganf, G.G. & Walker, K.F. (1999) Tolerance of riverine plants to flooding and exposure indicated by water regime. *Regulated Rivers: Research & Management*, 15, 43–62.

Chytrý, M., Tichý, L., Holt, J. & Botta-Dukát, Z. (2002) Determination of diagnostic species with statistical fidelity measures. *Journal of Vegetation Science*, 13, 79–90.

Clevering, O.A. (1995) Germination and seedling emergence of *Scirpus lacustris* L. and S*cirpus maritimus* L. with special reference to the restoration of wetlands. *Aquatic Botany*, 50, 63–78.

Clevering, O.A. & Hundscheid, M.P. (1998) Plastic and non-plastic variation in growth of newly established clones of *Scirpus* (*Bolboschoenus*) *maritimus* L. grown at different water depths. *Aquatic Botany*, 62, 1–17.

Colomina, I. & Molina, P. (2014) Unmanned aerial systems for photogrammetry and remote sensing: A review. *ISPRS Journal of Photogrammetry and Remote Sensing*, 92, 79–97.

Comaniciu, D. & Meer, P. (2002) Mean shift: A robust approach toward feature space analysis. *IEEE Transactions on Pattern Analysis and Machine Intelligence*, 24, 603–619.

Conners, R.W., Trivedi, M.M. & Harlow, C.A. (1984) Segmentation of a high-resolution urban scene using texture operators. *Computer Vision,*

Graphics, and Image Processing, 25, 273–310.

Coops, H. & Van der Velde, G. (1995) Seed dispersal, germination and seedling growth of six helophyte species in relation to water-level zonation. *Freshwater Biology*, 34, 13–20.

Coops, H. & Van der Velde, G. (1996) Effects of waves on helophyte stands: mechanical characteristics of stems of *Phragmites australis* and *Scirpus lacustris*. *Aquatic Botany*, 53, 175–185.

Coops, H., Vulink, J.T. & Van Nes, E.H. (2004) Managed water levels and the expansion of emergent vegetation along a lakeshore. *Limnologica - Ecology and Management of Inland Waters*, 34, 57–64.

Dey, V., Zhang, Y. & Zhong, M. (2010) A review on image segmentation techniques with remote sensing perspective. In: Wagner, W. & Székely, B. (eds.) *ISPRS Technical Commission VII Symposium: 100 Years ISPRS Advancing Remote Sensing Science*, 31–42. International Society for Photogrammetry and Remote Sensing (ISPRS) Archives, Volume XXXVIII, Part 7A. Online at: http://www.isprs.org/proceedings/XXXVIII/part 7/a/pdf/31_XXXVIII-part7A.pdf, accessed 03 Apr 2017.

Diekmann, M. (2003) Species indicator values as an important tool in applied plant ecology - a review. *Basic and Applied Ecology*, 506, 493–506.

Ehrenfeld, J.G. (2000) Defining the limits of restoration: The need for realistic goals. *Restoration Ecology*, 8, 2–9.

Engloner, A.I. (2009) Structure, growth dynamics and biomass of reed (*Phragmites australis*) – A review. *Flora - Morphology, Distribution, Functional Ecology of Plants*, 204, 331–346.

Faith, D.P., Minchin, P.R. & Belbin, L. (1987) Compositional dissimilarity as a robust measure of ecological distance. *Vegetatio*, 69, 57–68.

Franklin, J. (1995) Predictive vegetation mapping: geographic modelling of biospatial patterns in relation to environmental gradients. *Progress in Physical Geography*, 19, 474–499.

Frick, A., Steffenhagen, P., Zerbe, S., Timmermann, T. & Schulz, K. (2011) Monitoring of the vegetation composition in rewetted peatland with iterative classification of satellite imagery. *Fotogrammetrie, Fernerkundung, Geoinformation*, 2011, 109–120.

Haralick, R.M., Shanmugam, K. & Dinstein, I.H. (1973) Textural features for image classification. *IEEE Transactions on Systems, Man and Cybernetics*, 3, 610–621.

Hill, M.O. (1973) Diversity and evenness: a unifying notation and its consequences. *Ecology*, 54, 427–432.

Holden, J., Chapman, P. & Labadz, J. (2004) Artificial drainage of peatlands: hydrological and hydrochemical process and wetland restoration. *Progress in Physical Geography*, 28, 95–123.

Hoogland, T., van den Akker, J.J.H. & Brus, D.J. (2012) Modeling the subsidence of peat soils in the Dutch coastal area. *Geoderma*, 171–172, 92–97.

Inglada, J. & Christophe, E. (2009) The Orfeo Toolbox remote sensing image processing software. In: *2009 IEEE International Geoscience and Remote Sensing Symposium (IGARSS 2009)*, 3113–3116 (Vol. 4, pp. IV-733).

Jost, L. (2007) Partitioning diversity into independent alpha and beta components. *Ecology*, 88, 2427–2439.

Keddy, P.A. & Reznicek, A.A. (1986) Great Lakes vegetation dynamics: the role of fluctuating water levels and buried seeds. *Journal of Great Lakes Research*, 12, 25–36.

Klimkowska, A., van Diggelen, R., Bakker, J.P. & Grootjans, A.P. (2007) Wet meadow restoration in Western Europe: a quantitative assessment of the effectiveness of several techniques. *Biological Conservation*, 140, 318–328.

Klimkowska, A., van Diggelen, R., Grootjans, A.P. & Kotowski, W. (2010) Prospects for fen meadow restoration on severely degraded fens. *Perspectives in Plant Ecology, Evolution and Systematics*, 12, 245–255.

Klötzli, F. & Grootjans, A.P. (2001) Restoration of natural and semi-natural wetland systems in central Europe: progress and predictability of developments. *Restoration Ecology*, 9, 209–219.

Koebsch, F., Glatzel, S., Hofmann, J., Forbrich, I. & Jurasinski, G. (2013) CO_2 exchange of a temperate fen during the conversion from moderately rewetting to flooding. *Journal of Geophysical Research: Biogeosciences*, 118, 940–950.

Legendre, P. & Legendre, L. (1998) *Numerical Ecology*. Second edition, Elsevier, Amsterdam, 852 pp.

McGarigal, K. (2006) Landscape pattern metrics. In: El-Shaarawi, A.H. & Piegorsch, W.W. (eds.) *Encyclopedia of Environmetrics*. Second edition, John Wiley & Sons, Chichester. Online at: http://dx.doi.org/10.1002/9780470057339.val006

McGarigal, K. & McComb, W.C. (2011) Relationships between landscape structure and breeding birds in the Oregon Coast Range. *Ecological Monographs*, 65, 235–260.

Moore, P.D. (1989) The ecology of peat-forming processes: a review. *International Journal of Coal Geology*, 12, 89–103.

MLUV (2009) *Konzept zum Schutz und zur Nutzung der Moore* (*Programme for the Protection and Use of Mires*). Ministerium für Landwirtschaft, Umwelt und Verbraucherschutz Mecklenburg-Vorpommern, Schwerin, 107 pp. (in German). Online at: http://service.mvnet.de/_php/download.php? datei_id=11159, accessed 03 Apr 2017.

Pagter, M., Bragato, C. & Brix, H. (2005) Tolerance and physiological responses of *Phragmites australis* to water deficit. *Aquatic Botany*, 81, 285–299.

Pallis, M. (1916) The structure and history of Plav: the floating fen of the delta of the Danube. *Botanical Journal of the Linnean Society*, 43, 233–290.

Patzelt, A., Wild, U. & Pfadenhauer, J. (2001) Restoration of wet fen meadows by topsoil removal: vegetation development and germination biology of fen species. *Restoration Ecology*, 9, 127–136.

Pfadenhauer, J. & Grootjans, A. (1999) Wetland restoration in Central Europe: aims and methods. *Applied Vegetation Science*, 2, 95–106.

Ponti, M.P. (2013) Segmentation of low-cost remote sensing images combining vegetation indices and mean shift. *IEEE Geoscience and Remote Sensing Letters* 10, 67–70.

R Core Team (2011) *R: A Language and Environment for Statistical Computing*. R Foundation for Statistical Computing, Vienna. Online at: http://www.R-project.org

Richert, M., Dietrich, O., Koppisch, D. & Roth, S. (2000) The influence of rewetting on vegetation development and decomposition in a degraded fen. *Restoration Ecology*, 8, 186–195.

Riitters, K.H., O'Neill, R.V., Hunsaker, C.T., Wickham, J.D., Yankee, D.H., Timmins, S.P., Jones, K.B. & Jackson, B.L. (1995) A factor analysis of landscape pattern and structure metrics. *Landscape Ecology*, 10, 23–39.

Rosenthal, G. (2003) Selecting target species to evaluate the success of wet grassland restoration. *Agriculture, Ecosystems & Environment*, 98, 227–246.

Rosenthal, G. (2006) Restoration of wet grasslands - Effects of seed dispersal, persistence and abundance on plant species recruitment. *Basic and Applied Ecology*, 7, 409–421.

Roth, S., Seeger, T., Poschlod, P., Pfadenhauer, J. & Succow, M. (1999) Establishment of helophytes in the course of fen restoration. *Applied Vegetation Science*, 2, 131–136.

Scheller, W. & Voigtländer, U. (1996) *Pflege- und Entwicklungsplan für das Naturschutzgebiet "Heiligensee und Hütelmoor"* (*Development Plan for the Nature Reserve "Heiligensee und Hütelmoor"*). Consultancy report on behalf of the Ministry for Agriculture and Nature Protection, Mecklenburg-Western Pomerania. Salix-Büro für Landschaftsplanung, Waren, 135 pp. (in German).

Schrautzer, J., Sival, F., Breuer, M., Runhaar, H. & Fichtner, A. (2013) Characterizing and evaluating successional pathways of fen degradation and restoration. *Ecological Indicators*, 25, 108–120.

Shay, J.M., de Geus, P.M. & Kapinga, M.R. (1999) Changes in shoreline vegetation over a 50-year period in the Delta Marsh, Manitoba in response to water levels. *Wetlands*, 19, 413–425.

Shepard, R.N. (1962) The analysis of proximities: Multidimensional scaling with an unknown distance function. I. *Psychometrika*, 27, 125–140.

Spence, D. (1982) The zonation of plants in freshwater lakes. *Advances in Ecological Research*, 12, 37–125.

Succow, M. & Joosten, H. (eds.) (2001) *Landschaftsökologische Moorkunde* (*Peatlands from a Landscape Ecological Perspective*). Second edition, Schweizerbart'sche Verlagsbuchhandlung, Stuttgart, 622 pp. (in German).

Sweers, W., Horn, S., Grenzdörffer, G. & Müller, J. (2013) Regulation of reed (*Phragmites australis*) by water buffalo grazing: use in coastal conservation. *Mires & Peat*, 13(03), 1–10.

Timmermann, T., Margóczi, K., Takács, G. & Vegelin, K. (2006) Restoration of peat-forming vegetation by rewetting species-poor fen grasslands. *Applied Vegetation Science*, 9, 241–250.

Toogood, S.E. & Joyce, C.B. (2009) Effects of raised water levels on wet grassland plant communities. *Applied Vegetation Science*, 12, 283–294.

Tuomisto, H. (2010) A diversity of beta diversities: straightening up a concept gone awry. Part 1. Defining beta diversity as a function of alpha and gamma diversity. *Ecography*, 33, 2–22.

van der Walt, S., Schönberger, J.L., Nunez-Iglesias, J., Boulogne, F., Warner, J.D., Yager, N., Gouillart, E., Yu, T., and the scikit-image contributors (2014) Scikit-Image: Image Processing in Python. *PeerJ 2,* e453. Online at: https://doi.org/ 10.7717/peerj.453, accessed 27 Apr 2017.

van Dijk, J., Stroetenga, M., Bodegom, P.M. & Aerts, R. (2007) The contribution of rewetting to vegetation restoration of degraded peat meadows. *Applied Vegetation Science*, 10, 315–324.

Van Geest, G.J., Coops, H., Roijackers, R.M.M., Buijse, A.D. & Scheffer, M. (2005) Succession of aquatic vegetation driven by reduced water-level fluctuations in floodplain lakes: Vegetation

succession in floodplain lakes. *Journal of Applied Ecology*, 42, 251–260.

Walz, U. (2011) Landscape structure, landscape metrics and biodiversity. *Living Reviews in Landscape Research*, 5(3), 1–35. Online at: http://lrlr.landscapeonline.de/Articles/lrlr-2011-3/download/lrlr-2011-3BW.pdf, accessed 03 Apr 2017.

Xie, Y., Sha, Z. & Yu, M. (2008) Remote sensing imagery in vegetation mapping: a review. *Journal of Plant Ecology*, 1, 9–23.

Yu, Q., Gong, P., Clinton, N., Biging, G., Kelly, M. & Schirokauer, D. (2006) Object-based detailed vegetation classification with airborne high spatial resolution remote sensing imagery. *Photogrammetric Engineering and Remote Sensing*, 72, 799.

Zahid, F.M., & Tutz, G. (2009) Ridge estimation for multinomial logit models with symmetric side constraints. *Computational Statistics*, 28, 1017–1034.

Zerbe, S., Steffenhagen, P., Parakenings, K., Timmermann, T., Frick, A., Gelbrecht, J. & Zak, D. (2013) Ecosystem service restoration after 10 years of rewetting peatlands in NE Germany. *Environmental Management*, 51, 1194–1209.

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Author for correspondence:
Marian Koch, Landscape Ecology and Site Evaluation, Faculty of Agriculture and Environmental Sciences, University of Rostock, Justus-von-Liebig-Weg 6, 18059 Rostock, Germany
E-mail: marian.koch@uni-rostock.de