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Both management method as well as time since last management, reed bed age, impact reed bed vegetation diversity by creating distinct plant communities. Reed bed habitat structure is also affected with reed bed rejuvenation decreasing with increasing reed bed age. The results show the importance of considering reed bed age in management, optimally aiming for a mosaic of ages.

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Reed bed vegetation structure and plant species diversity depend on management type and the time period since last management

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Running title: Structural effect of reed bed management

Abstract

Question

Reed beds, dominated by common reed (*Phragmites australis*), have high ecological value. Several studies have examined the differences between managed and unmanaged reed beds without taking into account the time passed since the last management. In this paper, we seek to answer the question: How does the time passed since last management and the management method itself affect the plant community and the habitat structure of reed beds?

Location

'De Østlige Vejler', Northern Jutland, Denmark

Methods

We examined four reed bed treatments – beds either cut or harvested during the year of the study (0-year-old reed beds) and reed beds harvested 3 and 25 years ago, respectively. The reed bed plant communities and the reed bed habitat structure were determined in May and August. We tested the data for overall between-treatment differences (MANOVA and PCA) and specific differences in the plant community and habitat structure (Kruskal-Wallis).

Results

The plant community differed significantly between the four reed beds according to treatment, and each reed bed exhibited unique species. Species richness was significantly higher in the recently harvested reed beds (0 and 3 years since harvest) compared with the 25-year-old reed beds. Harvest sparked reed rejuvenation and increased the growth of new reeds. The 3-year-old reed bed had a habitat structure that equally resembled that of the newly harvested (e.g. similar green reed shoot density) and the 25-year-old reed beds (e.g. similar height). Cutting, as opposed to harvesting, created a plant community adapted to less light availability.

Conclusions

To secure most plant species and most variation in habitat structure, reed beds should contain a mosaic of differently aged and differently managed patches. Previous studies have disagreed on the effect of management on plant species diversity, which could be explained either by different reed bed age or different sampling periods.

Key words: *Phragmites australis*, reed swamp, plant community, habitat structure, species richness, biodiversity, harvest, moving, succession

Introduction

Reed beds, dominated by the sub-cosmopolitan common reed *Phragmites australis* (Cav.) Trin. Ex Steud (Lansdown 2017), are detritus-based wetland ecosystems that represent the early stage of succession from open water to woodland (Cowie et al. 1992; Valkama et al. 2008). Where new wetlands previously were formed at the same rate as others were lost, present-day drainage and eutrophication have halted natural wetland formation, resulting in a net loss of wetland areas (Vadász et al. 2008). Such wetland loss has been especially pronounced in Europe where 60–90% of all wetlands have disappeared during the 20th century (Čížková et al. 2013). Due to the limited herbivore grazing of reed beds, large amounts of litter accumulate and the reed bed eventually dries out and is gradually transformed through natural succession into other types of land cover (Hawke and José 1996). This succession can be stopped or reversed by different reed management methods, such as harvesting or burning of the reed bed, which slow down the litter accumulation rate (Cowie et al. 1992).

In Europe, reed beds have great economic value and common reed is used in a wide range of products, e.g. thatching material, and for the purpose of construction and gardening (Köbbing et al. 2013). In order to secure reed stems of high quality for commercial interests, reed beds should be harvested either annually or bi-annually (Valkama et al. 2008). Reed beds also have great ecological value being home to several rare plant species, numerous species of birds, and more than 700 species of invertebrates (Valkama et al. 2008). Therefore, it is important to evaluate how the management methodologies (i.e. frequency and/or type of management) affect reed bed plant communities and habitat structures.

Several studies have compared managed to unmanaged reed beds, but a potentially important confounding effect arises, namely the fact that the reed bed age (defined as time since last management action) varies considerably between studies (Decleer 1990; Cowie et al. 1992; Poulin and Lefebvre 2002; Schmidt et al. 2005). By merging reed beds of different ages into the same category "unmanaged", the effect of reed management might be confounded by the different successional stages of the non-harvested reed beds. Thus, it is largely unknown which reed bed age provides a favourable environment for the species inhabiting the reed beds. According to Güsewell et al. (2000), reed bed age is important, and they found that the habitat structural characteristics reed stem length, shoot number and stem diameter differed significantly between reed beds mown annually, every second year and every third year. The

reed age also matters to the animals inhabiting the reeds. For example, Greylag Goose (*Anser anser*) avoids both newly cut reed beds and reed beds older than 16 years (Kristiansen 1998). Time since reed management may even be speculated to explain some inconsistencies between studies as reed management has been documented to affect plant species richness both positively (Decleer 1990; Cowie et al. 1992) and negatively (Deák et al. 2015), and the effect may also depend on salinity (Valkama et al. 2008).

In the present study, we explored how reed bed age affected the species composition, plant community (species richness, Shannon diversity and habitat heterogeneity as well as Ellenberg indicator values (EIV), vegetation height and density) and reed bed habitat structure (i.e. height, diameter and density of common reed, both new (green) and old (brown)) of the reed bed. The effect on the harvested reed beds was examined for three age stages – time since last management 0 (young), 3 (intermediate) and 25 years (old). Additionally, we examined two management methods reed cutting and reed harvest. When cut, the stems of common reed were left behind and when harvested, the stems were removed. The difference between the four reed bed ages and management treatments was investigated during spring (May) before complete reed regrowth at the managed sites and in late summer (August) after regrowth to full height.

Methods

Study site

This study took place in a bird sanctuary and protected area with no access to the public in Northern Jutland, Denmark, named 'De Østlige Vejler' (57°04'N, 9°03'E). The entire Vejlerne is home to the largest coherent reed bed in Scandinavia, which covers approximately 2000 ha (Riis 2009). The 'De Østlige Vejler' contains more than 600 ha of reed bed.

Reed bed treatments

Common reed has been harvested from Vejlerne for more than 100 years. Since 1979, harvest have only been conducted during winter with the exception of limited summer harvest in 1991 and 1992 (Riis 2009). Throughout the years, different areas have been harvested, and it is therefore possible to locate areas with varying time since last harvest – here referred to as reed bed age. During 2018, we investigated four different areas comprising three different ages. The oldest reed bed area was last harvested in 1993, leaving the area unmanaged for 25 years (25-year-old reed bed). The second area was last harvested in 2015

(3-year-old reed bed). Two reed bed areas were managed during the year of the study (0-year-old reed beds) using two different management methods – cutting, where the reed stems are left behind, and traditional harvesting, where the reed stems are removed. Harvesting and cutting took place in February 2018. Thus, in total, four reed bed treatments were investigated.

For each of the four reed bed treatments, data were sampled in circular plots with a radius of 5 m with an area of 78.5 m^2 (called the 5 m circle). Twenty plots were sampled per treatment in May and another 20 plots in August, adding up to a total of 160 sampling plots. We did not sample the same 20 per treatment plots in May as in August since our sampling activity caused heavy disturbance within the 5 m circle due to trampling. The plots were distributed randomly within the four differently aged reed beds using QGIS 2.18.11 (QGIS Development Team 2016).

Data collection

In both May and August, it was noted whether the 5 m circle was dry or covered by water (Nygaard et al. 2016), and the percentage coverage of water within the circle was estimated. During spring (May), salinity was measured in the surface water at four points within each plot using a Cond 340i (WTW) after which average salinity was calculated. Salinity was not measured in August due to absence of surface water caused by a prolonged drought.

In order to obtain a full species list (presence/absence), all plant species were recorded and determined to species level within each plot. Plant abundance and species composition were further determined using the pinpoint method (Levy and Madden 1933) where a pinpoint frame of 0.5x0.5 m was placed at the centre of each 5 m circle. The pinpoint frame was carefully placed on the vegetation ensuring not to damage it in the process. The pinpoint frame had 16 intersection points at each of which a pin was inserted. All plants in contact with the pin were recorded and if several individuals of the same species touched the pin repeatedly, their total number was counted. We used the total number of counts of each species per pinpoint frame in the data analysis. The height at which each plant touched the pin was also recorded and if a species touched the pin at different heights, only the maximum height was registered. Vegetation cover was estimate as the number of pins touched by vegetation. Plants were identified to species level using primarily Frederiksen et al. (2006) and specific literature on graminoids (Mossberg and Stenberg 2014; Schou 2006; Schou et al. 2010; Schou et al. 2014).

Two types of observations were made in order to characterise the common reed bed structure within each plot. First, stem density was measured in the 0.5x0.5 m pinpoint frame where both the number of green (new) and the number of brown (old) stems were counted. This enabled us to calculate the reed density per m^2.

Second, the diameter of 20 randomly selected stems within the 0.5x0.5 m frame was measured. When possible, this was done for both green and brown stems; however, as 20 green stems could not be located in some of the frames, such registration was not always possible. Furthermore, data on common reed height obtained during the pinpoint analysis were also used to characterise the reed bed habitat structure.

Data analysis

Differences in salinity and water cover between reed bed treatments were tested using a Kruskal-Wallis test (Hollander et al. 2013). If a significant between-treatment difference was found, a post-hoc Dunn test was performed to determine which treatments differed from each other.

Using presence/absence data from the 5 m circle, we aimed to determine whether the species composition differed between the four reed bed treatments. First, we computed a PERMANOVA with 999 permutations based on the Jaccard metric using *Adonis2* in order to test for differences in species composition between treatments (McArdle and Anderson 2001; Oksanen et al. 2017). Second, we determined which species were unique to each of the treatments. Unique species are here defined as species occurring only in one of the treatments. Third, an indicator species analysis was used to determine which species were especially related to each treatment using the *indicspecies package* in R (Cáceres and Legendre 2009). This package assesses the statistical significance of the relationship between a number of sites and species on a presence/absence level. The number and identity of unique species may differ from the number of indicator species as a species occurring only once in a treatment is unique but might not qualify as an indicator species. The plant species presence/absence data from the 5 m circle were also used to estimate Ellenberg L (light), F (moisture) and N (nutrient) (Ellenberg et al. 2001) and we calculated the Ellenberg values for the plant community in each 5 m circle. Ellenberg indicator values are used as bioindicators of the environment (Ellenberg et al. 2001). We also calculated the Ellenberg values for the indicator species of each treatment and for the species unique to each treatment.

Data from the pinpoint frame were used to calculate vegetation cover, Pielou and Shannon diversity (Shannon 1948), while presence/absence species lists from the 5 m circle were used to determine species richness and within-treatment habitat heterogeneity. In order to investigate the within-treatment habitat heterogeneity defined as the dissimilarity of plot species composition (Willby et al. 2018), we calculated the dissimilarity for all pairwise combinations of plots within a treatment for each of the four treatments. The R package *vegan* (Oksanen et al. 2017) was used to calculate the binary Jaccard dissimilarity as it allowed use of the presence/absence data from the 5 m circles. We calculated the habitat heterogeneity for May and August separately.

We estimated the aboveground reed volume using the number of reed stems (reed stem density) in a square meter (RS) multiplied by the reed stem area (calculated using the reed stem radius (r)) and the reed height (h):

$$Reed\ volume\ (m^3) =\ RS \cdot \pi \cdot r^2 \cdot h$$

The reed volume was estimated for both green and brown reed.

We estimated total plant density within the pinpoint frame as the number of touches of the pinpoint pin. We divided the total density into the reed density (RD) and the density of all other plants.

Using the information on the number of green (GR) and brown reed (BR) stems in a pinpoint frame, the new to old reed ratio was calculated:

$$New\ to\ old\ ratio =\ GR/BR$$

To sum up, habitat structure consists of: green stem density (GR), brown stem density (BR), the new to old reed ratio (GR:BR), total density (RD), green reed diameter (d(g)), brown reed diameter (d(b)), reed height (h), brown volume and green volume.

In order to determine whether the four reed treatments differed significantly with regards to diversity and habitat structure, a non-parametric MANOVA with 10,000 permutations was conducted using the R package *npmv* (Burchett et al. 2017). Separate tests were run for May and August and for the plant community parameters (Ellenberg values; vegetation height, density and cover; species richness, Shannon diversity and habitat heterogeneity) and the reed bed habitat structure parameters (reed height; diameter of green and brown shoots; density of

green and brown shoots, total density and the new to old reed ratio; green and brown reed volume).

A Principal Component analysis (PCA) (Jolliffe 2002) with parameter scaling ($\mu = 0$, $\sigma = 1$) was conducted to visualise the degree of difference between treatments in May and August. The same parameters were considered for the PCAs as for the MANOVA. Highly correlated variables (correlation coefficient > 0.6) were removed (Zar 1999), and the final PCA included: new to old reed ratio, total reed density, red height, diameter of green and brown shoots, density of other plants, Ellenberg L and F, the Shannon diversity, habitat heterogeneity and species richness. Ellenberg N was included in the analysis in May but not in August.

For each reed and plant community parameter in May and August, we tested for significant differences between the four treatments for each parameter using a Kruskal-Wallis test (Hollander et al. 2013). We used the sequential Bonferroni Correction, also known as the Holm correction, to account for multiple testing (Holm 1979). When a significant between-treatment difference was found, a post-hoc Dunn test was performed to determine which treatments differed from each other.

All data analyses were conducted using R v.3.4.1 (R Core Team 2017). Graphs were created in ggplot2 (Wickham 2016).

Results

Abiotic conditions

The mean salinity levels were below 1 ppt in all four reed bed treatments (Appendix S1). The salinity differed significantly between treatments (Kruskal-Wallis, $p < 0.01$) and were significantly higher in the cut reed bed compared to the harvested (Dunn, $p < 0.01$), the 3-year-old (Dunn, $p < 0.01$) and the 25-year-old (Dunn, $p < 0.01$). The water cover did not differ between the treatments within the same sampling period, but there was a significant decrease in water cover from May (close to 100%) to August (close to 0%) between treatments (Appendix S1).

Plant community and habitat structure

We found 66 species across the four reed bed treatments, of which only 22 were found across all four treatments (Appendix S4). Across May and August, unique species counted five in

the cut reed bed, seven in the 0-year-old harvested bed, one in the 3-year-old reed bed and nine in the 25-year-old bed (Appendices S2 and S3). Subsequently, the plant species composition differed significantly between treatments in May (PERMANOVA, $p < 0.01$) and August (PERMANOVA, $p < 0.01$).

The indicator species analysis found that one species (*Alisma plantago–aquatica*) was associated with the cut reed bed, four (*Carex elata*, *Myosotis laxa ssp. caespitose*, *Carex disticha* and *Eriophorum angustifolium*) with the harvested and three (*Solanum dulcamara*, *Cicuta virosa*, *Phalaris arundinacea*) with the 25-year-old bed across May and August, whereas no particular species was mainly associated with the 3-year-old bed (Table 1). The plant species exclusively found in the 0-year-old harvested treatment exhibited the highest values of Ellenberg L and F but the lowest values of Ellenberg N compared with the other treatments (Table 1 and Appendix S3).

By visual inspection of the PCA from May, we found that the 0-year-old harvested and 25-year-old reed beds were clearly separated and that the 3-year-old reed bed could be found in-between the two (Fig, 1a). Further, the 0-year-old cut reed bed was more similar to both the 3-year-old and 25-year-old reed beds than to the 0-year-old harvested reed bed (Fig. 1a). The first two principal components explained 37% of the variation in the data, with the new to old reed ratio, species richness and Ellenberg N best explaining the partitioning on PC1 and Ellenberg L, Ellenberg F and the total reed density best described PC2.

Visually inspecting the PCA from August, we found that the 0-year-old cut and harvested reed beds were clearly distinct from each other (Fig. 1b). The 3-year-old and 25-year-old reed beds were similar, and separated themselves from both the 0-year-old cut and harvested reed beds (Fig. 1b). The first two principal components explained 38.8% of the variation in the data. Vegetation height, species richness and diameter of green shoots had the highest loadings on PC1 while Ellenberg L, Ellenberg F and species richness explained most variation on PC2 (Fig. 1b).

Overall, the plant community characteristics differed significantly (p-value < 0.001, non-parametric MANOVA) between the three reed bed ages and the two types of management treatments in year-0 in both May and August. In May, the plant community parameters species richness, Pielou, habitat heterogeneity, cover, vegetation height, Ellenberg N and Ellenberg L differed significantly between treatments (Kruskal-Wallis with sequential Bonferroni correction, $p < 0.05$) (Table 2). For example, median species richness was

significantly higher in the 3-year old reed bed compared with both the 0-year-old harvested bed and the 25-year-old reed bed in May (Fig. 2, Table 2). The opposite trend was found for Shannon diversity, which was significantly higher in the 0-year-old and 25-year-old reed beds than in the 3-year-old bed in August (Fig. 2, Table 2). Boxplots of the remaining plant community parameters can be found in Fig. 2 and Appendix S5.

Reed bed habitat structure characteristics differed significantly (non-parametric MANOVA, p-value < 0.001) between the three reed bed ages and the two management treatments in both May and August (Fig 1c and 1d), with significant between-treatment differences found across all parameters (Kruskal-Wallis with sequential Bonferroni correction, $p < 0.05$). For example, reed height was significantly lower in the 0-year-old cut and the 0-year-old harvested reed beds compared with the 3-year-old and 25-year-old harvested beds in May. In August, reed height was only significantly lower in the 0-year-old cut reed bed than in the other treatments (Table 2, Fig. 3). The density of green reed shoots was significantly higher in the 0-year-old harvested reed bed compared with the 3-year-old bed, which in turn had a significantly higher number of green reed shoots than the 25-year-old reed bed (Table 2, Fig. 3). The 25-year-old reed bed had a significantly lower ratio of new to old shoots compared with the other reed bed treatments (Table 2, Fig. 3). Boxplots of the remaining habitat structure parameters can be found in Appendix S6.

Discussion

Overall, we found that both management method and time since last harvest significantly affected the plant community, plant diversity and habitat structure. It is not uncommon that management actions that change the habitat structure also radically change the species composition across habitats as seen in both grasslands and abandoned rice fields (Mesléard et al. 1999; Kitazawa and Ohsawa 2002).

One aspect of the different plant communities found across treatments were the presence of unique species and several indicator species (Table 2, Appendix S2). In this context, use of different management treatments seems especially important since less than half of the species were found in all the treatments, the majority occurring in either one, two or three treatments (Appendix S2). Similarly, Kitazawa and Ohsawa (2002) found that different management treatments of rural herbaceous vegetation resulted in dominance of species that were uniquely adapted to the living conditions created by the particular management regimes.

The different species compositions between treatments were also apparent by the difference in Ellenberg values, where cutting decreased the Ellenberg L-values of the plant community in May, likely due to the fact that the reed left behind shaded the underlying plants. In contrast, harvesting increased the Ellenberg L-values (Table 2). Ellenberg L of grassland plant communities has also been observed to increase with enhanced cutting frequency (Moog et al. 2002). As the Ellenberg values were based on presence/absence data, they highlight the characteristics of plants co-occurring with the dominant species common reed rather than focus on common reed itself. We therefore suggest that, on a large scale, the most diverse habitat will be achieved by a mosaic of differently managed reed beds.

Our results partly explain some of the disagreement about the effect of management on species richness in reed beds as the response of species richness to management is dependent on both reed bed age and time of the sampling. We found that species richness peaked 3 years following last management, whereas Schmidt et al. (2005) found that species richness did not differ between managed and 5-year-old reed beds. In accordance with our result, Decleer (1990) found a higher species richness in managed compared with old (35-year-old) reed beds, which is also in agreement with our finding that species richness was higher in the recently harvested than in the 25-year-old reed bed. This indicates that species richness is positively affected by management, but that the effect only lasts for a few years before it abates, and we therefore encourage more studies to be undertaken including reed beds of intermediary age. In tall-herb fens, species richness increased after 2-4 years of grazing due to a decrease in the abundance of common reed (Ausden et al. 2005), and in our study the initial increase in species richness following management could be explained by the removal of common reed and decreased reed density in the young compared with the old reed beds. In our case, grazing of the reed bed would likely also result in reed bed drawback since the area adjacent to the study reed beds is a grazed marsh where common reed growth is limited (Andersen et al. 2020a). We only observed an age effect on species richness in May, where the species richness was significantly higher in recently harvested (0- and 3-year-old) compared to the 25-year-old reed bed, and by August, species richness no longer differed between the treatments. One explanation could be that the increases in species richness seen during spring in the younger reed beds, where the reed density was lower compared to the 25-year-old reed bed, had already been reduced by late summer due to the high competitive ability of common reed. The timing/season of the fieldwork may therefore also explain the inconsistencies across studies on the effect of management on species richness.

An equal proportion of plant community parameters differed between the 0-year-old harvested and 3-year-old harvested as between the 3-year-old and 25-year-old harvested, which indicates the importance of including reed bed age of unmanaged reed beds (Table 2). Only one plant community parameter differed significantly between the 0-year-old harvested and 3-year-old reed bed in May. This highlights the importance of age of the reed bed used as a control. Had we only conducted fieldwork in either May or August, or only included either the 3-year-old or 25-year-old reed bed as a control, the results would have been significantly different.

We found that harvesting promoted reed bed rejuvenation as the growth of new reed was strongly related to both reed age and management, which is in agreement with previous studies (Björndahl 1985; Ostendorp 1999; Deák et al. 2015). Further, the rejuvenation effect following management seems to last for at least three years, which highlights the importance of taking time since last management into account when studying reed beds and the effects of harvesting. In other investigations, winter harvesting was found to increase reed density compared with unmanaged reed beds (Bresciani et al. 2011; Valkama et al. 2008; Ostendorp 1999). This is partly in agreement with our finding that green reed density was significantly higher in the recently managed reed beds and in the early successional stage compared with reed beds left unmanaged for many years. We encourage more studies to include multiple ages of unmanaged reed beds to confirm this observed trend and discuss the optimal period for leaving reed beds unmanaged; however, based on the results of the present study and those of Schmidt et al. (2005) plant richness seems to peak 3-5 years following harvesting.

No clear habitat structure responses of reed beds to management treatments such as harvesting, cutting, burning and grazing have been identified (Valkama et al. 2008). Therefore, we looked at species richness and diversity relative to two management methods, as the effects of different management methods have been poorly addressed when considering reed bed conservation (Valkama 2008). We found that the method of management did not affect species richness but that cutting led to a lower Shannon diversity than harvesting. According to Cowie et al. (1992), cutting also results in lower species diversity compared with burning, another reed management practice that also increases species richness. Further, we found that cutting and harvesting created different habitat structures; thus, the growth of green reed and reed height were significantly smaller in the 0-year-old cut reed bed than in the 0-year-old harvested bed. The reduced reed growth in the cut compared with the harvested reed bed can likely be explained by light limitations.

Though many parameters differed between reed bed treatments and ages as discussed above, the first two axes of the PCA only explained a limited amount of the variation in the data. This could be caused by parameters not measured in this study, and we therefore suggest that future studies include more variables on for instance the environment, e.g. moisture levels along with water cover and nutrient levels along with Ellenberg N.

Reed beds are home to numerous birds and invertebrates that all depend on different habitat structures, a high habitat heterogeneity and various plant species (Baldi and Kisbenedek 1999, Mero et al. 2018, Sjöberg and Danell 1983, Valkama et al. 2008) with several species of birds avoiding newly harvested reed beds (Nielsen and Clausen 2019; Vadász et al. 2008). Denser vegetation protect nests from discovery by predators (Polak 2016; Wang et al. 2019), lead to higher breeding success (Mérő and Žuljević 2014) and a higher number of fledglings (Ille and Hol 1995). As harvest increased green shoot density in our study, it could have increased nest protection in May though it is important to consider that the reed height was lower thereby exposing nests. However, reed density dropped over the season, with the lowest die off in the old reed bed that had the highest density in August. Thus, higher protection in old reed beds in August might be expected although this is outside the breeding season.

In conclusion, we found that management method affects the plant community and that cutting resulted in a community with a significantly lower Ellenberg L compared with harvesting. Furthermore, the two management methods created different reed bed habitat structures with higher regrowth in the harvested than in the cut reed beds. We observed that plant species richness peaked 3-5 years after last harvesting; this finding, though, may be dependent on the timing of the fieldwork. While reed harvesting resulted in reed bed rejuvenation and increased green shoot density, reed die off throughout the season meant that the highest overall reed density occurred in the old reed bed and that this therefore provided the best protection for breeding birds. Thus, in order to create optimal conditions and favourable habitats for most species in reed beds comprising both heterogeneous and homogenous areas, a mosaic of beds exhibiting different management treatments and time since last management is likely the most optimal.

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Author contribution

DB, KT, SB, TLL and LHA conceived the idea of the research. LHA, MPK, JF and CMSF collected the data. LHA analysed the data under the guidance of CP and discussed first results with DB and PN. LHA wrote the first draft of the manuscript with contributions from DB. All authors discussed and commented on the final manuscript.

Data availability statement

Data available on zenodo.org doi 10.5281/zenodo.3794685 (Andersen et al. 2020b).

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Figure 1. Separation of the four reed bed treatments into 0-year-old cut, 0-year-old harvested, 3-year-old harvested and 25-year-old harvested reed beds. The top row represents separation of the four reed bed treatments in May (a) and August (b). Abbreviations used are SR: species richness; SD: Shannon diversity; HH: habitat heterogeneity; D: density of plants other than reed; EIV L: Ellenberg Indicator Value for light; EIV N: Ellenberg Indicator Value for nutrients; EIV F: Ellenberg Indicator Value for moisture; h: height; TR: total reed density; GR:BR: new to old reed ratio; d(g): diameter, green shoots; d(b):diameter, brown shoots.
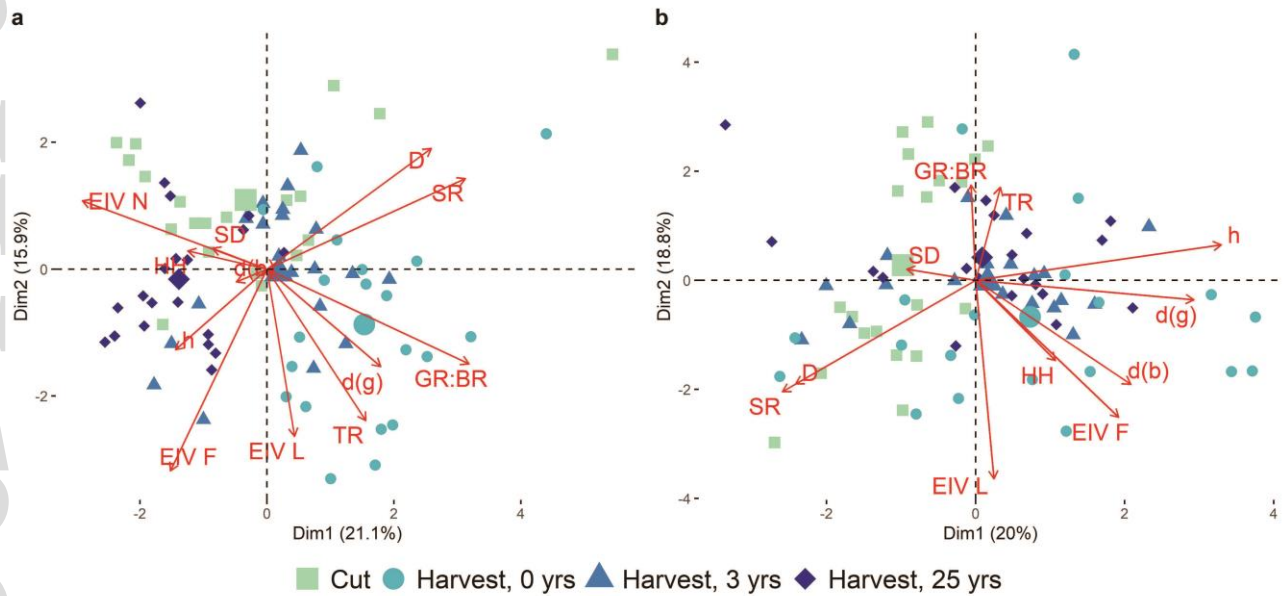
Figure 2. Median species richness (a), Shannon diversity (b), Pielou diversity (c) and habitat heterogeneity (d) for each of the four reed bed treatments in May and August. Boxes represent 25th and 75th percentiles, whiskers are the smallest/largest value within 1.5 times the interquartile range below/above the 25th/75th percentiles. Dots are outliers. Letters indicate whether two reed bed treatments are significantly different (different letter) or not (same letter) within May or August.

Figure 3. Median reed height (cm) (a), density of green shoots (b) and new to old reed shoot ratio (c) for each of the four reed bed treatments in May and August. Boxes represent 25th and 75th percentiles, whiskers are the smallest/largest value within 1.5 times the interquartile range below/above the 25th/75th percentiles. Dots are outliers. Letters indicate whether two reed bed treatments are significantly different (different letters) or not (same letter) within May or August.
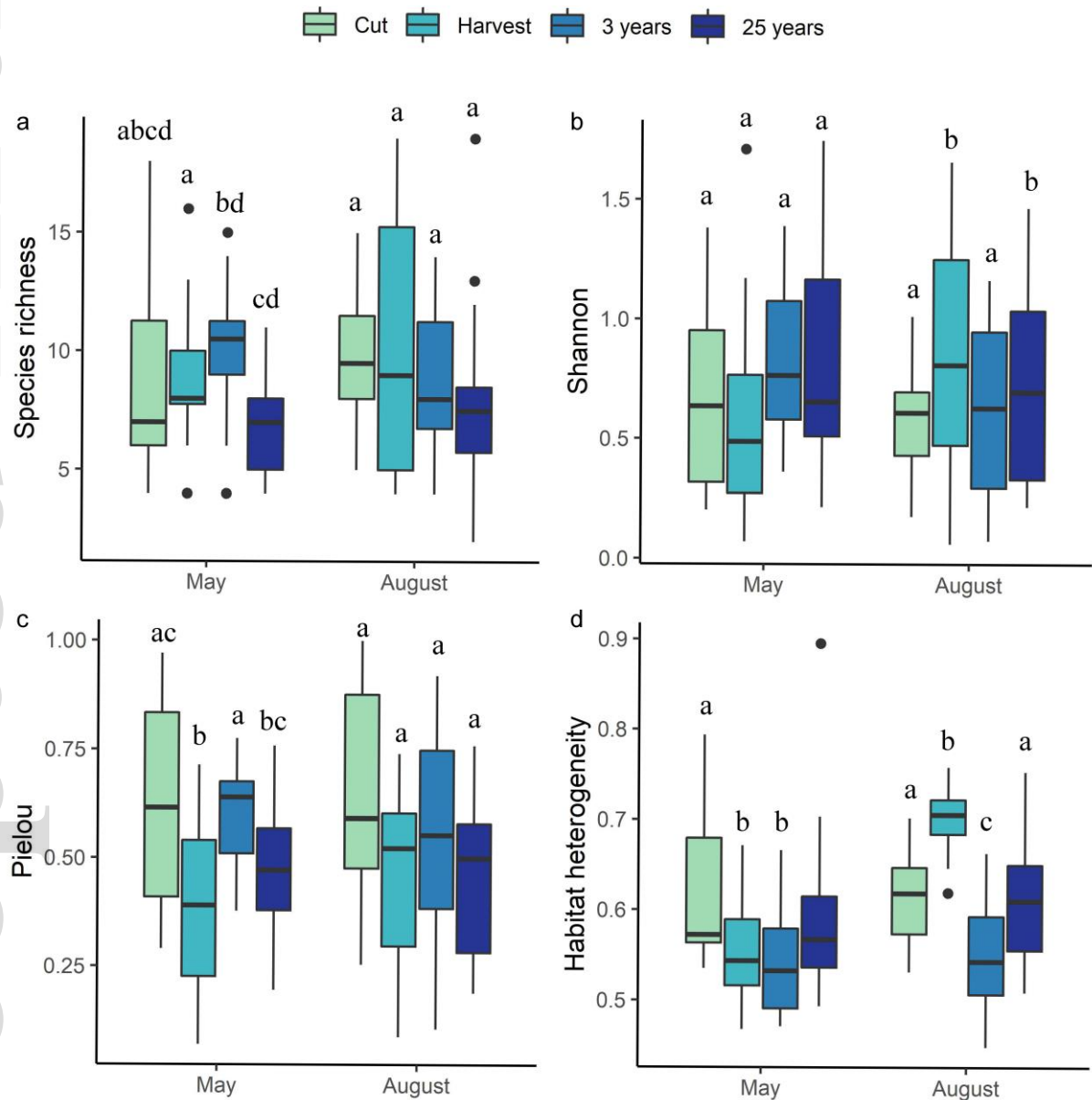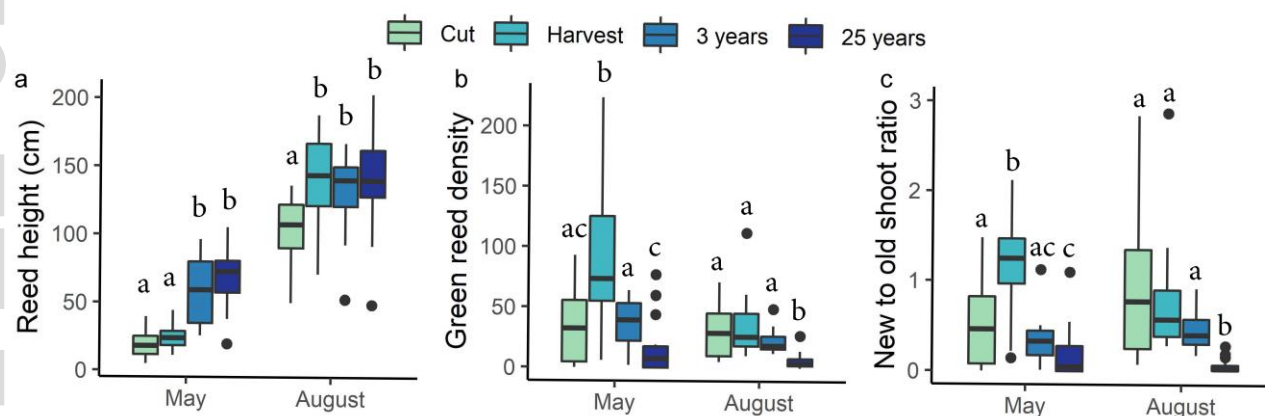
Table 1. Results of indicator species analysis. One species was linked to the cut, four to the harvested, none to the 3-year-old and three to the 25-year-old habitats. A/P: annual/perennial, EIV: Ellenberg Indicator Value, L: Ellenberg value for light, F: moisture, N: nutrients. All species are listed as least concern on the Danish Red List (Wind and Pihl 2010).

	Species	*p*-value	A/P	EIV L	EIV F	EIV N
Cut	*Alisma plantago–aquatica*	0.005	P	7	10	8
Harvested	*Carex elata*	0.005	P	8	10	5
Harvested	*Myosotis laxa ssp. caespitosa*	0.015	A	7	9	7
Harvested	*Carex disticha*	0.015	P	8	9	5
Harvested	*Eriophorum angustifolium*	0.015	P	8	9	2
25-year-old	*Solanum dulcamara*	0.005	P	7	8	8
25-year-old	*Cicuta virosa*	0.015	P	7	9	5
25-year-old	*Phalaris arundinacea*	0.025	P	7	8	7

Table 2. Between-treatment differences in plant community and reed bed habitat structure parameters. If Kruskal-Wallis with sequential Bonferroni correction was significant, post hoc Dunn test results for between-treatment differences are shown. The accumulated difference show the percentage (%) of parameters that differ between the reed bed treatments. Non-significant Kruskal-Wallis results are indicated by '-'. *** $p < 0.001$, ** $p < 0.01$, *$p < 0.05$, . $p < 0.1$, n.s. non-significant.

	Month	Cut: Harvested	Cut:3-year-old	Cut:25-year-old	Harvest:3-year-old	Harvested:25-year-old	3-year-old:25-year-old
Plant community							
Species richness	May	n.s.	.	n.s.	n.s.	*	***
	August	-	-	-	-	-	-
Shannon	May	-	-	-	-	-	-
	August	***	n.s.	***	*	n.s.	*
Pielou	May	**	n.s.	.	***	n.s.	*
	August	-	-	-	-	-	-
Habitat heterogeneity	May	**	***	n.s.	n.s.	n.s.	n.s.
	August	***	*	n.s.	***	***	*
Cover	May	**	***	***	n.s.	n.s.	n.s.
	August	-	-	-	-	-	-
Veg. height	May	n.s.	n.s.	**	n.s.	*	**
	August	n.s.	**	*	**	**	n.s.
Ellenberg N	May	***	**	n.s.	n.s.	***	**
	August	-	-	-	-	-	-
Ellenberg L	May	***	*	**	n.s.	n.s.	n.s.
	August	*	.	n.s.	n.s.	*	*
Ellenberg F	May	-	-	-	-	-	-
	August	-	-	-	-	-	-
Reed bed habitat structure							
Green density	May	***	n.s.	.	**	***	*
	August	n.s.	n.s.	***	n.s.	***	***
Brown density	May	n.s.	**	**	**	*	n.s.
	August	n.s.	n.s.	***	n.s.	***	***
Total density	May	**	**	n.s.	n.s.	.	n.s.
	August	n.s.	n.s.	***	n.s.	**	***
Green diameter	May	***	n.s.	n.s.	**	***	n.s.
	August	*	*	n.s.	n.s.	**	**
Brown diameter	May	n.s.	n.s.	***	n.s.	*	*

	August	**	n.s.	n.s.	***	**	n.s.
Reed stem ratio	May	**	n.s.	*	***	***	.
	August	n.s.	n.s.	***	n.s.	***	***
Green reed volume	May	***	**	n.s.	n.s.	***	**
	August	.	n.s.	***	n.s.	***	***
Brown reed volume	May	n.s.	***	***	***	***	n.s.
	August	**	n.s.	***	n.s.	*	***
Reed height	May	n.s.	***	***	***	***	n.s.
	August	***	**	***	n.s.	n.s.	n.s.

Online appendices:

Appendix S1: Water cover and salinity levels across treatments in May and August

Appendix S2: Venn Diagram depicting the number of species within each habitat
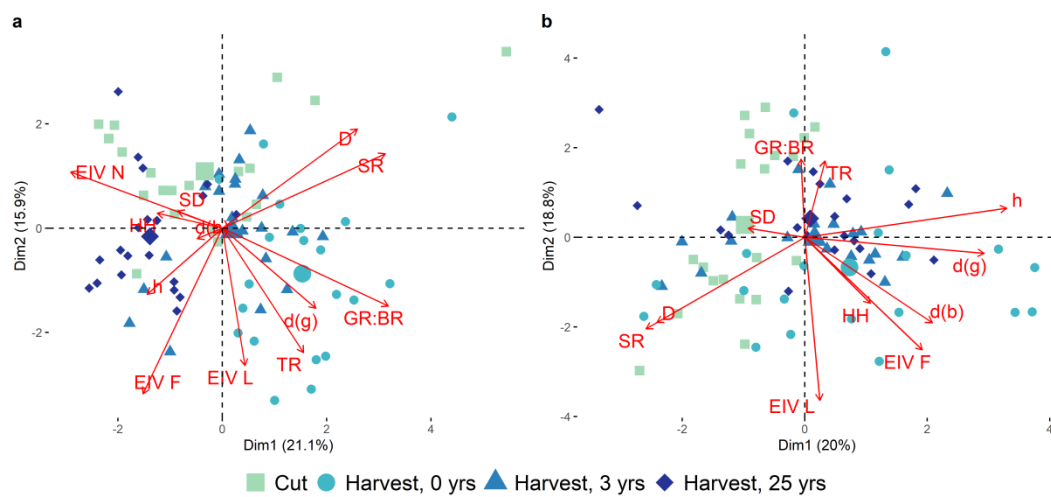
Appendix S3: Unique species per treatment

Appendix S4: A complete species list with frequencies for each reed bed treatment

Appendix S5: Boxplots, plant community

Appendix S6: Boxplots, reed bed habitat structure

	Species	*p*-value	A/P	EIV L	EIV F	EIV N
Cut	*Alisma plantago–aquatica*	0.005	P	7	10	8
Harvested	*Carex elata*	0.005	P	8	10	5
Harvested	*Myosotis laxa ssp. caespitosa*	0.015	A	7	9	7
Harvested	*Carex disticha*	0.015	P	8	9	5
Harvested	*Eriophorum angustifolium*	0.015	P	8	9	2
25-year-old	*Solanum dulcamara*	0.005	P	7	8	8
25-year-old	*Cicuta virosa*	0.015	P	7	9	5
25-year-old	*Phalaris arundinacea*	0.025	P	7	8	7

	Month	Cut: Harvested	Cut:3- year-old	Cut:25- year-old	Harvest:3- year-old	Harvested:25- year-old	3-year-old:25- year-old
Plant community							
Species richness	May	n.s.	.	n.s.	n.s.	*	***
	August	-	-	-	-	-	-
Shannon	May	-	-	-	-	-	-
	August	***	n.s.	***	*	n.s.	*
Pielou	May	**	n.s.	.	***	n.s.	*
	August	-	-	-	-	-	-
Habitat heterogeneity	May	**	***	n.s.	n.s.	n.s.	n.s.
	August	***	*	n.s.	***	***	*
Cover	May	**	***	***	n.s.	n.s.	n.s.
	August	-	-	-	-	-	-
Veg. height	May	n.s.	n.s.	**	n.s.	*	**
	August	n.s.	**	*	**	**	n.s.
Ellenberg N	May	***	**	n.s.	n.s.	***	**
	August	-	-	-	-	-	-
Ellenberg L	May	***	*	**	n.s.	n.s.	n.s.
	August	*	.	n.s.	n.s.	*	*
Ellenberg F	May	-	-	-	-	-	-
	August	-	-	-	-	-	-
Reed bed habitat structure							
Green density	May	***	n.s.	.	**	***	*
	August	n.s.	n.s.	***	n.s.	***	***
Brown density	May	n.s.	**	**	**	*	n.s.
	August	n.s.	n.s.	***	n.s.	***	***
Total density	May	**	**	n.s.	n.s.	.	n.s.
	August	n.s.	n.s.	***	n.s.	**	***
Green diameter	May	***	n.s.	n.s.	**	***	n.s.
	August	*	*	n.s.	n.s.	**	**
Brown diameter	May	n.s.	n.s.	***	n.s.	*	*
	August	**	n.s.	n.s.	***	**	n.s.
Reed stem ratio	May	**	n.s.	*	***	***	.
	August	n.s.	n.s.	***	n.s.	***	***
Green reed volume	May	***	**	n.s.	n.s.	***	**
	August	.	n.s.	***	n.s.	***	***
Brown reed volume	May	n.s.	***	***	***	***	n.s.
	August	**	n.s.	***	n.s.	*	***
Reed height	May	n.s.	***	***	***	***	n.s.

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