Danish wetlands remained poor with plant species 17-years after restoration

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Danish wetlands remained poor with plant species 17-years after restoration

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HIGHLIGHTS
• We investigated plant communities in wetlands 7-17 years after restoration.
• Plant communities did not approach those characterising natural riparian wetlands.
• Target species dispersal from source populations may restrict restoration success.
• Continuous high nutrient input may be another major constraint for recovery.

ABSTRACT
For more than two decades, wetland restoration has been successfully applied in Denmark as a tool to protect watercourses from elevated nutrient inputs from agriculture, but little is known about how the flora and fauna respond to restoration. The main objective of this study was therefore to: (1) examine plant community characteristics in 10 wetland sites in the River Odense Kratholm catchment, restored between 2001 and 2011 by re-meandering the stream and disconnecting the tile drains, and (2) explore whether the effects of restoration on plant community characteristics change with the age of the restoration. Specifically, we hypothesised that plant community composition, species richness and diversity would improve with the age of the restoration and eventually approach the state of natural wetland vegetation. We found that the prevailing plant communities could be characterised as humid grasslands, moist fallow fields and improved grasslands, whereas the abundance of natural wetland plant communities (e.g., rich fens, fen-sedge beds and humid grasslands) was lower in both the recently restored as well as in older restored wetlands. Additionally, species richness and diversity did not seem to improve with the age of the restoration. We suggest that the continued high nutrient input at the restored sites in combination with restricted dispersal of wetland plant species may hamper the recovery of natural plant communities and that the sites therefore may stay botanically poor for many decades.

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1. Introduction
Over the past 30 years, thousands of hectares of drained wetlands have been rewetted in Europe, North America and other

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parts of the world (Vasander et al., 2003; Lamers et al., 2015; Andersen et al., 2017; Chimner et al., 2017). Rewetting is consistent with Target 12 of the 4th Strategic Plan of The Ramsar Convention, which advocates the restoration of degraded wetlands for biodiversity conservation, disaster risk reduction, improvement of livelihoods and climate change mitigation and adaptation (The Ramsar Convention Secretariat, 2015). The focus on wetland restoration is also evident in the European Union’s Biodiversity Strategy for 2030, which aims for restoration of degraded ecosystems and addresses key drivers of biodiversity loss (European Commission, 2020).

There is an ongoing debate among scientists and stakeholders to justify realistic and effective wetland restoration measures (Zak et al., 2011). We know that wetland restoration can mitigate climate change impacts by curbing carbon dioxide emissions from drained peat soils (Günther et al., 2020) or even re-establish carbon sequestration and reduce eutrophication of water bodies (Kimmel and Mander, 2010), but the knowledge about long-term effects and the rate of the recovery is sparse, also when it comes to the succession of the vegetation (Jurasisinki et al., 2020). However, examining the outcome of wetland restoration is crucial to build on former experience when planning and implementing new projects as this may help set realistic goals for protected wetland habitats and species that can be balanced against the need to ensure that Europe’s biodiversity is on the path to recovery by 2030 (European Commission, 2020).

Denmark is one of the most active EU member states regarding wetland restoration and has 25 years of experience in this field (Hoffmann et al., 2020). So far, more than 200 Danish wetland sites have been restored (Carl Christian Hoffmann 2019a, personal communication). Most of the wetland restoration projects have been undertaken within the framework of the Action Plans on the Aquatic Environment (Ministry of Environment and Food of Denmark, 2020) and have involved various practical restoration measures such as stream re-meandering, disconnection of tile drains and re-establishment of lakes (Hoffmann et al., 2011; Audet et al., 2020). Usually, the restoration projects have been made in areas that were in agricultural use (42%) or, more specifically, used for hay production (meadows; 39%) (Hoffmann and Baattrup-Pedersen, 2007).

Danish restoration projects have generally focused on mitigating nitrogen and phosphorus losses from agricultural lands (Hoffmann and Baattrup-Pedersen, 2007; Audet et al., 2015), whereas no clear aims have been set for the biodiversity in the wetland areas subject to restoration activities (Audet et al., 2015). In this study, we evaluate the outcome of 10 wetland restoration projects in the Kratholm catchment of River Odense located on the Danish island of Funen. The wetlands in this catchment were rewetted to remove nitrogen and mitigate phosphorus leaching by re-establishing the natural hydrological conditions and, thereby, biogeochemical processes. It was anticipated that this would be beneficial for the flora and fauna and that species characterising natural wetlands would re-establish or become more abundant (Miljø- og Fødevareministeriet, 1998). However, no long-term follow-up monitoring was conducted to verify this anticipation. The main objective of this study was therefore to: (1) describe plant communities in the restored sites in the Kratholm catchment of River Odense and compare them to those characterising natural wetlands in Denmark, e.g., rich fens, fen-sedge beds and humid grasslands (Baattrup-Pedersen et al., 2014; Audet et al., 2015), and (2) explore whether plant community characteristics change with the age of the restoration and whether a certain time span is needed to restore communities resembling those characterising natural wetlands. Specifically, it was hypothesised that plant community composition, species richness and diversity would improve and eventually approach that of natural wetland vegetation with increasing time since restoration.

2. Materials and methods

2.1. Study sites and experimental design

The study was carried out in 10 restored wetlands within the Kratholm catchment, located in Denmark on the island of Funen in the southern part of the River Odense basin (Fig. 1). The total area of the catchment is 486 km². The catchment is characterised by a temperate and humid climate with an average annual precipitation of 744 mm and a mean annual temperature of 9.0 °C, the mean temperature of the warmest month, July, being 17.6 °C and the mean temperature of the coldest month, February, 1.3 °C (means for 2006–2015 for Odense weather station derived from the Danish Meteorological Institute) (Hashemi and Kronvang, 2020; Danmarks Meteorologiske Institut, 2020). The landscape is dominated by moraine plains, covered with moraine clay deposits, which were left by the base of the ice sheet formed during the Weichsel glaciation period. The most common soil types in the area are loamy sandy soils, found in 40% of the area, and sandy clay soils, found in 36% of the area. The land use is mainly agriculture, covering 71% of the area, while 15% are forested areas and 8% are urban areas (Kronvang et al., 2012).

Numerous wetland restoration projects have been conducted in the catchment of Kratholm, starting from 2000 (Windolf et al., 2016). The total area of the 10 studied wetlands is 859 ha. The size of the restored wetlands varies from 9.8 ha in Hammerdam to 296 ha in the second stage of the River Odense restoration project. The eldest restored wetland is Karlsmosen (rewetted in 2001), while the most recently restored one is River Silke (rewetted in 2011). The main restoration measures implemented are stream re-meandering and disconnection of tile drains and ditches. Before the restoration, the area in crop rotation varied from 1.9 to 146.9 ha and direct upland area from 75 to 734 ha (Table 1). The main rooting zone (0–30 cm soil depth) of the sites contained between 1.4% and 20.3% organic matter as determined at three sampling spots per area (Table 1; for method details see Zak et al., 2010).

2.2. Vegetation inventory

The vegetation was characterised in June 2018. In total, 172 vegetation plots were investigated varying between 5 and 70 per site, depending on area size (Table 1). The position of the plots was stratified to cover the most significant types of vegetation. The size of the vegetation plots was 2 × 2 m. If a plot was located next to the stream, the size was 1 × 4 m, placed parallel to the stream to avoid heterogeneous conditions. All vascular plants and bryophytes were identified in the plots according to Atherton et al. (2010) and Mossberg and Stenberg (2014), and abundance was assessed applying the Braun-Blanquet cover – abundance scale (Braun-Blanquet, 1932).

2.3. Data analysis

To achieve a standardised description of the vegetation types encountered in the investigated areas, we used the definitions given in the CORINE biotopes manual (Commission of The European Communities, 1991), applying a species-based classification model that was developed for semi-natural and natural wetlands and grassland vegetation in Denmark (Nygaard et al., 2009; Dybkjær et al., 2012). The model applies the definitions given in the CORINE biotopes manual (Commission of The European Communities, 1991), including habitat types protected by the Habitats Directive (European Council, 1992). The model uses full species names with rare exceptions, for example, Typhastrum sp. Therefore, subordinate species determined to genus level only were deleted from our data set, eight in total, before classifying the plots. We used passive ordination, i.e., the plots were passively projected into the classification model by applying species scores from the classification model to determine the community type to which the plot had the
highest resemblance (Økland, 1990). Following the classification, some of the identified plant communities were combined into groups due to overlap in dominant species characterising the plant communities, for example, humid grasslands and moist fallow fields. In one plot, *Petasites hybridus* was dominant and will in the following be referred to as *P. hybridus* stands.

We used the Shannon species diversity index, also known as the Shannon-Wiener index (Shannon, 1948), to describe species diversity in the plant communities and average indicator values for light, moisture and soil fertility (Ellenberg et al., 1992) to explore linkages between abiotic factors and the plant communities (Brunbjerg et al., 2018). Average plant indicator values (i.e., Ellenberg indicator values; Ellenberg et al., 1992) are commonly used in vegetation studies to assess local conditions (e.g., Diekmann, 2003) and the validity of these have been confirmed by direct measurement of the environmental conditions and by plant growth experiments (e.g., Schaffers and Sýkora, 2000; Bartelheimer and Poschlod, 2016). Ellenberg indicator values were available for 164 species out of 172. If indifferent values occurred, the species were eliminated from the data set. To calculate the indicator values for each plot or community, community-weighted mean values were used. The calculations were done by multiplying the indicator value by the abundance of the species, summing it up for all species and dividing it by total abundance. As there was only one plot where *P. hybridus* was dominant, it was not possible to calculate some of the statistical parameters, for example, standard deviation.

Table 1

<table>
<thead>
<tr>
<th>Restored site</th>
<th>Restoration year</th>
<th>Area, ha</th>
<th>Crop rotation, ha</th>
<th>Direct upland, ha</th>
<th>Type of restoration</th>
<th>OM&lt;sub&gt;soil&lt;/sub&gt;, %</th>
<th>Vegetation plots</th>
</tr>
</thead>
<tbody>
<tr>
<td>Karlsmosen</td>
<td>2001</td>
<td>62.5</td>
<td>62.5</td>
<td>171</td>
<td>Re-meandering, tile drain cut</td>
<td>8.9 (2.0)</td>
<td>10</td>
</tr>
<tr>
<td>River Odense near Brobyværk</td>
<td>2003</td>
<td>104.4</td>
<td>–</td>
<td>234</td>
<td>Re-meandering, tile drain cut</td>
<td>20.3 (2.6)</td>
<td>25</td>
</tr>
<tr>
<td>Sandholt Mallebakken</td>
<td>2003</td>
<td>54.7</td>
<td>57.5</td>
<td>83</td>
<td>Re-meandering, tile drain cut</td>
<td>5.7 (2.9)</td>
<td>7</td>
</tr>
<tr>
<td>Grevedbakken</td>
<td>2003</td>
<td>44.1</td>
<td>24.0</td>
<td>85</td>
<td>Tile drain cut</td>
<td>1.4 (0.0)</td>
<td>7</td>
</tr>
<tr>
<td>Hammerdam</td>
<td>2005</td>
<td>9.8</td>
<td>1.9</td>
<td>75</td>
<td>Re-meandering, tile drain cut</td>
<td>2.9 (0.9)</td>
<td>5</td>
</tr>
<tr>
<td>Brahetrolleborg Gods</td>
<td>2008</td>
<td>45.6</td>
<td>45.6</td>
<td>76</td>
<td>Re-meandering, tile drain cut</td>
<td>2.5 (0.0)</td>
<td>6</td>
</tr>
<tr>
<td>River Odense, stage 1</td>
<td>2009</td>
<td>68.8</td>
<td>46.8</td>
<td>91</td>
<td>Re-meandering, tile drain cut</td>
<td>6.8 (0.3)</td>
<td>9</td>
</tr>
<tr>
<td>Posens Mose</td>
<td>2009</td>
<td>26.1</td>
<td>–</td>
<td>465</td>
<td>Tile drain cut</td>
<td>1.7 (0.3)</td>
<td>8</td>
</tr>
<tr>
<td>River Odense, stage 2</td>
<td>2010</td>
<td>255.7</td>
<td>–</td>
<td>734</td>
<td>Re-meandering, tile drain cut</td>
<td>8.8 (5.2)</td>
<td>70</td>
</tr>
<tr>
<td>River Silke</td>
<td>2011</td>
<td>146.9</td>
<td>~146.9</td>
<td>261</td>
<td>Re-meandering, tile drain cut</td>
<td>1.4 (0.3)</td>
<td>25</td>
</tr>
</tbody>
</table>

* Data from Lewandowska et al. (2020).
LEDa Traitbase – a database of life history traits of the Northwest European flora – was used to allocate dispersal traits to species registered in 10 or more vegetation plots, amounting to 45 species in total (Kleyer et al., 2008). Equisetum palustre was excluded as no information on its dispersal was available in the database, while information about the dispersal of Taraxacum officinale was available only at genus level.

Data analysis was done using R version 3.5.3 as well as R Studio (R Studio, 2020; The R Foundation, 2020). To analyse the effect of time since restoration on the plant community, the FREQ and GLM procedures in Statistical Analysis Software SAS/STAT® version 9.4 were applied (SAS Institute Inc, 2017). We used a space-for-time substitution assuming that the spatial and temporal variation would be comparable within the studied catchment to test whether plant community characteristics approached that of natural wetland vegetation with increasing time since restoration. We defined three age classes for conducting the statistics: 7.5 (plots with wetland age 7 and 8 years), 11 (plots with wetland age 9, 10 and 13 years) and 16 (plots with age 15 and 17) as well as five plant community groups created relative to the characteristic plant species and ecology. As there was only one vegetation plot representing P. hybridus stands and as it differed from the rest of the plots regarding characteristic species, it was excluded from the analysis. Maps were created in QGIS Desktop 3.12.3.

3. Results

3.1. Plant communities

A total of 11 different plant communities were identified in the investigated areas based on the outcome of the supervised classification (Fig. 2a). The most common vegetation types were humid grassland and moist fallow field vegetation (combined 220 ha or 26%), improved grassland vegetation dominated by common, formerly sown grasses (217 ha or 25%), and reed bed vegetation, consisting of tall helophytes (105 ha or 12%) (for details see Table 2).

Indicator species for the most common plant communities were Agrostis stolonifera, Ranunculus repens and Rumex crispus in moist fallow field vegetation, Deschampsia cespitosa, Epilobium parviflorum and Filipendula ulmaria in humid grassland vegetation, Lolium perenne, Phleum pratense and Taraxacum sp. in improved grassland vegetation, Epilobium hirsutum, Glyceria maxima and Phalaris arundinacea in reed bed vegetation (for the complete list see Appendix 1; Nygaard et al., 2009).

We did not find evidence that plant community characteristics changed with the age of the restoration since no significant changes occurred in the abundance of any of the communities with time (Fig. 2b; Table 3).

3.2. Species richness and Shannon index

The species richness and Shannon index were similar for all plant community types. The mean vascular plant and bryophyte species richness was 9.5 ± 4.5 species per plot. Species richness was highest in mesophile grasslands (11.9 ± 7.3) and rich fens (11.8 ± 7.2) and lowest in improved grasslands (8.4 ± 2.7) and reed beds (7.8 ± 3.7) (Appendix 2). The average species richness did not change significantly with restoration age (r = 0.03, p = 0.61, Kendall’s rank correlation). We observed a mean richness ranging from 8.7 ± 4.7 species per plot at sites restored 10 years before sampling to 10.1 ± 4.7 species per plot at sites restored 17 years before sampling (Fig. 3a). The largest range of values was found in plots restored eight years prior to sampling, with values varying from one to 36 species per plot.

The mean Shannon index for all plots was 1.2 ± 0.5. The highest value was 1.5 ± 0.3 observed in plots categorised as humid grasslands and moist fallow fields, while the lowest values were recorded in P. hybridus stands (0.7; only one plot) and Molinia caerulea meadows (0.7 ± 0.1) (Appendix 3). The average Shannon index values varied from 1.1 ± 0.5 in plots restored eight years before sampling to 1.3 ± 0.7 in the plots restored 13 years before sampling (Fig. 3b), again without any significant pattern (r = 0.1, p = 0.06, Kendall’s rank correlation). The largest variation in the Shannon index was recorded in plots restored seven and 17 years before sampling.

3.3. Species dispersal

Most of the species had several dispersal strategies. The main types of dispersal of the most common plant species were hydrochory (41 species), zoochory (40 species), hemerochory (34 species) and anemochory (32 species). The most common types of dispersal in wetlands restored 7 to 11 years prior to sampling were zoochory, hydrochory (32 species for each type), hemerochory (26 species) and anemochory (25 species), while dispersal by zoochory, hydrochory, hemerochory (16 species for each type) and anemochory (13 species) was most common in wetlands restored 13 to 17 years before sampling. A total of 12 species displayed all four dispersal types, while 24 species displayed three of the four main dispersal types.

3.4. Ellenberg indicator values for light, moisture and soil fertility

The community-weighted mean for the Ellenberg indicator value for light was 7.2 ± 0.5, corresponding to half-light conditions. We observed rather similar values for all the analysed community types, ranging from 6.9 for P. hybridus stands to 8.0 ± 0.0 for M. caerulea meadows, representing the interval between half-light and light conditions (Appendix 4).

The community-weighted mean for Ellenberg indicator values for moisture was 7.3 ± 1.4. The highest mean was found in fen-sedge beds (9.5 ± 0.5), which characterise aquatic plants that can survive for long periods without flooding, while the lowest mean value was found in improved grasslands 5.7 ± 0.9 and mesophile grasslands 5.7 ± 1.1, representing a state between fresh and humid soils (Appendix 4).

The community-weighted mean for Ellenberg indicator values for soil fertility was 6.4 ± 1.3. The highest value was found in P. hybridus stands with an indicator value of 7.9. Humid tall herb fringe communities had the second highest indicator value, 7.6 ± 0.9. These high values indicate that the levels of available nutrients were high. The lowest value was found in the M. caerulea meadows, 3.6 ± 0.1, which is indicative of nutrient levels between nutrient poor and moderately nutrient rich (Appendix 4).

The community-weighted means for Ellenberg indicator values for light, moisture and soil fertility resemble those previously found in semi-natural and natural wetland and grassland vegetation in Denmark (Fig. 4; Nygaard et al., 2009). The only exception was M. caerulea meadows where the average community-weighted mean for Ellenberg indicator values for light from our studied wetlands was slightly higher, 8.0 ± 0.0.

Overall, there was no significant correlation between wetland age and the average community-weighted mean for Ellenberg indicator values for light, moisture or soil fertility (p > 0.05). The lowest average community-weighted mean for Ellenberg indicator values for light was 7.0 ± 0.4 in plots restored 17 years prior to sampling, while the highest value was 7.4 ± 0.4 in plots restored 10 years prior to sampling (Fig. 5a). The average community-weighted mean for Ellenberg indicator values for moisture ranged from 6.8 ± 1.4 in plots restored seven years prior to sampling to 7.9 ± 1.5 in plots restored 13 years prior to sampling (Fig. 5b). The average value of community-weighted Ellenberg indicator values for soil fertility ranged from 5.6 ± 1.2 in plots restored 13 years prior to sampling to 7.0 ± 1.1 in plots restored 15 years prior to sampling (Fig. 5c).

4. Discussion

4.1. Plant communities

We hypothesised that restored wetland plant communities would change over time with an increase in the abundance of communities

characterising natural wetland vegetation. Thus, we expected that the longer time since the restoration, the higher the resemblance to communities characterising natural wetlands in contrast to younger wetlands, which would show a stronger legacy of the land use practice prior to restoration. However, this hypothesis must be rejected for our study sites. We found that the abundance of improved grassland vegetation was rather high, while the abundance of natural plant communities (e.g., rich fens, fen-sedge beds and humid grasslands) was lower. This was observed both in recently restored wetlands and in wetlands restored a longer time ago. Specifically, in River Silke (restored in 2011) and in both stages of the River Odense restoration project (from 2009 and 2010, respectively), improved grassland vegetation covered more than 25% of the restored area. Moreover, in Karlsøen (restored in 2001) improved grassland vegetation covered 19% of the restored area.

4.2. Species richness and Shannon index

The mean species richness of the plant communities in the studied areas was low (Section 3.2). In comparison, species richness varied from 6.4 to 40.8 species/m² in areas along six naturally meandering streams, with an average species richness of 24 species/m² in the fen community (Audet et al., 2015). In a monitoring report on wetland restoration success, species richness in calcareous fens in River Sønderå in Southern Jutland was 26.0 species/m² and 15.1 species/m² in River...
All these community types were rather productive (et al., 2006; Audet et al., 2015), characterised by high plant diversity, productive wetland community types, such as rich fens (Verhoeven et al., 2003), and this may have consequences for other plant-linked ecosystem functions (Göthe et al., 2016; Zak et al., 2019).

Statistical parameters of the generalized linear models on wetland age effect on plant communities in the Kratholm catchment.

Table 3

<table>
<thead>
<tr>
<th>Plant community</th>
<th>River Silke</th>
<th>River Odense stage 2</th>
<th>River Odense stage 1</th>
<th>Posers Mose</th>
<th>Brahetrolle-høg Gods</th>
<th>Hammer-dam</th>
<th>Gedde-balken</th>
<th>Sandholtt Melle-balken</th>
<th>River Odense near Brøby-værk</th>
<th>Karl-mosen</th>
<th>In total</th>
</tr>
</thead>
<tbody>
<tr>
<td>Humid grasslands</td>
<td>4.2</td>
<td>38.4</td>
<td>13.9</td>
<td>1.3</td>
<td>13.7</td>
<td>4.6</td>
<td>1.6</td>
<td>0.1</td>
<td>25.6</td>
<td>0.3</td>
<td>141.5</td>
</tr>
<tr>
<td>%</td>
<td>29</td>
<td>13</td>
<td>20</td>
<td>5</td>
<td>30</td>
<td>47</td>
<td>4</td>
<td>0</td>
<td>25</td>
<td>0</td>
<td>17</td>
</tr>
<tr>
<td>Moist fallow fields</td>
<td>10.3</td>
<td>44.8</td>
<td>3.1</td>
<td>1.0</td>
<td>0.0</td>
<td>0.0</td>
<td>3.7</td>
<td>11.3</td>
<td>2.2</td>
<td>1.6</td>
<td>78.0</td>
</tr>
<tr>
<td>%</td>
<td>7</td>
<td>15</td>
<td>5</td>
<td>4</td>
<td>0</td>
<td>0</td>
<td>8</td>
<td>21</td>
<td>2</td>
<td>3</td>
<td>9</td>
</tr>
<tr>
<td>Moist fallow fields and humid grasslands combined</td>
<td>52.3</td>
<td>83.2</td>
<td>17.0</td>
<td>2.3</td>
<td>13.7</td>
<td>4.6</td>
<td>5.3</td>
<td>11.4</td>
<td>27.8</td>
<td>1.9</td>
<td>219.5</td>
</tr>
<tr>
<td>%</td>
<td>36</td>
<td>28</td>
<td>25</td>
<td>9</td>
<td>30</td>
<td>47</td>
<td>12</td>
<td>21</td>
<td>27</td>
<td>3</td>
<td>26</td>
</tr>
<tr>
<td>Improved grasslands</td>
<td>37.5</td>
<td>108.6</td>
<td>26.4</td>
<td>1.1</td>
<td>16.8</td>
<td>1.1</td>
<td>1.0</td>
<td>9.0</td>
<td>11.1</td>
<td>1.6</td>
<td>217.4</td>
</tr>
<tr>
<td>%</td>
<td>26</td>
<td>34</td>
<td>38</td>
<td>4</td>
<td>37</td>
<td>11</td>
<td>2</td>
<td>17</td>
<td>11</td>
<td>19</td>
<td>25</td>
</tr>
<tr>
<td>Reed beds</td>
<td>16.0</td>
<td>30.8</td>
<td>7.1</td>
<td>3.9</td>
<td>9.7</td>
<td>0.4</td>
<td>5.4</td>
<td>0.7</td>
<td>15.4</td>
<td>15</td>
<td>104.5</td>
</tr>
<tr>
<td>%</td>
<td>11</td>
<td>10</td>
<td>10</td>
<td>15</td>
<td>21</td>
<td>4</td>
<td>12</td>
<td>1</td>
<td>15</td>
<td>24</td>
<td>12</td>
</tr>
<tr>
<td>Dry fallow fields</td>
<td>10.3</td>
<td>7.0</td>
<td>2.4</td>
<td>1.9</td>
<td>0.0</td>
<td>0.0</td>
<td>7.5</td>
<td>0.0</td>
<td>6.8</td>
<td>8.6</td>
<td>44.5</td>
</tr>
<tr>
<td>%</td>
<td>7</td>
<td>2</td>
<td>3</td>
<td>7</td>
<td>0</td>
<td>0</td>
<td>17</td>
<td>0</td>
<td>6</td>
<td>14</td>
<td>5</td>
</tr>
<tr>
<td>Humid tall herb fringes</td>
<td>1.8</td>
<td>4.5</td>
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</tr>
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<td>4</td>
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</tr>
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</tr>
<tr>
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<tr>
<td>%</td>
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<tr>
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<td>%</td>
<td>0</td>
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<td>0</td>
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<td>In total</td>
<td>118.1</td>
<td>234.0</td>
<td>53.3</td>
<td>9.5</td>
<td>41.2</td>
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<tr>
<td>%</td>
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<td>46</td>
<td>43</td>
<td>61</td>
<td>61</td>
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Hellegård å in Central Jutland (Hoffmann et al., 2006). The most common plant communities found in the studied wetlands in the Kratholm catchment were humid grasslands, which can be considered a target community, moist fallow fields, improved grasslands and reed beds. All these community types were rather productive – even the humid grasslands indicated high nutrient availability. In contrast, low-productive wetland community types, such as rich fens (Verhoeven et al., 2006; Audet et al., 2015), characterised by high plant diversity, were rare in the studied areas.

Similar to species richness, the mean values of the Shannon diversity index were low (Section 3.2). In comparison, Baattrup-Pedersen et al. (2013a) found a higher Shannon index for the same communities along medium-sized naturally meandering streams, being 1.9 in reed beds, 2.4 in meadows and 2.9 in rich fens. Concurrently, a turnover in community types occurred along a gradient in nutrient availability, with a decline in rich fen species and an increase in productive and fast-growing helophytes.

We did not find a significant effect of wetland age on either plant communities, species richness or the Shannon species diversity index in the restored wetlands, not even after combining the plant communities into larger groups and wetland age into different age classes (Fig. 3). This finding demonstrates that a restoration period of almost 20 years might not in itself be sufficient for natural plant communities to recover and this may have consequences for other plant-linked ecosystem functions (Göthe et al., 2016; Zak et al., 2019).

4.3. Species dispersal

It has been shown that species of fens and fen meadows generally have transient and short-term persistent seeds, while species of degraded systems have mainly long-term persistent seeds and, additionally, that the abundance of plants that regenerate from seeds and form persistent seed banks increase with increasing degradation level (Klimkowska et al., 2010b). Consequently, seed banks are not always reliable regarding the recovery of wetland vegetation (Middleton, 2003; Ma et al., 2011) and the prospects for restoration of degraded wetlands can therefore be hampered (Klimkowska et al., 2010b). The streams in the Kratholm catchment were straightened in the 1940s and since then most of the adjacent areas have been used for agriculture until the implementation of restoration measures. Hence, the local wetland plant seed bank is likely highly degraded with mostly persistent species, and this may act as an important barrier for the development of species-rich wetland plant communities (Målson et al., 2008; Stroh et al., 2012).

Instead, species recovery in the restored areas had to rely on long-distance dispersal of species. We found that hydrochorous, zoochorous, hemerochory and anemochory were the most common dispersal types among the recorded species and also that most species displayed several dispersal types. Anemochorous, hydrochorous and zoochorous species have a high potential for long-distance dispersal (Nilsson et al., 2010; Schöpke et al., 2019). However, anemochory is rather unimportant for dispersal of wetland propagules in contrast to hydrochory as a
A considerable number of viable seeds can be deposited in restored areas following a flooding episode (Nilsson et al., 2010). This also means that restoring the natural hydrological regime, including flooding, can be important for species recruitment since dispersal pathways are connected (Middleton, 2003). The diversity of the deposited seeds can be low in catchments with high levels of agriculture (Baattrup-Pedersen et al., 2013b; Baattrup-Pedersen et al., 2013c). Thus, previous investigations have revealed that mainly seeds from species such as Urtica dioica, Juncus effusus and J. bufonius germinated from sediments following inundation (Riis et al., 2014). Both Juncus species are abundant in natural wetlands in Denmark, but they are also common and, consequently, they are not likely to improve the overall diversity of the area. To improve conditions for species recovery diaspor transfer could be applied as done in fen meadows and wet meadows in Europe (Klimkowska et al., 2007; Klimkowska et al., 2010a).

**Fig. 3.** a. Species richness in wetlands with a different wetland age in the Kratholm catchment (no significant differences, \( r = 0.03, p = 0.61 \), Kendall’s rank correlation). Fig. 3b. Shannon species diversity index for vegetation plots described in restored wetlands in the Kratholm catchment (no significant differences, \( r = 0.1, p = 0.06 \), Kendall’s rank correlation). The size of a vegetation plot was 4 m². In the box plots, the bottom and top of the box show the 25th and 75th percentiles, the band near the middle of the box is the 50th percentile (the median); the ends of the whiskers represent the minimum and maximum of the data. The circles show outliers, while red stars indicate mean values. Sample size is given above each box.

**Fig. 4.** Comparison of average Ellenberg indicator values for light, moisture, and soil fertility for 17 Danish semi-natural and natural wetland and grassland plant communities based on a total of 13,000 plots covering a gradient ranging from natural habitats with spontaneous vegetation (e.g., mires and springs) to meadows and pastures (Nygaard et al., 2009) with the studied plant communities from Kratholm catchment (marked in red), community-weighted means for each of the communities are shown as an orange star, values for humid grasslands and moist fallow fields were combined. In the box plots, the bottom and top of the box describe the 25th and 75th percentiles, the band near the middle of the box is the 50th percentile (the median); the ends of the whiskers represent the minimum and maximum of the data. The circles show outliers, while red stars indicate mean values. Sample size is given above each box.
4.4. Abiotic conditions and restoration success

Despite the fact that the restorations in the Kratholm catchment were undertaken many years ago, the establishment of natural wetland plant communities did not occur. As discussed above, this may reflect poor seed banks and an inadequate restoration of the hydrology of the areas but also that the abiotic conditions necessary for their establishment and growth within the areas were inadequate. A closer study of the Ellenberg indicator values conducted to get insight into the abiotic conditions revealed that the plants preferring half-light conditions were most abundant in the wetland sites. This coincides with the Danish fen habitat assessment based on information from 4154 vegetation plots, where the average Ellenberg indicator value was found to be 7.0, describing half-light conditions (Andersen et al., 2013). Most of the studied areas in Kratholm catchment were managed by mowing or grazing, thus preventing the development of dense halophyte stands and woody vegetation. However, in some areas we observed a relatively high abundance of Phragmites australis and different species of Salix sp. and Alnus sp., indicative of succession, as also observed along the River Skjern in Central Jutland following restoration (Pedersen et al., 2007). If this succession continues, the light availability in the herb and bryophyte layer will be restricted, but, at the same time, it will open up for colonisation of new species associated with trees and shrubs, which may contribute to the overall diversity of the area.

As expected, the majority of species in the restored areas were adapted to humid conditions, which is comparable with the Ellenberg indicator values for moisture in fens (7.5 – indicator for state between humidity and wetness) found by Andersen et al. (2013). However, 1/4 of the total restoration area in the Kratholm catchment was classified as improved grasslands (217 ha) corresponding to the rather dry and thus unfavourable soil conditions for the development of wetland plant communities.

Regarding the Ellenberg indicator values for soil fertility, a majority of the recorded plant species are found on soils of intermediate and high nutrient availability. These levels are markedly higher than in Danish fens having a mean Ellenberg indicator value of 4.7 corresponding to moderately nutrient-rich sites (Andersen et al., 2013). The high Ellenberg indicator value suggests that the productivity of the plant community types was higher than that found in natural rich fen vegetation (Baattrup-Pedersen et al., 2014) and this may be a major obstacle for the establishment and growth of target species in the restored areas. It is well documented that species richness is higher in wetlands with a low nutrient input (Zedler, 2000; Güsewell et al., 2005; Audet et al., 2015) and vice versa, a decrease in species richness occurred at

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**Fig. 5.** Average community-weighted Ellenberg indicator values for light, moisture, and soil fertility in wetlands in the Kratholm catchment with a different restoration age (no significant differences, $p > 0.05$). The size of a plot was 4 m². In the box plots, the bottom and top of the box describe the 25th and 75th percentiles, the band near the middle of the box is the 50th percentile (the median); the ends of the whiskers represent the minimum and maximum of the data. The circles show outliers, while red stars indicate mean values. Sample size is given above or under each box. Indicator values for light conditions: 1 – deep shade, 2 – between 1 and 3, 3 – shade, 4 – between 3 and 5, 5 – semi-shade, 6 – between 5 and 7, 7 – half-light, 8 – light, 9 – full light. Indicator values for moisture: 1 – strong drought indicator, 2 – between 1 and 3, 3 – damp soil, 4 – between 3 and 5, 5 – fresh soils, 6 – between 5 and 7, 7 – humidity indicator, 8 – between 7 and 9, 9 – wetness indicator, 10 – aquatic plants that can survive for long periods without flooding, 11 – aquatic plants rooted under water, 12 – permanently or almost permanently submerged aquatic plants. Indicator values for soil fertility: 1 – nutrient-poorest sites, 2 – between 1 and 3, 3 – nutrient-poor sites, 4 – between 3 and 5, 5 – moderately nutrient-rich sites, 6 – between 5 and 7, 7 – nutrient-rich sites, 8 – pronounced nutrient indicator, 9 – very nutrient-rich sites (Ellenberg et al., 1992).
increased productivity (Older Venterink et al., 2003; Kotowski and Van Diggelen, 2004). In accordance, the highest species richness in riparian areas typically occurs in groundwater discharge areas characterised by low nutrient contents and at the same time these areas also tend to be more resistant to human-induced regulation of the hydrological regime, which together allows the assembly of larger and more stable wetland plant populations (Jansson et al., 2007).

The nutrient input will likely continue to be high at the restored sites in the Kratholm catchment due to intensive agricultural land use. Arable land occupies 60–70% of the catchment (Kronvang et al., 2012; Kronvang et al., 2016) and the nutrient input to the restored wetlands varies from 24 to 396 kg/ha/year, while phosphorus deposition rates via sedimentation vary between 1 and 674 kg/ha/36 days per year (Lewandowska et al., 2020). Similar to other wetland restoration projects, the continued elevated level of nutrients can therefore be the most important barrier for the recovery of diverse plant communities (Pedersen et al., 2007; Moreno-Mateos et al., 2012; Zak et al., 2015).

5. Conclusions

The hypothesis that the restored wetland plant communities in the Kratholm catchment would improve with time following restoration was not confirmed. Instead, the dominant plant communities were humid grasslands, moist fallow fields and improved grasslands. We find it likely that continuous high nutrient input to the areas is a main reason why no directional changes in the plant communities occurred. As a consequence, it seems to be a highly challenging task to achieve improvements in biodiversity if relying on spontaneous processes in wetland areas restored to mitigate nutrient losses from agricultural lands. Additionally, lack of local source populations and restricted dispersal of species characterising natural wetlands may contribute to explain the absence of directional changes. To enhance the process, top soil removal and diaspore transfer may be considered for inclusion in the restoration actions implemented to facilitate the development of natural wetland vegetation but such a measure should be considered carefully as it may fail if elevated nutrient input continues.

Conflict of interest

None.

Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.scitotenv.2021.149146.

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