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RESEARCH ARTICLE

Landscape-level vegetation conversion and biodiversity improvement after 33 years of restoration management in the Drentsche Aa brook valley

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Effects of restoration management on peatlands formerly used for intensive agriculture are rarely evaluated or discussed over larger spatial and temporal scales. Here, restoration of the Drentsche Aa brook valley was evaluated at the landscape level. Detailed vegetation maps were used with 1982 serving as the baseline, 1994 representing vegetation before rewetting, and 2015 after rewetting. Based on the mapping typology and phytosociological records, 15 main vegetation types were distinguished. Species richness and Shannon index values were calculated as plant diversity indicators, and the number of rare species was used as a rarity indicator. Basic landscape metrics were evaluated as measures of spatial heterogeneity. Results after restoration measures showed extensive vegetation type conversions clearly pointed to lower nutrient levels, and an increase in marsh vegetation at the cost of wet meadows. Significantly higher landscape heterogeneity was achieved, while biodiversity indicators showed small differences over time due to a mixture of positive and negative changes at different locations. This study shows that long-term restoration management on agricultural peatlands can be successful at landscape level. Our experience highlights the importance of continuity in management given the prolonged influence by intensive agriculture, both from former land uses and from the surrounding valley flanks.

Key words: landscape restoration, peatland rewetting, species rarity, species richness, vegetation mapping

Implications for Practice

- Implementing long-term landscape restoration on former intensive agricultural peatland can improve biodiversity by lowering nutrient levels, increasing spatial heterogeneity, and restoring typical marsh vegetation.
- High soil nutrient availability is the major constraint for the success of peatland restoration, even after decades of management for nutrient removal. Rewetting with unpolluted anoxic groundwater and continuous management are the key solutions to this problem.
- Landscape-scale biodiversity restoration requires clear objectives focusing on either general biodiversity value or specific target species (given the different performances of species richness and rarity), and spatially explicit planning due to the contrasting changes at patch level.

Introduction

Drastic anthropogenic influences on ecosystems and ambitious goals to repair these damages are boosting the need for large-scale ecological restoration (Crossman & Bryan 2006; Jones et al. 2018). However, the success of restoration varies substantially among sites despite the increasing amount of money and labor being invested (Holl et al. 2003). Much of the potential insight from the past and ongoing restoration studies still needs to be explored by long-term monitoring to understand the ecological mechanisms underlying success (Holl et al. 2003).

Peatlands, including both living peat-forming vegetation (mires) and their replacement communities on peat soils that no longer form peat, are unique ecosystems with characteristics favorable for hosting many specialist species. These characteristics include high soil moisture content, low oxygen content, and limited nutrient availability (Lamers et al. 2015; Minayeva et al. 2017). Peatlands also yield a vast variety of ecosystem services, including prevention of pollution through uptake by plants and microbes (Vymazal 2007), hydraulic buffer function

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through soil water retention (Ahmad et al. 2020), and provisioning of biomass as raw material (Wichmann et al. 2020). Peatlands are also very important for mitigating greenhouse gas emissions, which are driving climate change (Leifeld & Menichetti 2018). However, peatlands have suffered severe degradation due to human activities, such as drainage, peat extraction, and intensive agricultural production (Leifeld & Menichetti 2018; Swindles et al. 2019). From a technical point of view, it is clear that peatland restoration requires improved hydrological regimes, water quality, and microclimate. Measures to achieve these conditions include rewetting, biomass removal without fertilization, and mulching (Bakker 1989; Gorham & Rochefort 2003; Van Dijk et al. 2007; Schumann & Joosten 2008). From a practical perspective, these measures require different spatial and temporal scales (Lamers et al. 2015). For example, rewetting requires landscape-level measures that include the wetland's catchment, whereas topsoil removal may be applied at a smaller scale. To make the optimal policy decision on restoration measures, it is vital to obtain knowledge about key factors and processes at different scales. Effective monitoring of integrated, landscape-scale restoration programs for a long period is therefore needed.

Currently, studies on large-scale experimentation in long-term restoration projects are scarce. According to Wagner et al. (2008), only 13% of the experiments on wetland restoration deal with the landscape scale, whereas the majority of cases only focus on area less than 1 ha. With respect to time period, "long-term" responses of peatlands to restoration have been studied mainly over time spans of less than two decades (Grootjans et al. 2002).

Meanwhile, results of biodiversity assessments strongly depend on the chosen spatiotemporal scale, and conclusions are not transferable between different scales (Waldhardt 2003). Spatially, peatlands have a significant impact on biodiversity far beyond their borders by regulating the hydrology and microclimate of adjacent areas (Parish et al. 2008). Temporally, long-term effect of single restoration measures, like the influence of raised water tables on biogeochemical and physical properties, strongly affect the success of restoration projects (Lamers et al. 2015). Previous studies have demonstrated considerable variations in the outcome of peatland restoration at different scales. Guo et al. (2017) reported an effective natural succession-based restoration measure on cultivated peatlands in northeastern China that reached 64% similarity to a natural peatland in 15 years. Similarly, Strobl et al. (2020) observed a progressive plant diversity development toward reference conditions within two decades of rewetting in central Germany. Meanwhile, with a much shorter time period within 5 years after implementation, Van Dijk et al. (2007) found that rewetting in formerly intensively fertilized agricultural fields was not effective in restoring species-rich fen vegetation.

Given the scarcity of studies on the effect of restoration both on larger scales and over longer periods of time, and the uncertainties in the results of restoration management across different spatiotemporal scales, our research questions address (1) what is the overall effect of long-term peatland restoration on vegetation type and biodiversity value at landscape level, and (2) what is the spatial pattern of local-scale vegetation conversion and biodiversity changes within the landscape.

Methods

Study Area

The restored site is located in the Drentsche Aa brook valley in the province of Drenthe in the northeast of the Netherlands (Fig. 1; 53°7′12.39″N, 6°37′34.45″E). The 30,000 ha brook valley area has a long history of ongoing agricultural drainage for over 300 years and has been intensively fertilized for decades, during which natural mires were deeply drained and fertilized for dairy production. Nearly 40 years ago, restoration of the degraded peatlands started through gradual retreat of agricultural activities, cessation of fertilization, topsoil removal, and mowing of biomass (Bakker 1989; Olff & Bakker 1991). Since 1996, more than 600 ha of land in this area have been rewetted by removing drainage ditches, with the aim of reinstating upward groundwater discharge and facilitating recovery of species-rich meadow vegetation. Since 2002, one third of the brook valley has become part of a designated nature reserve (Fig. 1). During restoration, the central part of the brook valley was mapped in detail three times to monitor vegetation changes in 1982, 1994, and 2015. In this study, the vegetation map of 1982 is regarded as the baseline representing an early stage of restoration, while the 1994 and 2015 maps represent the stages of restoration before and after rewetting.

Vegetation Mapping and Type Conversions

Vegetation of the restored areas was repeatedly mapped following a regionally specific typology system (Everts et al. 1980; Everts & de Vries 1991) using the Braun-Blanquet approach (Braun-Blanquet 1964). The typology was adopted from phytosociological classification systems of the Netherlands (Schaminée et al. 1995) and Germany (Ellenberg 1978). Nomenclature of plant communities follows Schaminée et al. (1995) and vascular plants follow Van der Meijden (1996). In all three vegetation surveys, a ground-based mapping technique was applied using aerial photographs as base maps, based on the presence and coverage of dominant and characteristic plant species of each vegetation unit defined in the typology. In the 1994 and 2015 surveys, the typology was further underpinned by detailed vegetation sampling (749 and 395 relevés 2×2 m in size, respectively) for 288 vegetation communities (association level according to the Dutch vegetation classification system, Schaminée et al. 1995). These relevés were also used in assessing the biodiversity values of the distinguished vegetation types. The mapping area was expanded in each survey. In the present study, only the overlapping 1,102 ha area in all three surveys was used.

The environmental conditions of the landscape were estimated based on bioindication by the vegetation communities. Nutrient level of the vegetation was classified according to phytosociological literature into oligotrophic, mesotrophic, eutrophic, and hypertrophic (Ellenberg 1978; Pott 1992; Schaminée

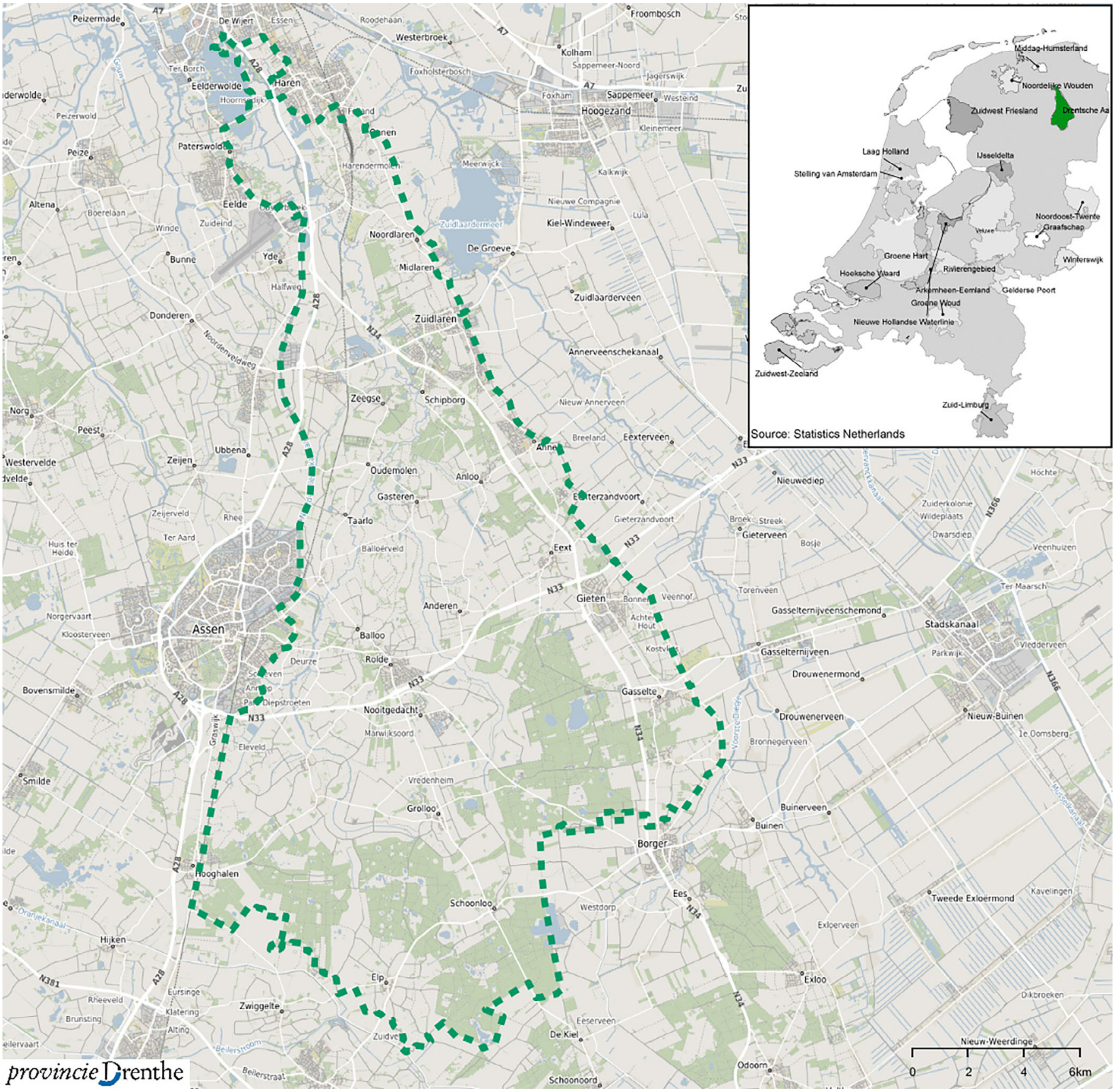

Figure 1. Location of the study area. The distribution of Dutch nature parks at the top right corner was retrieved from Statistics Netherlands (www.cbs.nl). The borders of the National Park Drentsche Aa (green dashed line, including infrastructures and build-up areas) were retrieved from the park website (www.drentscheaa.nl).

et al. 1995 as described in Everts & de Vries 1991). The indicated range of groundwater fluctuation was based on literature data from Western Europe (e.g. De Haan 1992; Grootjans & Ten Klooster 1980 as described in Liu et al. 2020). For comparison at the landscape level, the basic vegetation communities were clustered into 15 main vegetation types indicating similar environmental conditions and based on the Dutch vegetation classification system (Table S1; Schaminée et al. 1995). These vegetation types range from typical mire vegetation (living peat-forming vegetation such as *Sphagnum* and sedge vegetation types) to other vegetation on peatlands (such as wet meadows and grasslands). The original maps at the vegetation community level were then reclassified into main vegetation types. Overlaying the three vegetation maps resulted in 1,102 ha of matched area. These distribution maps of main vegetation types were then used to calculate areas and assess trends in vegetation change.

Specific categorical conversions in vegetation cover from one vegetation type to another were calculated using conversion matrices according to the systematic transition assessment as introduced by Pontius et al. (2004), which has been widely used to detect trends in land-use changes and landscape mosaic variations (Takada et al. 2010; Malatesta et al. 2019). This approach was also used to evaluate conversions in vegetation type (Greer & Stow 2003). The vegetation type distribution maps were overlaid to identify patches (mapped features) with specific directional changes in vegetation type. The resulting data were exported as spreadsheets summarizing the areas of individual vegetation types into a matrix format (Table S3). All data preparation and spatial analyses were carried out using ArcGIS 10.5 software.

Biodiversity Indicators and Landscape Metrics

Biodiversity of the main vegetation types as well as the whole landscape was assessed using the relevé data collected during the mappings of 1994 and 2015. Midpoints of the recorded Braun-Blanquet cover-abundance scales were used in calculating the biodiversity indexes for each of the relevés (Wikum & Shanholtzer 1978). Species richness (S) and Shannon index (H) were calculated as plant biodiversity indicators. Number of endangered species in the relevés were identified according to the Dutch red list (Sparrius et al. 2014) as an indicator of plant species rarity.

Plot-scale biodiversity values were allocated and up-scaled to vegetation type level and landscape level (Wagner et al. 2000; Tasser et al. 2008; Zimmermann et al. 2010). For the main vegetation type level, indicator values of individual relevés from both 1994 and 2015 were grouped into main vegetation types and calculated as mean indicator values. Mean richness and Shannon index were combined to indicate diversity level, while mean richness of rare species indicates rarity, defined as representing the likelihood of a certain vegetation type to host rare species in this study. For the landscape level, area-weighted indicator values were calculated to represent the biodiversity of the whole area.

In addition to the selected biodiversity indicators, landscape pattern metrics including number of patches (NP), patch density (PD, the number of patches per unit area), and mean patch size (MPS, average area of the patches) were calculated at the vegetation-type level and the landscape level using the software FRAGSTATS v4 software (McGarigal et al. 2012). Distribution maps of the main vegetation types were converted into raster format and fed into the software with a cell size of 15 m. These landscape metrics are basic measurements of spatial patterns and distributions of the main vegetation types (Pătru-Stupariu et al. 2017; Szilassi et al. 2017). Landscape diversity metrics, such as Shannon's and Simpson's diversity and evenness indexes, were tested but not included. Differences between these indexes among years were negligible and therefore not interpretable due to the fixed number of vegetation types (i.e. patch classes) according to the vegetation typology in this study. Descriptions and formulas of the indicators are summarized in Table S2.

Biodiversity Changes Associated to Vegetation Type Conversion

Differences of mean richness, Shannon index, and rarity values among main vegetation types were tested by Tukey's post hoc multiple comparison method using the software R version 4.0.2 (R Core Team 2020) with the package emmeans (Lenth et al. 2020). Results of the multiple comparison were exported in a matrix form. Only significant differences were considered. Results of richness and Shannon index were combined to represent species diversity. Differences between the two types were included in further analysis when either of the two indicators showed a significant difference. Rarity was considered in parallel to species diversity, representing the possibility of a vegetation type to harbor rare species. Magnitude of the differences was omitted so that the differences were simplified into positive and negative directions. The resulting matrix of biodiversity change per vegetation type conversion was then combined with the vegetation maps to generate a spatially explicit visualization of the directions in biodiversity changes.

Results

Vegetation Type Conversions

Vegetation composition of the Drentsche Aa brook valley showed drastic changes indicating significantly lowered nutrient levels (Figs. 2 & S1), following different trends of vegetation type conversion in the two mapped periods (Table S3). In the first period of restoration before rewetting (1982–1994), approximately 46.5% of the area in the landscape shifted into another vegetation type (Table S3A). After rewetting (1994–2015), these shifts were even more pronounced (approximately 62.5% of the total area changed to other types; Table S3B). The most pronounced change was the decrease in hypertrophic moist grasslands (12, the number of main vegetation type according to Table 1), of which 41% shifted to eutrophic moist grasslands (11) during the first period (Table S3; Fig. 2A). This corresponded to an almost 50% decrease in hypertrophic areas (Fig. 2B). The remainder of this hypertrophic type practically disappeared during the second period, which gave rise to a 20% increase in eutrophic moist grasslands. Mesotrophic areas showed a significant increase, especially in the second period (Fig. 2B). The area covered by open-water vegetation (1), and reed and sedge communities (2–4) doubled during this period (Fig. 2A), with conversions mainly from eutrophic/hypertrophic moist grasslands and mesotrophic wet meadows (Table S3). Meanwhile, a modest loss of wet meadows (9) that had been changed into sedges (3, 4), eutrophic grasslands (11), and ruderal (unmanaged) communities (15) occurred (Table S3; Fig. 2). A number of mesotrophic wet meadows (10) also changed into eutrophic grasslands (11) despite its overall increased coverage (Table S3; Fig. 2). In addition, woody (14) and ruderal (15) vegetation types showed significant increases in the second period, mainly converted from eutrophic/hypertrophic grassland (11, 12) and wet meadows (9).

Biodiversity Indicators and Landscape Metrics

Biodiversity indicators and landscape metrics values differed largely between main vegetation types, whereas the differences

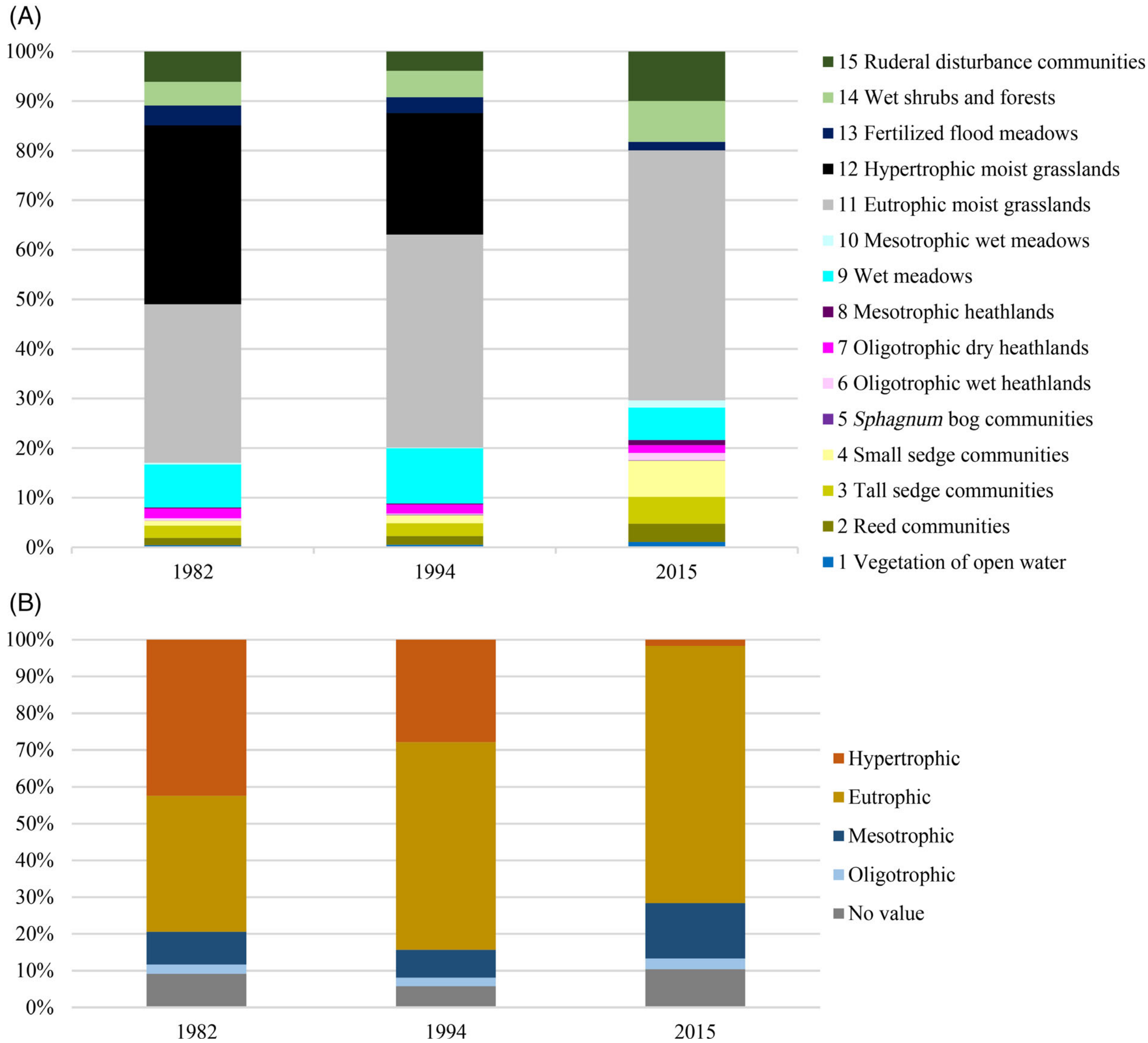

Figure 2. Proportional area coverage of (A) main vegetation types and (B) indicated nutrient levels.

between landscape level values per mapped year seem trivial (Table S4). Species-rich wet meadows (9, 10) have the highest Shannon index and rarity values. Hypertrophic types (12, 13) have the lowest values on all of the three biodiversity indicators. In general, typical mire vegetation (e.g. small sedges and *Sphagnum* bogs) perform differently in these two aspects with low species diversity but relatively high rarity, and especially small sedge communities (4) have the highest rarity. Wet shrubs and forests (14) and ruderal disturbance communities (15) are among the lowest in rarity value, although having species richness values near the average level. At the landscape level, the differences between periods were small. Both richness and rarity had increased values over the three vegetation surveys, while the Shannon index first increased then decreased again during the two periods. However, these changes are all marginal with a magnitude of less than one standard error.

The NP and PD increased substantially in the first period (1982–1994). This is characterized by large increases in sedges communities (3, 4), wet meadows (9), eutrophic grasslands (11), and woody and ruderal communities (14, 15). The negligible changes in NP and PD in the second period (1994–2015) result from a mixture of further increases from sedges, woody, and ruderal communities (3, 4, 14, 15), and drastically decreased patches of hypertrophic types (12, 13). Sedge communities (3, 4) cover a relatively large NP, despite their low occupation of areas and small patch size. At the landscape level, MPS is highly variable for all types and is generally small in magnitude (<1 ha), except for eutrophic moist grasslands (11) with patches up to over 5 ha.

Biodiversity Changes Associated to Vegetation Type Conversion

The post hoc multiple comparison revealed mixed positive and negative consequences of vegetation type conversions on biodiversity indicators (Tables 1 & S5). Conversions

Table 1. Conversion matrix of biodiversity indicators corresponding to main vegetation type conversions. Species diversity represents a combination of species richness and Shannon index. Rarity represents the number of rare species. "+" and "−" indicate positive and negative changes, respectively, and "n.s." indicates nonsignificant differences. p values and mean differences are presented in Table S5.

		To															
Species Diversity		*1*	*2*	*3*	*4*	*5*	*6*	*7*	*8*	*9*	*10*	*11*	*12*	*13*	*14*	*15*	*Main Vegetation Type*
From	1		n.s.	+	+	n.s.	+	+	+	+	+	+	+	n.s.	+	+	Vegetation of open water
	2	n.s.		n.s.	+	n.s.	n.s.	n.s.	+	+	+	+	n.s.	n.s.	+	n.s.	Reed communities
	3	−	n.s.		+	n.s.	n.s.	n.s.	+	+	+	+	n.s.	n.s.	+	n.s.	Tall sedge communities
	4	−	−	−		−	−	−	n.s.	+	+	n.s.	n.s.	−	−	−	Small sedge communities
	5	n.s.	n.s.	n.s.	+		n.s.	n.s.	+	+	+	+	n.s.	n.s.	n.s.	n.s.	*Sphagnum* bog communities
	6	−	n.s.	n.s.	+	n.s.		n.s.	n.s.	+	+	+	n.s.	n.s.	n.s.	n.s.	Oligotrophic wet heathlands
	7	−	n.s.	n.s.	+	n.s.	n.s.		n.s.	+	+	+	n.s.	n.s.	n.s.	n.s.	Oligotrophic dry heathlands
	8	−	−	−	n.s.	−	n.s.	n.s.		+	+	n.s.	n.s.	n.s.	n.s.	−	Mesotrophic heathlands
	9	−	−	−	−	−	−	−	−		n.s.	−	−	−	−	−	Wet meadows
	10	−	−	−	−	−	−	−	−	n.s.		−	−	−	−	−	Mesotrophic wet meadows
	11	−	−	−	n.s.	−	−	−	n.s.	+	+		−	−	−	−	Eutrophic moist grasslands
	12	−	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	+	+	+		n.s.	n.s.	n.s.	Hypertrophic moist grasslands
	13	n.s.	n.s.	n.s.	+	n.s.	n.s.	n.s.	n.s.	+	+	+	n.s.		n.s.	n.s.	Fertilized flood meadows
	14	−	−	−	+	n.s.	n.s.	n.s.	n.s.	+	+	+	n.s.	n.s.		−	Wet shrubs and forests
	15	−	n.s.	n.s.	+	n.s.	n.s.	n.s.	+	+	+	+	n.s.	n.s.	+		Ruderal disturbance communities

		To															
Rarity		*1*	*2*	*3*	*4*	*5*	*6*	*7*	*8*	*9*	*10*	*11*	*12*	*13*	*14*	*15*	*Main Vegetation Type*
From	1		n.s.	n.s.	+	+	n.s.	n.s.	n.s.	+	+	n.s.	n.s.	n.s.	n.s.	n.s.	Vegetation of open water
	2	n.s.		+	+	+	n.s.	n.s.	n.s.	+	+	n.s.	n.s.	n.s.	n.s.	n.s.	Reed communities
	3	n.s.	−		+	n.s.	n.s.	n.s.	n.s.	+	n.s.	n.s.	−	n.s.	−	n.s.	Tall sedge communities
	4	−	−	−		n.s.	−	−	−	n.s.	n.s.	−	−	−	−	−	Small sedge communities
	5	−	−	n.s.	n.s.		n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	−	n.s.	−	n.s.	*Sphagnum* bog communities
	6	n.s.	n.s.	n.s.	+	n.s.		n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	−	n.s.	Oligotrophic wet heathlands
	7	n.s.	n.s.	n.s.	+	n.s.	n.s.	−	n.s.	+	+	n.s.	n.s.	n.s.	n.s.	n.s.	Oligotrophic dry heathlands
	8	n.s.	n.s.	n.s.	+	n.s.	n.s.	n.s.		+	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	Mesotrophic heathlands
	9	−	−	−	n.s.	n.s.	n.s.	−	−		n.s.	−	−	−	−	−	Wet meadows
	10	−	−	n.s.	n.s.	n.s.	n.s.	−	n.s.	n.s.		−	−	−	−	−	Mesotrophic wet meadows
	11	n.s.	n.s.	n.s.	+	n.s.	n.s.	n.s.	n.s.	+	+		n.s.	n.s.	n.s.	n.s.	Eutrophic moist grasslands
	12	n.s.	n.s.	+	+	+	n.s.	n.s.	n.s.	+	+	n.s.		n.s.	n.s.	n.s.	Hypertrophic moist grasslands
	13	n.s.	n.s.	n.s.	+	n.s.	n.s.	n.s.	n.s.	+	+	n.s.	n.s.		n.s.	n.s.	Fertilized flood meadows
	14	n.s.	n.s.	+	+	+	+	n.s.	n.s.	+	+	n.s.	n.s.	n.s.		n.s.	Wet shrubs and forests
	15	n.s.	n.s.	n.s.	+	n.s.	n.s.	n.s.	n.s.	+	+	n.s.	n.s.	n.s.	n.s.		Ruderal disturbance communities

toward wet meadows (9) and mesotrophic wet meadows (10) from almost all other types have positive effects on biodiversity from both aspects. Conversions from grasslands (11–13) and woody vegetation (14) toward typical mire vegetation (3–5) have positive rarity changes in half of the cases but have less significant or even negative effects on species diversity. Meanwhile, conversions toward woody and ruderal types (14 and 15) from (mesotrophic) wet meadows (9, 10) and small sedges (4) have consistently negative effect on all the biodiversity indicators.

The application of the conversion matrices to the vegetation maps resulted in spatially explicit demonstrations of biodiversity changes (Fig. S2). The biodiversity changes corresponding to vegetation type conversion showed mixed effects for all indicators and both periods. Overall, there was a positive change across the whole landscape. During the first period (1982–1994), the percentage area having positive and negative changes was 27 and 11% for species diversity, and 8 and 6% for rarity, respectively. Similarly, percentages of the second period (1994–2015) were 29% positive and 19% negative for species diversity, and 10 and 8% for rarity.

A few prevailing directions of biodiversity change can be observed when indicator changes are combined with vegetation type conversion. An NP in the middle part of the map (Fig. 3) did not show changes between 1982 and 1994 but showed positive changes between 1994 and 2015. Examples of such positive changes are conversions from hypertrophic grasslands (12) into other vegetation types (Fig. 3A). Contrasting directions of change in biodiversity between the two periods were also observed, with positive change during the first period and negative change during the second period. This was largely characterized by patches converted into wet meadows (9) during the first period but, after rewetting, shifting to various mire vegetation types such as open water (1) and sedges (3, 4) (Fig. 3B).

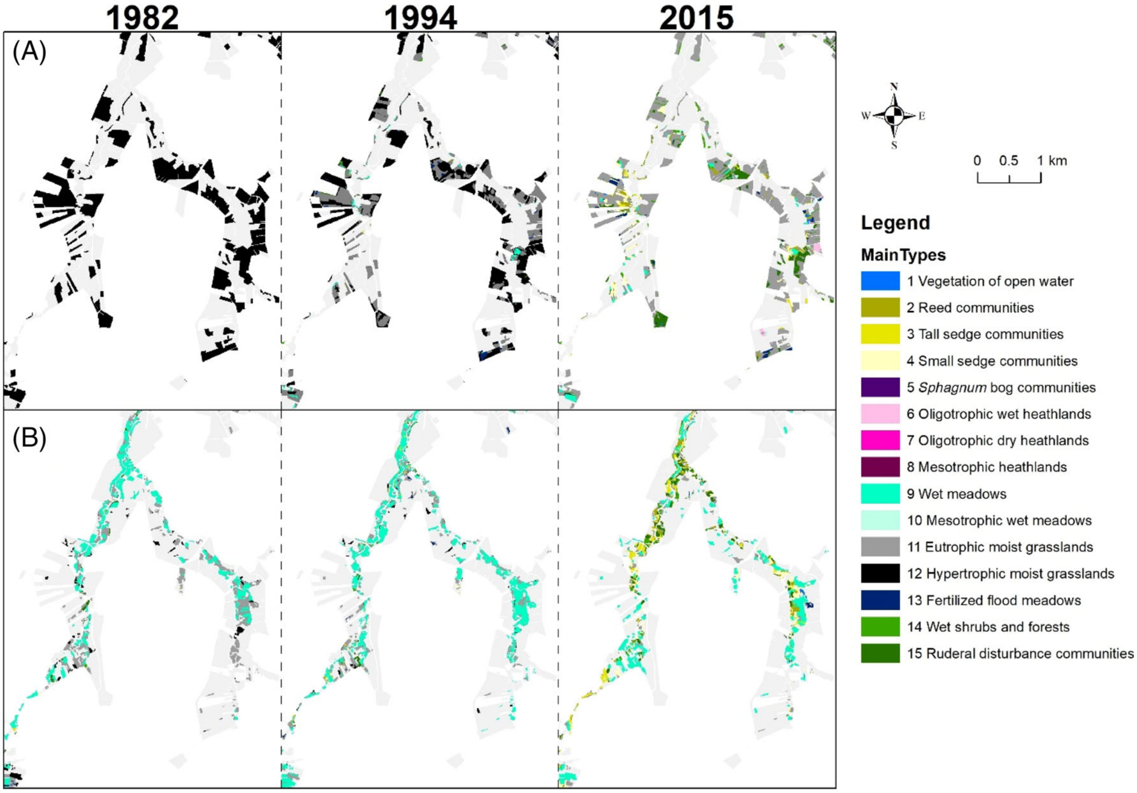

Figure 3. Examples of vegetation type conversions at middle-stream of the brook valley, illustrating key vegetation type conversions that characterized some prevailing directions of biodiversity changes: (A) conversion from hypertrophic moist grasslands to less eutrophic vegetation types; (B) conversion from wet meadows to marsh vegetation types. The complete maps are presented in Figure S1.

Discussion

Overall Improvement of Landscape-Level Biodiversity

Starting from the baseline map of 1982 that was largely dominated by hypertrophic vegetation, restoration has driven conversions toward vegetation types with lower nutrient levels during both periods. Since 1994, rewetting measures were successful and led to distinctly higher groundwater levels at the landscape level. Liu et al. (2020) estimated that 80% of the landscape had raised groundwater levels, up to an average of 9 cm higher in the center of the rewetted areas. Changes in environmental conditions introduced greater heterogeneity and complexity into the homogeneous dry and hypertrophic landscape, providing a much wider range of habitats that could support higher vegetation biodiversity (Moser et al. 2002; Caners et al. 2019). This is reflected in the substantial increases in landscape metrics in the first period from 1982 to 1994 and the subsequent improvement in species diversity and rarity. Rewetting did not further improve the heterogeneity of the landscape in the second period from 1994 to 2015. However, a larger increase in mean rarity comparing to the previous period highlighted the benefit from rewetting on supporting the occurrence of rare species.

Mixed Effects of Vegetation Conversions at Local Scale

Although an overall positive restoration effect on vegetation type conversion could be inferred at the landscape level, the co-occurring positive and negative changes of biodiversity indicators cannot be ignored. These changes, however, did not result in significant changes in landscape-level area-weighted indicator values. Looking at patch-level differences, vegetation type conversion from species-poor hypertrophic types to types associated with lower nutrient levels led to a wide-spread improvement of biodiversity. This matches the expectation that nutrient load is negatively correlated with plant diversity and is likely to lead to dominance of highly productive species (Drexler & Bedford 2002; Káplová et al. 2011), such as reed (e.g. *Phragmites australis*) or other productive grass species (e.g. *Holcus lanatus*). Lowering nutrient load should therefore remain as one of the focal points for restoration of agriculturally intensified peatlands (Walker et al. 2004; Lamers et al. 2015).

The observed vegetation type conversions and the subsequent biodiversity changes have a clear implication on the effectiveness of management practices that have taken places. Large proportions (41 and 75% in the first and second period, respectively) of the hypertrophic moist grasslands converted into eutrophic grassland with higher biodiversity values. This is in agreement with the proven benefits of topsoil removal (Patzelt et al. 2001) and mowing (Káplová et al. 2011) on reducing nutrient availability and restoring plant biodiversity. In the second period, conversions from eutrophic grassland (nearly 20%) to species-rich wet meadows and sedge communities with high rarity values highlighted the effect of rewetting in promoting mire vegetation (Tuittila et al. 2000). Meanwhile, some of the negative biodiversity changes in the second period can be associated to losses of sedges and species-rich wet meadows into woody and ruderal types. Dominance of such highly productive vegetation type could be a signal of lack of management at small scales (Lamers et al. 2015). This further stresses the need for continued active management (such as mowing and further raising groundwater levels, e.g. Middleton et al. 2006; Rochefort et al. 2016) that will in turn support a further increase in plant populations of target species.

The present analysis of repeated vegetation mapping did not allow for firm conclusions on the effect of management on the development of individual plant communities or habitat types with high conservation values. Yet, recent observations have shown positive development of rare species and habitat types in various sites where the combination of rewetting and topsoil removal had been carried out on a local scale (5–20 ha). Many nationally rare species and even locally extinct species, e.g. *Parnassia palustris*, *Epipactis palustris*, *Carex oederi*, *Carex flava*, and *Gentiana pneumonanthe*, are now present with hundreds of individuals, whereas some very rare species (e.g. *Carex hostiana* and *Liparis loeselii*) also occurred despite the small amount. These species are partly characteristic of habitat types under the framework of the European Natura 2000 legislation (e.g. alkaline fens 7,230), some of which (e.g. fen orchid, *Liparis loeselii*) are on the annex list of species with the highest protection status.

It is noteworthy that typical mire vegetation, such as the small sedges communities, have relatively low species richness values compared to wet meadows. Therefore, a shift from wet meadows to peat-forming vegetation during the second period resulted in some negative effects on biodiversity at the landscape scale. However, natural mires harbor highly specialized plant and animal species, which was reflected in the rarity values of small sedges and *Sphagnum* bogs that are similar to wet meadows and significantly higher than grassland vegetation types. In consequence, underestimation of the value of peatland biodiversity may occur if only species richness is considered (Minayeva et al. 2017). In addition, the functional significance of natural mires vegetation, such as their tolerance to high groundwater levels and importance for peat formation, cannot be fully assessed when using only richness and rarity indicators. Therefore, indicators for the assessment of peatland restoration projects need to be tailored to the targets at the respective scales. For example, indicators that address functional diversity (Laine et al. 2021), naturalness (Mendes et al. 2019), etc., might be more suitable in different situations with specific objectives such as preservation of functioning peatlands or restoration of pristine ecosystems, comparing to the basic uses of species richness or rarity indices.

Uncertainties in Indication

There are two possible sources of uncertainty in this analysis. First of all, the ground-based mapping approaches may cause uncertainties despite their advantage in providing detailed species-level information (Shuman & Ambrose 2003). Vegetation patches were manually determined on aerial photographs in the field and digitized afterwards. Borders of the patches did not always match perfectly between different years, which may have created small polygons not representing the correct vegetation type conversion after overlaying the maps. This, however, would not have had large influence on the area-weighted indicator calculations, and may not even be visible in the full-extent maps, because only less than 0.5 ha of the landscape was occupied by patches with a size smaller than one sample size (4 m^2). Meanwhile, subjective judgment by different mapping personnel may have led to inconsistent vegetation classification when dealing with similar types. However, with a working typology clearly showing the dominant and character species, such misjudgments would only happen between subtypes. The integration of 15 main vegetation types would reduce this uncertainty.

On the other hand, calculation and usage of the biodiversity indicators may cause uncertainties as well. With calculations of indicators using the entire relevé dataset due to lack of data from the year 1982, one important assumption was that biodiversity of a certain vegetation type does not change over time. However, within one main type, vegetation may either shift to its more optimum form under favorable environmental conditions or degrade due to pollution or lack of management (Patzelt et al. 2001; Káplová et al. 2011). This may cause uncertainties in the evaluation of indicator values per main type as well as in the area-weighted landscape-level values. Meanwhile, species diversity itself is largely variable under different climate, environmental, and management conditions (e.g. different species richness reported for wet meadows from Vinther & Hald 2000; Van De Riet et al. 2010; Kołos & Banaszuk 2013). Therefore, our semiqualitative approach focusing only on the significant differences tried to avoid these uncertainties. More consistent comparison can be achieved within our studied spatiotemporal scale and relatively between main vegetation types at the cost of direct comparisons of biodiversity values with other systems.

Implications: Success of Rewetting

In this study, rewetting as a measure for restoring species-rich wet meadows was successful for the Drentsche Aa. In contrast to the various cases in which rewetting of formerly intensively drained and fertilized sites would hamper restoration efforts due to eutrophication (Van Dijk et al. 2004; Smolders et al. 2010; Zak et al. 2010), our study highlights a consistent trend in vegetation change toward types associated with lower nutrient levels. This trend was even more prominent after rewetting, together with significant increases in typical peat-forming vegetation types, such as reed and sedge communities. Besides the consensus on the ability of raised water tables to promote developments of wet vegetation types (Tuittila et al. 2000), the overall success of rewetting in the Drentsche Aa brook valley can be ascribed to two aspects.

One important factor is the water source supplying the raised water level (Grootjans et al. 2002; Lucassen et al. 2005). In our case, the raised water level was realized by restoring the upward discharge of clean, anaerobic, and iron-rich groundwater. In contrast, failed rewetting cases using nutrient-rich surface water as the source for raising groundwater levels has led to allochthonous input of nutrients, but also provoked rapid and excessive mobilization of "internal" nutrients in the subsoil (Smolders et al. 2006, 2010). However, we cannot ignore the fact that 70% of the landscape in our study still exhibits relatively eutrophic conditions, and loss of mesotrophic meadows to eutrophic types was observed after rewetting. These could result from the high nutrient load as well as incoming pollution from upstream agricultural activities and valley flanks. Therefore, the importance of soil nutrient concentration as a major constraint (Van Dijk et al. 2007; Lamers et al. 2015) in restoring species-rich grassland on former agricultural land should be further considered in an integrated approach that also includes surrounding regional factors.

Rewetting in the Drentsche Aa brook valley was introduced in addition to mowing over a prolonged period of time (nearly 40 years since the initial restoration). This combination of management practices has been shown to be successful in gradually reducing high nutrient stocks (Grootjans et al. 2002; Káplová et al. 2011; Jabłońska et al. 2021). However, rewetting on the landscape scale sometimes leads to termination of management in areas that are difficult to reach. This may result in highly productive vegetation types outcompeting typical mire vegetation (Lamers et al. 2015; Minayeva et al. 2017). This could explain the doubling in coverage of woody and ruderal vegetation during the rewetted period. Therefore, consistent management is important to avoid invasion by tall woody and herbaceous species, e.g. through resuming a mowing regime with machinery adapted to very wet sites (Kozub et al. 2019) or by shrub removal (Kotowski et al. 2013).

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Supporting Information

The following information may be found in the online version of this article:

Figure S1. Distribution maps of main vegetation types.
Figure S2. Direction in biodiversity changes corresponding to vegetation type transitions.
Table S1. List of main vegetation types and their characteristics.
Table S2. List of biodiversity indicators from plot to landscape level.
Table S3. Transition matrix of main vegetation types.
Table S4. Mean biodiversity indicator values (standard error) and vegetation type level landscape metrics per main vegetation and at landscape level.
Table S5. Results of the Tukey's HSD post hoc multiple analysis of (A) species richness, (B) Shannon-index, c) rarity between main vegetation types.

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