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Herbivore exclusion and active planting stimulate reed marsh development on a newly constructed archipelago

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ABSTRACT

Wetlands provide vital services on which human societies depend. As they have been rapidly degrading due to anthropogenic impacts worldwide, wetland restoration is increasingly applied. When a return to the original state of a wetland is constrained, forward-looking restoration can provide a new way to enhance an ecosystem's ecological integrity. However, the direction in which new ecosystems will develop is strongly coupled to the initial environmental conditions and may benefit from active decisions on (future) management.

To improve the natural values of a degrading freshwater lake in the Netherlands, a forward-looking restoration project was initiated in lake Markermeer in 2016, involving the construction of a 700-ha archipelago called the "Marker Wadden". This archipelago should provide new habitat to higher trophic levels in the lake's food web through the development of currently missing Common reed (*Phragmites australis*) dominated marshlands with gradual land-water transitions. However, the restoration project faces strong grazing pressure by Greylag geese (*Anser anser*) that possibly inhibit reed establishment.

Here, we aimed to unravel the effect of herbivory by Greylag geese (using exclosures) and the introduction of reed rhizomes on early vegetation development and carbon dynamics on the bare soils of this new ecosystem in a manipulative field experiment. Our results showed that excluding herbivores strongly increased reed-vegetation cover, density and maximum height, but only when reed rhizomes were actively introduced. Spontaneous vegetation development on bare soils was limited, and colonization by Broadleaf cattail (*Typha latifolia*) dominated over reed. Net ecosystem exchange of carbon and ecosystem respiration were strongly linked to vegetation development, with highest methane emissions in the most densely vegetated plots.

We conclude that the establishment of reed marshes can strongly benefit from excluding herbivores and the introduction of reed, and that otherwise other vegetation types may establish more slowly in newly created wetlands. This illustrates how active management of vegetation development has the potential to benefit novel ecosystems.

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1. Introduction

Worldwide, wetland ecosystems are rapidly degrading due to anthropogenic influences, notably overexploitation, eutrophication, land-use changes and climate change (Díaz et al., 2020). Ecosystem degradation often results in a loss of vital ecosystem services, such as water purification, carbon storage and the provision of staging and breeding habitat for (migratory) water birds (Gibbs, 2000; Mitsch et al., 2015). To counteract these losses, ecosystem restoration is an increasingly important approach (Gibbs, 2000; Suding, 2011), as emphasized by the currently ongoing UN Decade on Ecosystem Restoration. However, classical ecosystem restoration – the return of an ecosystem to its historic and pre-human-use conditions – is often difficult and questions arise which historical reference situation should be aimed for (Hobbs and Norton, 1996; Higgs et al., 2014; van Leeuwen et al., 2021).

An innovative solution to overcome these issues associated with classical ecosystem restoration is to develop degraded ecosystems into a novel and forward-looking direction (Suding, 2011). Forward-looking restoration does not aim to return an ecosystem to its former state, but applies other modifications to enhance the functioning of severely altered and degraded landscapes (Hobbs et al., 2009). Degraded landscapes may profit from the construction of entirely novel types of ecosystems, despite that these may be rather unrelated to the historical ecosystem state. Although such forward-looking restoration does not require a historical reference state to return to, it still requires decisions on how to develop and manage an ecosystem that is moving towards a new situation. Ecosystem development can be managed and steered in a very controlled way and direction (Grumbine, 1994; Seastedt et al., 2008), or can be left passively to natural processes (e.g. rewilding, Corlett, 2016). Therefore, management choices have direct consequences for the ecosystem services that an ecosystem can ultimately provide.

The type of vegetation that develops in a novel ecosystem is crucial for its further ecological development, the higher trophic levels that it may sustain, and the ecosystem services that it can provide (Hobbs et al., 2006). Nature managers therefore often aim to facilitate and steer in the vegetation that develops by the introduction of transplants, sowing and mowing (Johst et al., 2006; Lepŝ et al., 2007; Temmink et al., 2020). However, the development is determined by complex interactions within and between biotic processes and abiotic conditions that are not always fully understood (Lamers et al., 2015; Bakker et al., 2018; Reijers et al., 2019). For example, establishment of a valuable marshland with helophytes depends on the availability of seeds for germination or possible source populations that can facilitate clonal expansion (Chambers et al., 1999; Yu et al., 2012), and water table and nutrient conditions to allow germination and growth (Ekstam et al., 1999; Yu et al., 2012; van Leeuwen et al., 2014). Following establishment, subsequent biotic interactions such as grazing by herbivorous water birds can steer vegetation development in yet another direction (Bakker et al., 2018, Reijers et al., 2019). Hence, if nature managers target development of a specific novel ecosystem with particular vegetation types and ecosystem functions, active knowledge-based management may be necessary to facilitate or accelerate ecosystem development.

An important function of wetland ecosystems is their ability to store a large amount of carbon in the soil and in above- and belowground biomass (González-Alcaraz et al., 2012). Yet, wetlands are not carbon neutral by definition (Dalal and Allen, 2008; Bridgham et al., 2013). The decomposition of organic material in the sediment may lead to microbial production of carbon dioxide (CO_2) and of methane (CH_4), which can end up in the atmosphere via diffusion, ebullition or via plants (Aben et al., 2017; Oliveira Junior et al., 2019; van den Berg et al., 2020). For example, wetland plants can function as a conduit for CH_4, which then bypasses the oxygen-rich layer in the sediment, thereby escaping oxidation and resulting in direct emissions to the atmosphere (Dingemans et al., 2011; van den Berg et al., 2020). Hence, the plant community assembly is pivotal for the functioning of wetland ecosystems, and in that light, it is important to understand the effects of the establishment of vegetation in new wetlands on carbon dynamics.

Lake Markermeer in the Netherlands is an example of a degrading shallow freshwater lake in need of restoration (Fig. 1a). The 70,000 ha lake used to be an inland sea, which was converted into a freshwater lake by dam constructions in the 20th century (Supplementary Fig. S1). The Dutch Society for Nature Conservation (Natuurmonumenten) started a forward-looking ecosystem restoration project in 2016 called the "Marker Wadden", in which they started building a completely new 700 ha-archipelago of five islands with the lake's own sediment (Fig. 1b). Their aim was to enhance the functioning and ecological integrity of the lake by creating a wetland dominated by helophyte marshes that would be able to sustain a high diversity of higher trophic levels of the food web and would perform key biogeochemical functions. On the Marker Wadden, nature managers actively introduced and stimulated reed growth, because it provides habitat for particularly insect and bird species in European wetlands (Den Hartog et al., 1989; Voslamber and Vulink, 2010). However, this approach is susceptible to herbivory by water birds – e.g. Greylag goose – during establishment (Pollet, 2001; Bakker et al., 2018; Reijers et al., 2019). However, it remains unknown how herbivory affects reed establishment and carbon dynamics in this new ecosystem.

To fill this knowledge gap, we studied the interactive effects of active planting of common reed *P. australis* (hereafter referred to as "reed") and top-down control by grazing of geese (e.g. *Anser anser*) on early vegetation development and carbon dynamics over the initial growing season by performing a manipulative field experiment. We hypothesized that (1) reed planting would accelerate reed vegetation development, but only if grazing by herbivorous water birds was prevented (Bakker et al., 2018), and that (2) such accelerated reed development would change carbon dynamics in the novel wetland, because both net CO_2 uptake (to estimate net ecosystem productivity) and CH_4 emissions would be highest in high-density vegetation where higher biomass captures more carbon, produces more organic compounds that facilitate methanogenesis, and plants may function as a chimney transporting CH_4 from the soil to the atmosphere (Dingemans et al., 2011, van den Berg et al., 2020).

2. Methods

2.1. Study site

Our study site is located in Lake Markermeer in the Netherlands, which historically was part of the Zuiderzee estuary (for a detailed history of the lake see van Leeuwen et al. 2021). The ecological integrity of this human-made lake with Nature-2000 status, however, decreased strongly over time (van der Velde et al., 2010; Noordhuis, 2014; van Riel et al., 2019; van Leeuwen et al., 2021). To boost the ecological integrity of the lake, shallow areas and soft land-to-water-transitions have been created by constructing a 700-ha archipelago named the Marker Wadden from 2016 till 2020 (coordinates 52°35′30″N 5°22′43″E). The islands were constructed by building ring dikes of sand (ranging from 1.5 to 4.0 km in length, width of 15 m), which were filled up with Holocene marine clay and silt that was pumped from the bottom of the lake up to a depth of −20 m (creating deep pits, Saaltink et al., 2016). The lake bottom itself is located 3.6 m below the water surface. In 2017, the construction of the first islands that consisted of multiple basins on which the experiment was conducted, were finished (Fig. 1a–b).

After construction, the islands harbored no vegetation and did not have a viable seedbank (see Supplementary Method S1, Supplementary Fig. S1 for details regarding our seed bank study). In the basins, the water level was managed to maintain a shallow water layer of approximately 20 cm depth up till early July 2017, after which the water was pumped out and the basins fell dry. Subsequently, the construction company refilled the basins with an extra layer of approximately 50 cm of fresh sediment in November 2017, which buried the vegetation. The

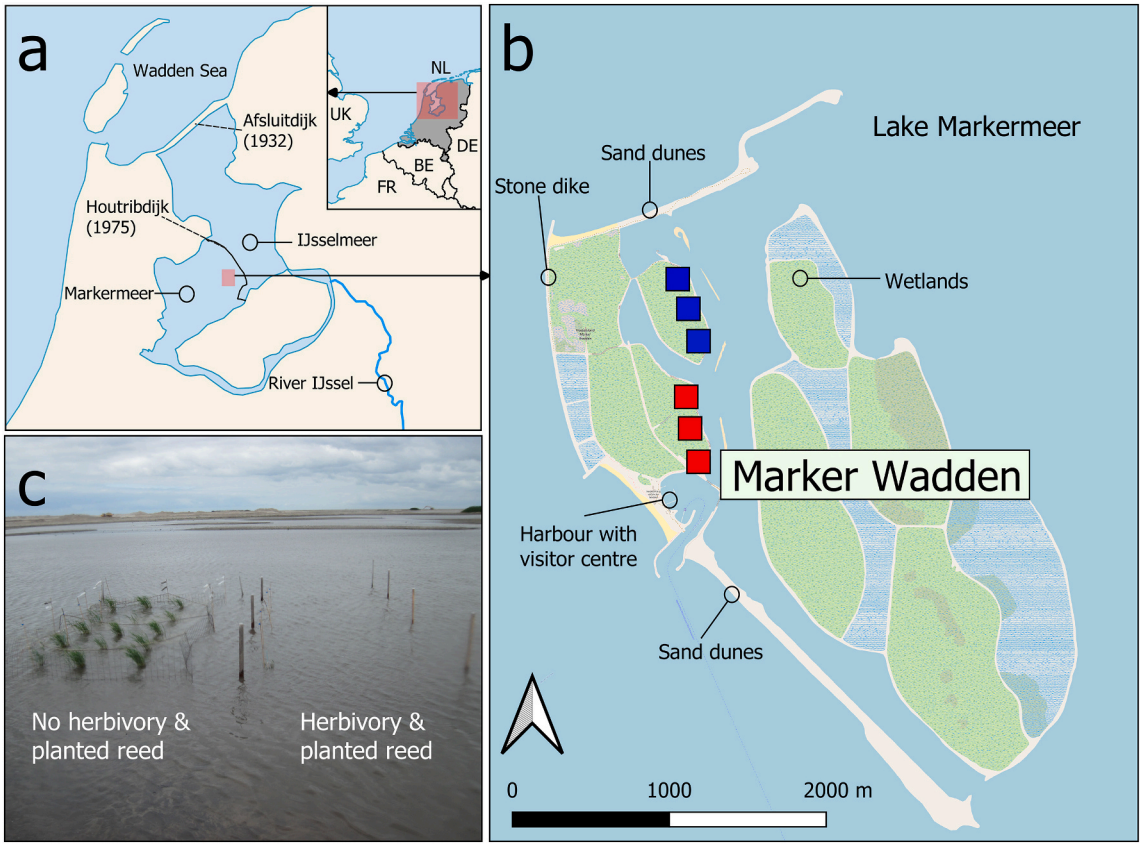

Fig. 1. Map of the experimental blocks on the newly constructed Marker Wadden. (a) The location of the Marker Wadden (red box) in the Netherlands (inset, grey) and (b) the newly constructed archipelago the Marker Wadden. Blue squares indicate the experimental blocks in basin 1 and red squares in basin 2. Note that an island can consist of multiple basins. (c) Plots without herbivory and planted reed (left) and with herbivory and planted reed (right) in June 2018 (circa 2 months after planting). The reed in the plot with herbivory is already grazed, hence not visible anymore above the water level. Map (a) created with Natural Earth and (b) with OpenStreetMap. Photo: M. v.d. Akker. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

water level was raised again in May 2018 to prevent willow (*Salix* spp.) germination, and lowered again in July 2018. Nutrient availability (plant available nitrogen and phosphorus) in the sediment top layer (10 cm) appeared to be high (Supplementary Fig. S2) and is expected to strongly facilitate high plant production rates (Smolders et al., 2008). Potential grazers on wetland vegetation in the area are water birds, in particular Greylag goose (*A. anser*), and possibly Coots (*Fulica atra*) and Mute swans (*Cygnus olor*), which frequented the area.

2.2. Experimental set-up

To study the interactive effect of reed planting and herbivory on early vegetation succession and carbon dynamics, we constructed a full-factorial field experiment. In six replicated blocks we applied each of four treatments: "no herbivory, planted reed", "herbivory, planted reed", "no herbivory, no planted reed" and "herbivory, no planted reed". To capture the spatial variability of the newly constructed islands, the experiment was divided over two basins with three-replicate blocks per basin (Fig. 1b). In each block, a "herbivory" and "no herbivory" plot was paired and one pair of "herbivory" and "no herbivory" was planted with reed in each block. All plots were 4 × 8 m. To prevent herbivory, exclosures were constructed in July and August 2017 by connecting steel-mesh-panels of 1 × 1 m (mesh size 10 × 15 cm) around the perimeter of the plot. Diagonal ropes on top of the grids prevented birds from flying in. Plots without exclosures were marked with wooden poles. Reed was planted on May 3, 2018 by transplanting 15 reed clumps consisting of plants including rhizomes (Fig. 1c), distributed in 3 rows of 5 clumps evenly in a plot. On average, a reed clump consisted of 11 ± 2 shoots (average ± SE) with a shoot length of 31.4 ± 3 cm ($n = 18$). At the time of planting, the plots were still completely devoid of plants. The transplanted reed clumps originated from a nearby site at Marker Wadden, where they were planted in 2017 and grown out enough to be collected for transplantation. Soil characteristics of all soils in the experimental treatments, namely, bulk density, organic matter content and water content, were 0.5 ± 0.02 kg DW L^{-1}, 13 ± 0.5% and 42 ± 0.9 g, respectively ($n = 24$; mean ± SE).

2.3. Sample collection and analyses

From 12 to 14 September 2018, by the end of the first growing season, we performed a vegetation survey and assessed a range of soil parameters and measured greenhouse gas (GHG) fluxes in the experimental plots. First, vegetation cover was determined visually to the nearest 10% per plot. This estimate was used to generate the Braun-Blanquet cover-abundance scale (Westhoff and Van Der Maarel, 1978), which we used to calculate the Simpson diversity index (Hunter and Gaston, 1988). Second, as a proxy for vegetation performance, in five standard subsections of 15 × 15 cm of each plot, the maximum height of the reed vegetation (measuring tape) and shoot density (count per subsection) of the reed was measured. Third, from each plot we collected four randomly distributed soil samples (5 cm deep, 5 cm diameter). These samples were pooled in the field to constitute one soil sample per plot. Soil samples were weighed and then stored at −20 °C until further analyses.

All soils were dried at 70 °C for 72 h and weighed to calculate soil moisture content. A 25 mL subsample of soil was used to determine

organic matter (OM) content by loss on ignition at 400 degrees °C. To determine nutrient porewater concentrations, from each plot two porewater samples were collected spaced 3–4 m apart using ceramic cups (poresize 2.5 μm) attached to a vacuumized syringe (Eijkelkamp, Giesbeek, the Netherlands). Next, each water sample was split and we filled 1) a 10 mL vial containing 0.1 mL of 65% nitric acid that was stored at 4 °C (HNO_3) (ISO 17294-2:, 2016) and 2) a 20 mL cup that was stored at −20 °C until further analysis. For analyses, nitrate (NO_3^-) and ammonium (NH_4^+) concentrations were measured on thawed samples colorimetrically with an Auto Analyzer system coupled to a spectrophotometer (Bran and Luebbe, Norderstedt, Germany). For methodological details see Geurts et al. (2008). In the acidified subsamples, phosphorus (P) was measured using inductively coupled plasma optical emission spectrometry (ICP-OES; Thermo Fischer Scientific, Bremen, Germany).

Greenhouse gas (GHG) measurements were performed in all plots, except for the ones in the "no herbivory, no planted reed" treatment, which due to logistical constraints could not be sampled (see **Fig. S3** for a schematic overview of the measurements). One day prior to GHG measurements, 20 cm long PVC collar (diameter 50 cm) were inserted into the sediment (15 cm deep) to make a seal with the sediment. We selected vegetated patches when present. Closed transparent or darkened flux chambers (diameter 50 cm, height variable and depending on the vegetation, fitted with a circulating fan) were placed on the collar to make an air tight seal. Net Ecosystem CO_2 Exchange (NEE) measurements with transparent chambers were used to approximate net ecosystem productivity. Ecosystem respiration (R_{eco}; autotrophic and heterotrophic respiration) was measured in darkened chambers. Methane (CH_4) fluxes were measured under light and dark conditions. CO_2 and CH_4 concentrations in the chambers were measured using a Los Gatos Greenhouse Gas Analyzer (model 915–0011-1001, Los Gatos Research, Mountain View, California, USA) over a three-minute interval. The linear change in gas concentration over time was used to calculate the diffusive flux of CO_2 and CH_4 (van Bergen et al., 2019). In case of an abrupt increase in gas concentration – indicating ebullition – we removed the chamber, vented and replaced the chamber (Oliveira Junior et al., 2019). In each collar, reed shoot number was counted.

2.4. Statistical analyses

We analysed how vegetation and carbon dynamics (dependent variables) were influenced by reed planting and herbivory (fixed effects) using multiple general linear mixed-effects models using package "nlme" to fit a Gaussian error distribution (Bates et al., 2015; Pinheiro et al., 2017). We used Tukey-adjusted comparisons to test differences among treatments using "emmeans" (Lenth, 2018) in R for statistics (v 3.6) (R Core Team, 2020) following Zuur et al. (2009). All models were fitted with a Gaussian error distribution with a nested random effect; block (six in total, one block consisting of four plots replicated three times in each basin) was nested in basin (2 levels). Normality and heterogeneity of residuals of the models were assessed using histograms, Q-Q plots and Shapiro-Wilk tests, and if assumptions were not met, we transformed the data (see below). All data are shown with their average ± Standard Errors (SE), and in all hypothesis testing procedures the significance level was pre-set at $\alpha = 0.05$.

To assess the main effects of the fixed effects "herbivory" (access by waterbirds yes or no), "reed planting" (rhizomes sown or not, treatment for brevity) and their interaction, the models were fitted with one of three possible dependent variables: 1) vegetation cover in percentage, 2) log-transformed reed shoot number (density, count per m^2), 3) log-transformed maximum reed height (cm from sediment) and 4) Simpson's diversity index. For reed shoot number we were unable to fit a Poisson error distribution because of overdispersion caused by many zeros.

Effects of the treatments on carbon and nutrient dynamics in porewater were analysed in similar mixed-effects models. For carbon, we analysed effects of the fixed effects – treatments – on three dependent variables: 1) NEE, 2) R_{eco} and 3) CH_4. Data on CH_4 fluxes from light and dark measurements were averaged per plot. To assess the effect of vegetation density on carbon dynamics, we performed linear regressions with the variables NEE or R_{eco} and the reed shoot density in the collar. For the linear regressions, we followed the procedure of the "Gaussian model" as described above. For porewater nutrient concentrations, we first averaged the data per plot, and then we assessed effects of treatments on dependent variables, namely, porewater concentrations of three nutrients 1) NH_4^+, 2) NO_3^- and 3) P.

3. Results

3.1. Vegetation development

Reed planting and the exclusion of herbivores resulted in a higher vegetation cover (Fig. 2). Vegetation cover was affected by herbivory ($F_{1,15} = 78.5$, $p < .001$), reed planting ($F_{1,15} = 158.1$, $p < .001$) and their interaction ($F_{1,15} = 78.4$, $p < .001$). Specifically, in treatments with planted reeds and without herbivory, the highest vegetation cover was present (94 ± 2%; mean ± SE), while this was lowest in plots that were not planted and subjected to herbivory (10 ± 9%, Fig. 3a). Without herbivory but with planting, reed dominated the vegetation. However, in unplanted plots, Broadleaf cattail (*Typha latifolia*) dominated with on average 6 ± 5 and 15 ± 8% cover in the unplanted plots with herbivory respectively. Other species that occurred at low density (~1%) were *Atriplex prostrata*, *Epilobium hirsutum*, *Leontodon* spp., *Lolium perenne*, *Senecio congestus*, *Salix viminalis*, and *Tussilago farfara*, with generally a low diversity (Simpson diversity index <0.4; Supplementary Fig. S4). Reed grew only in planted treatments and did not spontaneously colonize the unplanted treatments (Fig. 3b). Reed performance, measured as reed shoot number and reed height was affected by herbivory ($F_{1,15} = 17.5$, $p < .001$), reed planting ($F_{1,15} = 231.1$, $p < .001$) and their interaction ($F_{1,15} = 17.5$, $p < .001$). Reed shoot number was highest in the treatment without herbivory with planted reed (94 ± 15 shoots m^{-2}) and was three times lower in treatments with planted reeds with herbivory (31 ± 9 shoots m^{-2}). Similar to shoot number, reed maximum height was negatively affected by herbivory ($F_{1,15} = 29.2$, $p < .001$) and positively affected by reed planting ($F_{1,15} = 336.3$, $p < .001$), which resulted in a significant interaction ($F_{1,15} = 29.2$, $p < .001$). Maximum reed height was highest when reed was planted in the absence of herbivory (116 ± 6 cm), and was 5.8 times lower (20 ± 10 cm) in planted plots with herbivory (Fig. 3c).

3.2. Carbon dynamics

Reed planting and herbivory affected greenhouse gas fluxes ($F_{2,10} = 14.9$, $p = .001$, Fig. 4). The treatment without herbivory and with reed

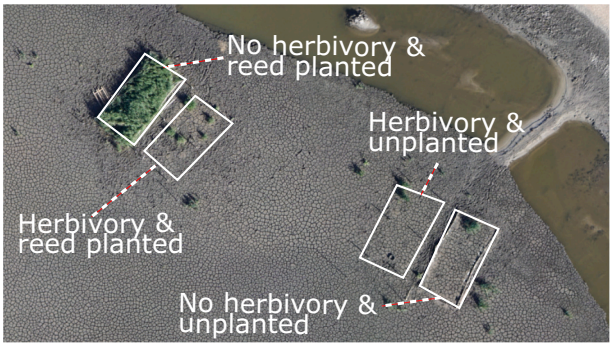

Fig. 2. Aerial view of an experimental block. Results of experimental treatments on early vegetation establishment after one growing season in one block in September of 2018. Drone picture by Boskalis.

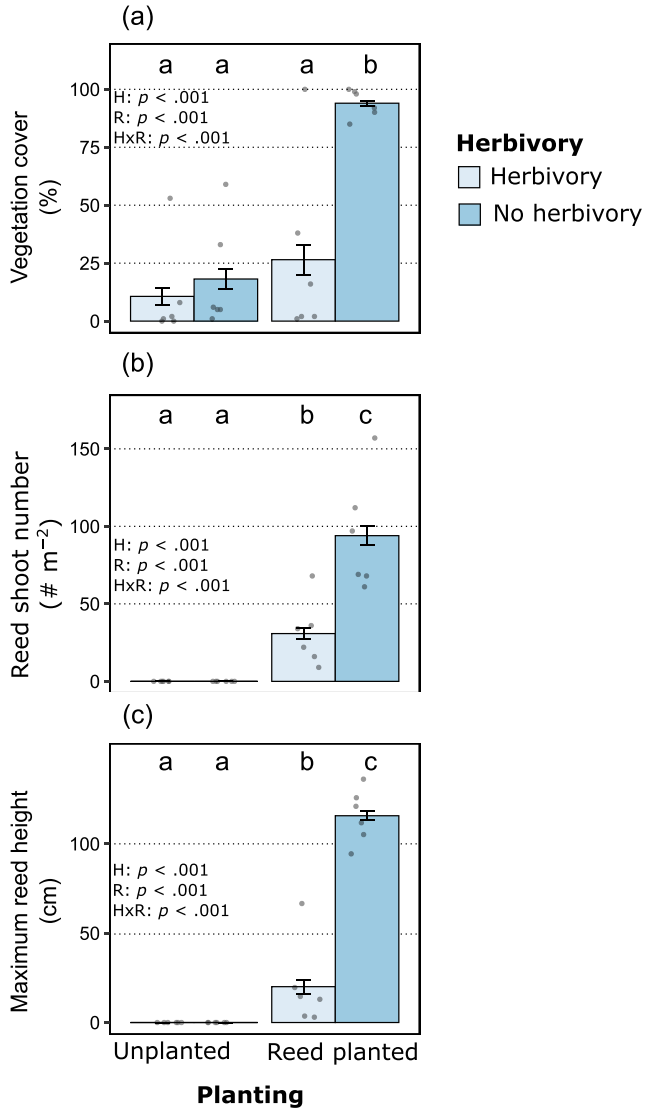

Fig. 3. Impacts of herbivory and reed planting on vegetation cover, reed shoot number and maximum reed height. (a) Vegetation cover (%), (b) reed shoot number (# m^{-2}) and (c) maximum reed height (cm) for each treatment. Bars are means with SEs ($n = 6$). Grey dots depict actual data points. Different letters depict significant differences. Significance for main (H, herbivory; R, reed planting) and interactive effects (HxR, herbivory x reed planting) effects are shown with *P* values. Statistical indices of the presented parameters can be found in Supplementary Table S1.

planting resulted in the highest Net Ecosystem CO_2 Exchange (NEE, -78.3 ± 10 g CO_2 m^{-2} d^{-1}, Fig. 4a; a negative number shows carbon uptake), representing the highest net ecosystem productivity. In the treatment with herbivory and planted reed, carbon uptake was 2.4 times lower (-32.7 ± 16 mg CO_2 m^{-2} d^{-1}). NEE was almost zero in the treatment that was not planted and with herbivores present (0.3 g CO_2 m^{-2} d^{-1}). Ecosystem respiration (R_{eco}) showed a similar trend ($F_{2,10} = 12.3$, $p < .001$, Fig. 4a). R_{eco} was highest in the treatment without herbivory and with planted reed (34.1 ± 5 g CO_2 m^{-2} d^{-1}) and was three times lower in treatments with herbivory and planted reed (11.1 ± 7 g CO_2 m^{-2} d^{-1}). R_{eco} was negligible in the treatment that was unplanted with herbivory (1.0 ± 0.6 g CO_2 m^{-2} d^{-1}). Similar to CO_2 fluxes, treatments affected CH_4 fluxes ($F_{2,10} = 5.7$, $p = .02$). The treatment that was unplanted with herbivory showed near-zero CH_4 emissions (1.1 ± 0.4 mg CH_4 m^{-2} d^{-1}, Fig. 4b). Interestingly, CH_4 emissions were only positive when plants were present. Methane fluxes were similar in the treatments with herbivory and planted reed (88.2 ± 40 mg CH_4 m^{-2} d^{-1}) and treatments with planted reed, but with without herbivory (154.4 ± 50 mg CH_4 m^{-2} d^{-1}). Both the NEE and R_{eco} were strongly correlated to the number of reed shoots in the GHG-measuring collar ($R^2 = 0.93$ and 0.92 for NEE and R_{eco}, respectively, Fig. 4c–d). A similar relation was found for CH_4, however, the fit was slightly weaker ($R^2 = 0.79$, Fig. 4c).

4. Discussion

In this paper, we show that early vegetation development in a novel forward-looking wetland restoration project on a landscape-scale can be strongly accelerated by the planting of helophyte rhizomes and by protecting their growth against herbivorous water birds. We found that both herbivory and reed planting steer vegetation establishment and succession. Herbivory altered the type of marshland that developed by stimulating the development of Broadleaf cattail over growth of Common reed, without increasing biodiversity. Without excluding avian herbivores, the newly created ecosystem would have developed into a cattail-vegetation, which typically results in a less diverse wetland in Europe, while the combination of reed planting and excluding grazers promoted the development of a targeted reed-dominated wetland. Reed performance was highest when comparing herbivory versus no herbivory, which in turn resulted in highest ecosystem productivity and carbon uptake. These results suggest that primarily herbivory controls vegetation development and corresponding functions of a novel wetland ecosystem. Thus, to enable the establishment of herbivory-sensitive target plant species, management strategies such as a combination of active planting of target species and excluding herbivores may be implemented to accelerate and steer wetland development. As such, active management during early phases of habitat restoration may accelerate their value in negating the rapid and global degradation of wetlands.

4.1. Vegetation development

Our data show that in a created wetland that is part of an archipelago, a reed vegetation will develop on the short term only when reed is planted and herbivory is absent. Indeed, herbivory by water birds (e.g. geese, coots and swans) is known to control vegetation type, structure and abundance in both aquatic and wetland ecosystems (Bakker et al., 2016, 2018). This implies that either nature should run its course or that active management is necessary to enable the establishment of target vegetation, such as reed (Bakker et al., 2018). Once reed reaches a certain density and patch-size, herbivorous birds hardly effect an established stand (Reijers et al., 2019), which might mean that a onetime management action may suffice to obtain a self-sustaining reed population. Furthermore, our results show that without the introduction of reed, another vegetation type will establish, which is not higher in plant biodiversity. Specifically, *Typha* spp. were only observed in the treatments without reed planting and with herbivory in our experiment. Consequently, other species that easily disperse, germinate and are a non-preferable food source, such as willow (*Salix* spp.) and willowherb (*Epilobium* spp.), may be expected in the future.

Taken together, it is crucial to have set clear goals regarding target vegetation, ecological knowledge about possible establishment thresholds and intended management in novel wetlands (e.g. intensive, extensive, none – rewilding; Gibbs, 2000, Corlett, 2016). Beyond the measured variables in our experiment, water level fluctuations in combination with herbivory and nutrient availability are other variables that can control vegetation establishment (Vera, 2009; Beemster et al., 2010). Although novel and innovative solutions exist to manage coastal and river works on a large scale, such as the “sand engine” in the Netherlands (de Vriend et al., 2014), the large-scale creation of an archipelago to boost ecosystem functioning with a forward-looking restoration perspective is unprecedented (van Leeuwen et al., 2021).

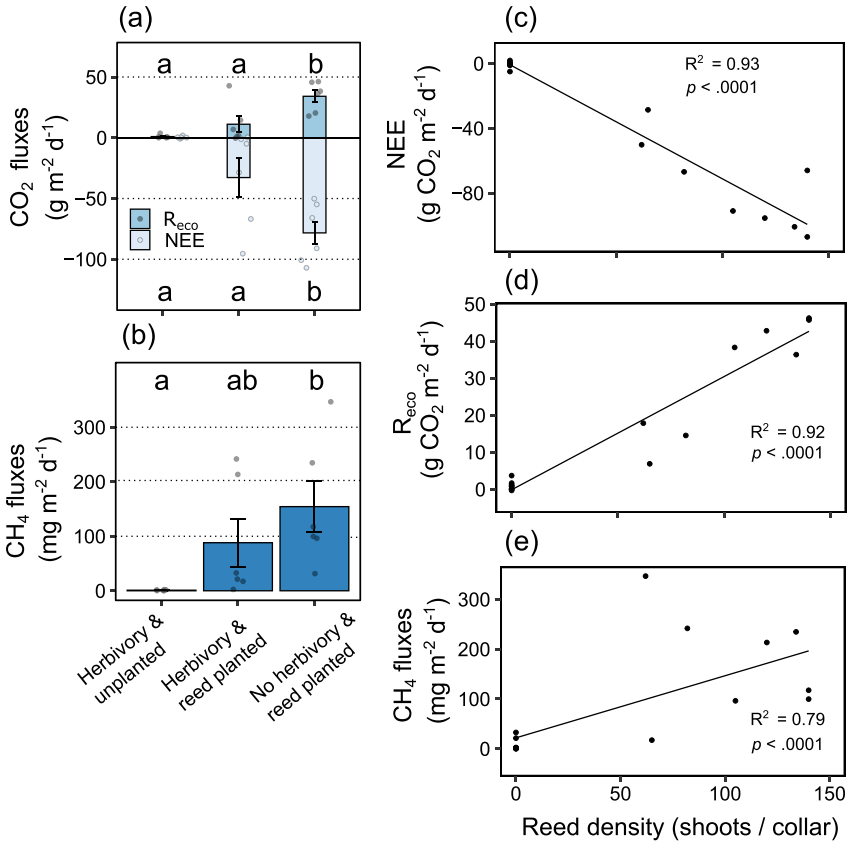

Fig. 4. Impacts of herbivory and reed planting on greenhouse gas fluxes. (a) CO_2 fluxes under light (Net Ecosystem Exchange – NEE) and dark conditions (Ecosystem Respiration – R_{eco}; g m^{-2} d^{-1}) and (b) CH_4 fluxes (mg m^{-2} d^{-1}) for each treatment. Bars indicate means with SEs ($n = 6$). Note that a negative value represents a CO_2 uptake and a positive value an emission to the atmosphere. Grey and black dots depict actual data points. Different letters depict significant differences. (c-e) Regressions between GHG fluxes and reed shoot number in the collar in which fluxes were measured. Significant relations are shown with their respective R^2 and P values. Statistical indices of the presented parameters can be found in Supplementary Table S1.

Next to the emerging field of 'building with nature' in which natural processes are harnessed to benefit human societies (Borsje et al., 2011; Temmerman et al., 2013), we here show the first results of a 'building for nature' project aiming to boost natural values on a landscape scale. As such, this project may be exemplary how to create marshes that may i) ultimately support a wide-range of species, ii) provide vital ecosystem services, and iii) negate the rapid and global degradation of wetlands (Lotze et al., 2006).

4.2. Carbon dynamics

Our data indicate that a high vegetation cover (and shoot number/shoot height) is associated to an increase in NEE (CO_2 uptake), but also in R_{eco} (CO_2 emissions). These results are in accordance with and in the same order of magnitude of many studies related to CO_2 emissions from wetland soils (Søvik et al., 2006; Zhou et al., 2009; Couwenberg et al., 2011). Next to CO_2, a high plant cover and shoot number positively correlates with CH_4 emissions. In our novel ecosystem, the measured CH_4 flux (~150 mg m^{-2} d^{-1}) was relatively low compared to other ecosystems dominated by reed (e.g. 500 mg m^{-2} d^{-1} for reed on peat; ~400 mg m^{-2} d^{-1} for grazed reed, but ~100 mg m^{-2} d^{-1} for ungrazed reed in a constructed lake (Dingemans et al., 2011) and on average 387 mg m^{-2} d^{-1} of several constructed wetlands in summer, Søvik et al., 2006, van den Berg et al., 2020). Typically, methanogenesis primarily takes place under anoxic soil conditions with ample availability of labile organic material (Valentine et al., 1994; Segers, 1998). CH_4 production can be stimulated by plants that secrete organic substances in the soil (e.g. as root exudates, dead roots and leaves, Lyu et al., 2018) or plants chimney soil-CH_4 to the atmosphere, thereby bypassing potential CH_4 oxidation in the oxygenated soil layer (Dingemans et al., 2011; van den Berg et al., 2020). However, it is not possible to determine which pathway was most important in our experiment.

Overall, in the case of reed dominance, a high CO_2 uptake combined with relatively low CH_4 emissions seemed to result in carbon in storage (12.2 ± 3 g CO_2-eq m^{-2} d^{-1}; GWP CH_4: 34, 13 h light, 11 h dark), which can aid in climate change mitigation (c.f. Velthuis et al., 2018), while bare areas were a source of carbon 0.7 ± 0.4 g CO_2-eq m^{-2} d^{-1}. However, to accurately determine this, it is crucial to make a carbon budget, preferably over multiple years (van Bergen et al., 2019), as the vegetation (including above- and belowground parts), soil and microbial community of this novel wetland will further develop. The negligible CO_2 and CH_4 respiration rates as measured in our experiment in the absence of plants, which agree with results obtained from experiments using this soil (Temmink et al., 2021b), highlight that soil development has not yet commenced and a functioning microbial community is absent. In that light, full ecosystem development, including important processes such as carbon sequestration, hinges on both the development of vegetation and the soil. Our data suggest that this can be achieved most rapidly by transplantation in combination with prevention of high herbivory pressure. Furthermore, in the case that such a forward-looking restoration project is initiated, it is key to use soil with an unactive or absent microbial community to prevent high methane fluxes under wet conditions.

4.3. Conclusions and implications

In a new wetland situated on a recently constructed archipelago, we performed a full-factorial field experiment to study the effects of herbivory and the introduction of reed on early vegetation development and key biogeochemical functions. We conclude that both the introduction of reed and exclusion of herbivores controlled vegetation development. Specifically, reed planting coupled with an absence of herbivory by geese, a targeted reed vegetation will establish, while this will develop into a cattail/willow vegetation under high herbivory pressure. Our data show that vegetation establishment has important implications for driving ecosystem productivity and carbon dynamics

including C-sequestration.

Beyond our experiment, these results imply that it is crucial to set clear goals for target vegetation (e.g. natural succession, reed marsh or cattail marsh), as it determines the potential biodiversity, carbon dynamics, biogeochemical functioning, and necessary management of such a novel ecosystem. Future work should focus on long-term vegetation development and carbon dynamics to better understand the direction in which the ecosystem will develop towards. To enable waterbirds to benefit from reed vegetations after their establishment, exclosures also need to be removed. However, this poses the risk the grazing waterbirds return and also forage on adult plants or further prevent establishment from the once protected core areas. Questions remain on the optimal timing, amount of core necessary and degree of protection during certain phases of the annual cycle that may still be needed. Furthermore, such novel approaches as presented here, are vital to create high quality natural landscapes in systems that are unsuitable for classical restoration approaches. Consequently, it can aid in halting the deterioration of ecosystems worldwide, as has been called in the United Nations Decade on Ecosystem Restoration (2021−2030) and the European Green deal, which marks restoration one of the key objectives. To do so, it is key to understand both the functioning of natural and novel ecosystems, such as environmental filters, stressors and establishment thresholds, which may challenge the (re)creation of sustainable landscapes for biodiversity.

Data statement

Data available via Archiving and Networked Services (DANS) EASY https://doi.org/10.17026/dans-2c3-uv9a (Temmink et al., 2021a).

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.ecoleng.2021.106474.

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