

RESEARCH ARTICLE

Active wetland restoration kickstarts vegetation establishment, but natural development promotes greater plant diversity

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Postdoctoral Fellowship Program (Grade C) of China Postdoctoral Science Foundation, Grant/Award Number: GZC20240601; Gieskes-Strijbis Fund, Grant/Award Number: -

Handling Editor: Dejun Li**Abstract**

1. Rapid vegetation establishment is an important goal for many freshwater wetland, coastal and terrestrial restoration projects. To accelerate the restoration process, managers often introduce target plant species, potentially generating priority effects that can lead to either divergence or convergence of community compositions over time, depending on the local biotic and abiotic conditions. These alternative trajectories pose the question of whether active restoration by initial steering of plant community composition results in a different long-term community assembly when compared to restoration via natural development.
2. Here, we tested vegetation development subject to active restoration or natural development strategies with plant introduction and protection against herbivory by geese (*Anser anser*). This was facilitated by a 1300 ha restoration project in which new, bare wetland habitat was created from soft sediments ("Marker Wadden", the Netherlands). We studied vegetation cover, plant community composition and soil elevation in a full-factorial experiment under grazed, ungrazed, planted and unplanted conditions for 6 years.
3. Without herbivory by geese, the planting of reed (*Phragmites australis*) accelerated vegetation establishment and resulted in greater vegetation cover. However, cover was dominated by reed, and plant diversity remained low. With herbivory, grazing on reed increased plant diversity. With herbivory and without reed planting, vegetation established slower. However, after 6 years, plant cover became similar to the treatment with planted reed rhizomes in the absence of herbivory—albeit with higher plant community diversity. Across all treatments, locations with higher vegetation cover decelerated soil subsidence, which maintained important abiotic conditions for the developing food web.

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4. *Synthesis and applications*: Active steering of wetland restoration by introducing target species and preventing herbivory accelerated vegetation development, while natural development took longer. However, natural development resulted in more diverse plant community compositions over time. These results imply that restoration projects face a trade-off between actively stimulating vegetation cover to facilitate food web development and prevent soil subsidence, or waiting for more diverse plant communities to develop naturally.

KEYWORDS

herbivore exclusion, Marker Wadden, *Phragmites australis*, priority effects, restoration, rewilding, *Typha latifolia*, wetland

1 | INTRODUCTION

The establishment and development of vegetation is crucial for the restoration success of degraded freshwater wetlands, coastal and terrestrial ecosystems (Hobbs et al., 2006; Temmink et al., 2020). Vegetation is often the foundation of ecosystem functioning through primary production, habitat provisioning for higher trophic levels, biogeochemical cycling, nutrient transport and carbon storage (Bakker et al., 2016, 2018; Hobbs et al., 2006). Furthermore, increased vegetation density can enhance soil accretion through the accumulation of organic matter and the entrapment of sediments or externally produced organic matter, or prevent soil erosion through biological armouring with dense roots (Barciela-Rial et al., 2023; Bouma et al., 2009; Saaltink et al., 2019; Tak et al., 2023). Together, these processes may aid the stabilization of newly deposited fine sediments (clays and silts) and organic matter (Bouma et al., 2009; Saaltink et al., 2019; Temmink et al., 2021; Wang et al., 2017). Therefore, nature managers often use vegetation transplanting, sowing, and mowing—known as facilitative priority effects (Stroud et al., 2024; Temmink et al., 2020, 2022)—as tools to ensure the rapid establishment and growth of target plant species in ecological restoration. Yet, consequential (i.e. vegetation-driven) changes in biotic (e.g. herbivory) and abiotic conditions (e.g. water level, nutrients) can also alter vegetation development and cause the development of plant communities and their functions to move into an alternative, non-desired or unforeseen direction (Bakker et al., 2016; Bouma et al., 2024; Reijers et al., 2019; Temmink et al., 2022). This non-desired or unforeseen direction can make nature restoration challenging. An alternative strategy is natural development, which involves the establishment of nature in a novel system. When occurring in degraded systems, this process is referred to as regeneration. Natural development minimizes human intervention by allowing natural successional processes to guide ecosystem recovery and establishment (Corlett, 2016).

While planting often results in an acceleration of vegetation development, it is unclear whether plant community assemblages that develop over longer timescales via natural successional processes differ from communities influenced by directed restoration. In forests, the planting of trees resulted in the rapid growth of some desired tree species and the recovery of some structural aspects of forests (Garcia

et al., 2016; Jones et al., 2018). However, other forest species that are an essential component of natural forests did not recover, even after 50 years (Garcia et al., 2016). In grasslands, the seeding of differing plant functional groups affected standing biomass, the number of species and community composition (Delory et al., 2019; Weidlich et al., 2017; Werner et al., 2016). Werner et al. (2016) showed that long-term benefits of priority effects (here seeding of grassland or forbs) can persist for at least 8 years and result in distinct community composition.

A systematic review on priority effects and a meta-analysis concluded that facilitative priority effects are increasingly used in restoration, but results are often from terrestrial ecosystems, while valuable wetland ecosystems are understudied (Jones et al., 2018; Weidlich et al., 2020). However, critical ecosystem processes in wetlands, such as community assembly or sediment consolidation, depend on the establishment of foundational plant species that often experience strong establishment thresholds (Reijers et al., 2019; Temmink et al., 2022). Yet, wetland restoration projects often do not resemble natural wetlands in terms of vegetation or functioning after a decade (Zedler & Callaway, 1999). Although introducing plant species and protecting their growth from herbivory is common practice during many restoration projects, few studies have directly compared different restoration actions in the same location for multiple years (Jones et al., 2018). For example, a one-season experiment in a freshwater marsh confirmed that rhizome planting (i.e. facilitative priority effects) accelerated reed bed development and was strengthened by additional protection against herbivory by waterbirds (Temmink et al., 2022). Particularly, high densities of greylag geese (*Anser anser*) prohibited reed growth in line with high grazing pressures induced by waterbirds (Bakker et al., 2016). Hence, the question arises 'how does active restoration such as the planting of target species and protection from herbivory independently and synergistically influence vegetation development over longer-term compared to a natural development strategy in an applied landscape restoration context?'

Here, we aimed to determine the impact of different forms of management on the longer-term development of vegetation composition in a freshwater wetland. We chose the degraded freshwater Lake Markermeer in the Netherlands as our study ecosystem, where societal constraints make a return to its former marine estuary state infeasible. Classical restoration would compromise newly acquired

ecosystem services, such as flood protection and freshwater supply (de Leeuw et al., 2024; Kelderman et al., 2012; Noordhuis, 2014; van Leeuwen et al., 2021). Therefore, nature managers initiated a forward-looking restoration project by constructing 1300 ha of new marshlands in an archipelago called "Marker Wadden" (van Leeuwen et al., 2021). We performed a 6-year field experiment in which we influenced vegetation development by full-factorial combinations of reed planting and herbivory (i.e. grazed, ungrazed, planted and unplanted treatments). We tested three hypotheses. First, we hypothesized that long-term exclusion of herbivory by geese combined with planting of reed rhizomes would result in more rapid vegetation establishment and denser reed vegetation than in control situations (i.e. with herbivory and without initial reed rhizomes planted) (Jobe et al., 2022; Temmink et al., 2022). Second, we hypothesized that lower levels of steering by nature managers would result in more species-rich plant communities because of less dominant priority effects (Jones et al., 2018; Temmink et al., 2022). Third, we hypothesized that higher vegetation density would be an important factor prohibiting soil subsidence in wetlands (Reijers et al., 2019), which is specifically important for management decisions involving newly constructed wetlands.

2 | MATERIALS AND METHODS

2.1 | Study site

The study site is located in Lake Markermeer in the Netherlands (52°35'30.2" N, 5°22'43.6" E). This 700 km² shallow lake (3–4 m depth) was originally part of a saltwater inland sea where the River Rhine met the North Sea (formerly called Zuiderzee, Figure 1). In 1932, a 32-km closure dike was constructed (*the Afsluitdijk*) for flood protection, which created a freshwater lake named Lake IJsselmeer. In 1976, the construction of a second dike (*the Houtribdijk*), divided Lake IJsselmeer into Lake Markermeer and Lake IJsselmeer.

Almost entirely devoid of riverine input, Lake Markermeer became stagnant (van Leeuwen et al., 2021). Furthermore, the combination of very fine clay sediment, an average depth of 3.6 m, and fetch lengths of >25 km, made lake sediments highly susceptible to wind-induced resuspension (Kelderman et al., 2012; van Leeuwen et al., 2021). This turbidity, combined with a lack of land-water transitions and low nutrient availability, caused a decrease in primary productivity (van Leeuwen et al., 2021). This impaired trophic transfer efficiency and thus lowered biodiversity at higher trophic levels (Jin et al., 2022). Both fish and bird populations diminished (de Leeuw et al., 2024; Noordhuis, 2014), with common bird species declining by more than 75% following the 1980s.

The degraded freshwater ecosystem could not be classically restored to its former marine estuary state (van Leeuwen et al., 2021). Therefore, to increase the lake's ecological integrity, the Dutch Society for Nature Conservation (Natuurmonumenten) constructed a 1300-ha, seven-island archipelago: Marker Wadden (Figure 1). The project aimed to increase the lake's primary productivity and biodiversity by increasing gradual land-water transitions and creating shelter between islands to decrease turbidity and sediment resuspension, while maintaining current ecosystem services (Jin et al., 2022; van Leeuwen et al., 2021). On Marker Wadden, like in the rest of the Netherlands, herbivory pressure due to greylag geese is high (Bakker et al., 2018; Reijers et al., 2019; van der Winden et al., 2024).

The first five islands were constructed between 2016 and 2020 by building ring dikes of locally extracted Pleistocene sands and filling the constructed basins with locally extracted marine clays and silts (see Temmink et al., 2021, 2022; van Leeuwen et al., 2021, for extra information). The basins were hydrologically connected to Lake Markermeer through multiple openings in the ring dikes. Water level was close to the soil level, and the clays were rich in nutrients (high P and N concentrations), on which vegetation rapidly developed (van Leeuwen et al., 2023). The last two islands were completed in 2023.

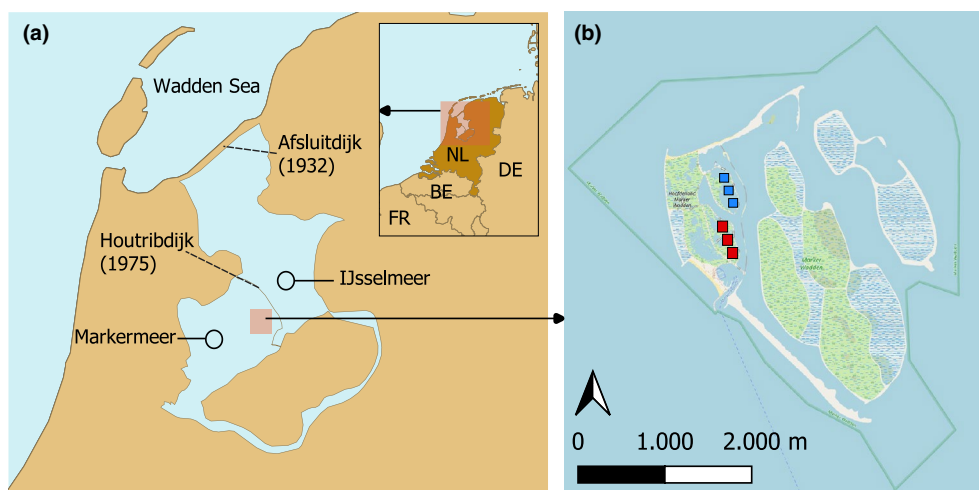


FIGURE 1 The location of Marker Wadden and the experimental design. (a and b) Marker Wadden in the Netherlands and the location of the experiment (blue-red squares). Blue squares indicate the location of experimental blocks on the northern basin and red squares on the southern basin. Each block consists of four experimental treatments ($n=6$).

2.2 | Experimental set-up

To study the interactive effects of herbivory and reed planting on vegetation and soil development, we carried out a full-factorial field experiment on Marker Wadden (Figure 1). In July and August 2017, 24 plots were constructed on the main island of the Marker Wadden archipelago (Figure 1b). Six replicated blocks, spaced 125 to 250 m apart, each included four 4.0×8.0 m plots with one of the following treatments: (1) no herbivory, planted reed; (2) no herbivory, no planted reed; (3) herbivory, no planted reed; and (4) herbivory, planted reed. To capture the spatial heterogeneity of the island, the blocks were equally divided between the northern and southern basins. Plots that needed to exclude herbivory (the exclosures) were enclosed by 1.0 m high steel mesh panels (mesh size 10×15 cm). Ropes were attached diagonally across the top of the panels to prevent birds from entering. The perimeter of all plots was marked with 1.0 m high wooden poles. Within each reed planting plot, 15 reed clumps with rhizomes were transplanted from a nearby site in early May 2018. Clumps were distributed in three rows of five clumps, with each clump consisting of 11 ± 2 shoots with a shoot length of 31.4 ± 3.0 cm (average $\pm$ SE). At the time of planting, every plot was entirely devoid of vegetation (for more details, see Temmink et al., 2022). After initial installation actions, plots were unmanaged (i.e. no removal of plants or trees). Plots were monitored five times over 6 years: in September 2018, 2019 and 2021, and August 2022 and 2023, hereafter referred to as 'year 1' until 'year 6'. Observations were conducted during typical summer conditions (dry and sunny) in the absence of extreme weather events. The mean air temperature from 2018 until 2023 was 11.2°C (minimum -13.1°C and maximum 37.4°C) with a mean precipitation of 780 mm year⁻¹ (see Table S1 for yearly values). The field research was conducted after approval by the nature manager of the Dutch Society for Nature Conservation.

2.2.1 | Data collection

Vegetation surveys were performed in each experimental plot in all years except year 3, because the site was inaccessible due to COVID mobility restrictions. For the entire 4.0×8.0 m experimental plots, we non-destructively recorded plant community composition by visually estimating the percentage cover of each plant species using the decimal Londo scale (Londo, 1976). Furthermore, as a proxy for vegetation performance, reed shoot density and maximum reed height were measured non-destructively in five 15×15 cm subsections of each plot (following a transect along the central length of each plot; every 1.5 m; except for year 3 and 4 due to COVID restrictions). These variables highly correlate to standing biomass (Reijers et al., 2019).

Soil elevation was measured in years 1, 2, 5 and 6 with a Differential Global Positioning System (DGPS; GRS-1 RTK Rover, Topcon, Tokyo, Japan (2018–2019), HiPer SR, Topcon, Tokyo, Japan (2021–2023)). Three DGPS measurements were taken every 1.5 m along the central length of each plot. The measurements at each point were then averaged, yielding six points per plot. Finally, the water level was recorded within the centre of every plot in year 5 and 6. To measure

groundwater, holes were cored until reaching the saturated zone. The hole was then left for 30 min, after which the water level relative to the surface was manually measured with a measuring tape.

Soil organic matter content was measured in year 5 and year 6. Four randomly distributed soil samples (5 cm depth, 5 cm diameter) were collected within each plot. These samples were homogenised in the field to constitute one soil sample per plot before being weighed and stored at -20°C until further analyses. To determine organic matter content, we used loss-on-ignition. For analysis, 25 mL subsamples of soil were heated until 400°C using a thermogravimetric analyser (LECO TGA701, LECO Corporation, Michigan, United States).

2.3 | Statistical analyses

We analysed the effect of reed planting and herbivory (i.e. the four treatments) on vegetation development for four variables: (1) vegetation cover (percentage), (2) the inverse of the Simpson's Diversity Index, (3) reed shoot density (count per m²) and (4) maximum reed height (cm from the sediment). The inverse of the Simpson's Diversity Index was calculated using species composition and abundance, as this is a more intuitive and appropriate metric for diversity, as a higher number indicates higher diversity (Jost, 2006).

To determine the effects of herbivory, reed planting, and time (as a factor with each sampled year as one level) on the dependent variables described above, multiple linear mixed-effects (LME) models were applied using the 'nlme' package (Pinheiro et al., 2017). All models were initially fitted with a Gaussian error distribution with a nested random effect; block (six levels, three per basin) was nested in basin (two levels). Residuals of the model were then assessed for normality and heterogeneity using histograms, QQ plots and Shapiro–Wilk tests. If the assumptions of normality and heterogeneity were not met, then the data were log-transformed to achieve normality. The 'emmeans' package was further used to test for significant differences among treatments using Tukey-adjusted comparisons (Lenth et al., 2018; Zuur et al., 2009). The significance level was pre-set at $\alpha=0.05$. All data are shown with their means and $\pm 95\%$ confidence intervals (CI). The statistical approach of supplementary figures are described in their respective captions.

To determine the effect of water level (cm) and 6-year average vegetation cover (%) on 6-year average elevation change (meter; note that the period spans 6 years but contains 5 years of data), a multiple linear regression model was applied; assumptions were assessed following the method described above.

3 | RESULTS

3.1 | Vegetation development

Over 6 years, herbivory, reed planting, time and their interaction affected vegetation cover ($p < 0.01$, Figure 2, Table S2). Specifically, the 'no herbivory, planted reed' treatment reached $94 \pm 6\%$ vegetation

cover after one growing season and gradually reached $100 \pm 0\%$ (average $\pm$ CI) (Figure 2a, Figure S1). By contrast, the vegetation cover in treatments of 'no herbivory, no planted reed' and 'herbivory, no planted reed' increased over five-fold from circa 10%–18% to 65%–96% in 6 years. The rate of change was similar for all treatments with a 10%–15% increase in cover per year except for 'no herbivory, planted reed', which was near zero as it reached 100% cover within 1 year (Figure S1). Time and herbivory positively affected diversity with highest diversity values in grazed plots ($p < 0.05$, Figure 2b). In year 6, the highest diversity was recorded in 'herbivory, no planted reed' with 2.2 ± 1.0 and the lowest in 'no herbivory, planted reed' with 1.2 ± 0.3 . We found a three-way interaction between herbivory, reed planting and time for reed shoot density ($p < 0.01$, Figure 2c) and a two-way interaction between herbivory and reed planting, and an effect of time on reed height ($p < 0.001$, Figure 2d). Specifically, for reed shoot density and maximum reed height, herbivory only had an effect in actively planted plots, where reed shoot density and maximum reed height was highest in the first 5 years in the 'no herbivory, planted reed' treatment. We found no difference in the slope of change over 6 years for all treatments (Figure S1).

Across all years, reed was the dominant plant species in the 'no herbivory, planted reed' treatment (Figure 3). Over time, these plots were gradually colonized by great willowherb (*Epilobium hirsutum*) resulting in an 84.5% average cover of reed and a 13% average cover of great willowherb (see Figure S2 for non-aggregated data). Year

5 marked an increase in the coverage of submerged aquatic plants, with an average cover of 15.6% (Figure 3). This increased two-fold by year 6, reaching an average cover of 36.4%. Vegetation cover and composition relate to water level, which differed per basin (Figures S3 and S4; the northern basin was relatively wet and submerged macrophytes established, while the southern basin was drier with a vegetation dominated by emergent wetland plants).

3.2 | Soil elevation development

Over 6 years, the soil elevation in our experiment decreased and exhibited a large variation (Figure 4; Figure S5). We found a strong positive relationship between vegetation and a 6-year change in elevation ($R^2 = 0.4$, $p = 0.002$). Specifically, the greatest changes in elevation (subsidence of between 44 and 56 cm) occurred in plots that had relatively low average vegetation cover (6.8% to 43.3%; Figure 4; Figure S6 with treatment categories). The least changes in elevation (c. 10 cm) occurred in plots with an average vegetation cover $> 75\%$. All plots with a vegetation cover of $< 45\%$ and elevation change > 40 cm were dominated by submerged macrophytes, while plots with a change of elevation < 19 cm were dominated by reed. Over time, we found an increase in soil organic matter (Figure S8) and a positive relationship between emergent macrophytes (such as reed and cattail) and elevation (Figure S7).

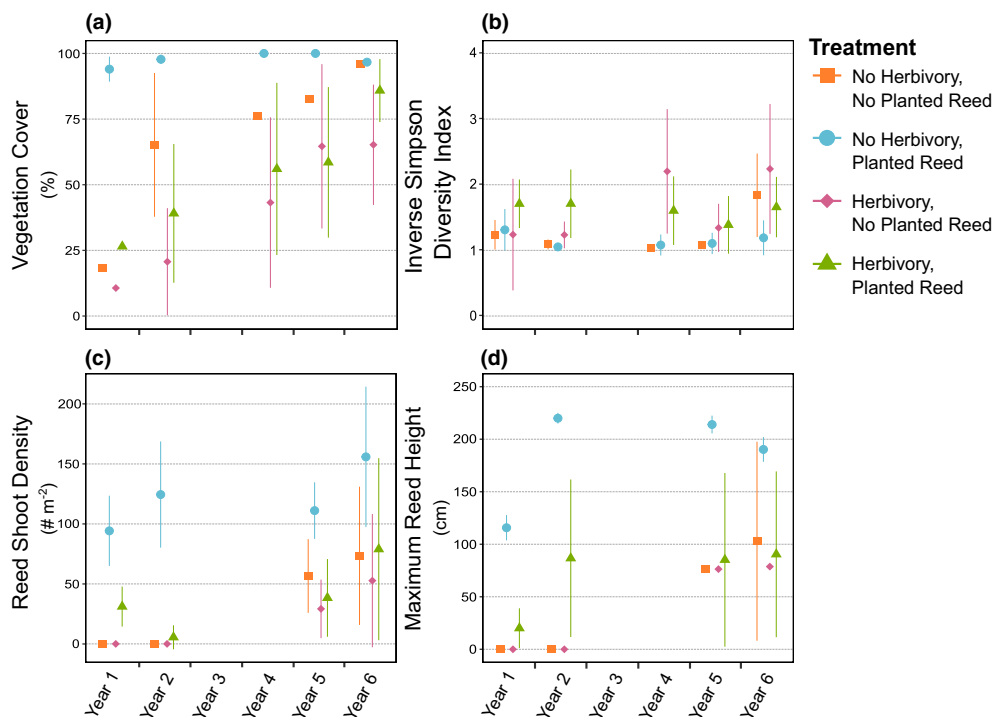


FIGURE 2 Impacts of reed planting and herbivory on vegetation cover, vegetation diversity, reed shoot density, and maximum reed height during late summer between year 1 and year 6. (a) Vegetation cover (%), (b) the inverse of the Simpson's Diversity Index, (c) reed shoot density ($\# \text{ m}^{-2}$) and (d) maximum reed height (cm). Symbols show means with 95% confidence intervals ($n = 6$).

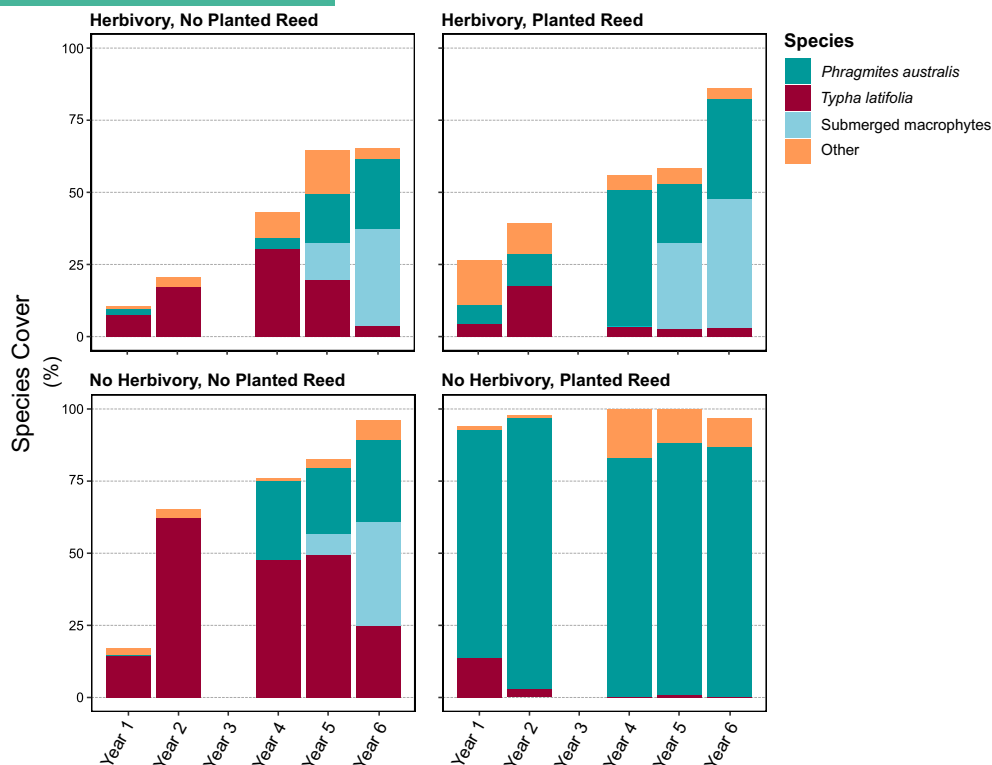


FIGURE 3 Species cover within each treatment during late summer between year 1 and year 6. Stacked bars display average vegetation cover (%) for each treatment and are shown for '*Phragmites australis*', '*Typha latifolia*', 'Submerged macrophytes' and 'Other'. See [Figures S2](#) and [S3](#) for all observed species.

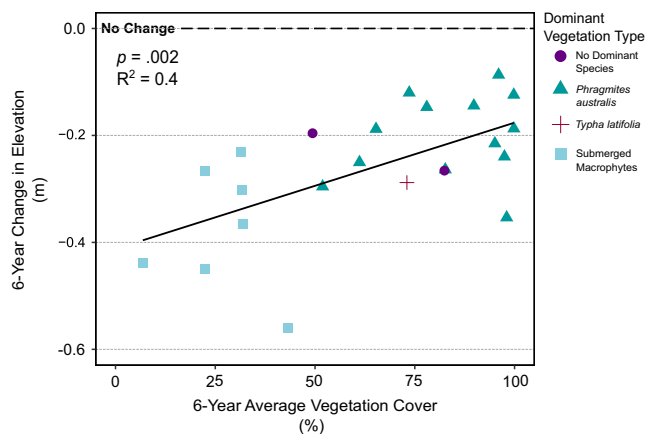


FIGURE 4 The relationship between the 6-year change in elevation and the 6-year average vegetation cover. Dots depict averages for each treatment ($n = 23$; one enclosure was damaged in year 6). Colour and shape show the dominant vegetation type in year 6.

4 | DISCUSSION

Our 6-year field experiment shows that vegetation cover in constructed wetland habitats can be accelerated by planting target vegetation and protecting its growth from grazing by herbivorous waterbirds. Such active restoration in a newly available marshland

environment rapidly led to stable and almost monospecific dense vegetation, which provided an important new habitat for higher trophic levels, such as fish and birds (van Leeuwen et al., 2023). Alternatively, with one or no restoration action (waiting for natural plant regeneration), vegetation established and developed more gradually over time to reach a similar cover with higher diversity after 6 years. These results and prior work in wetlands conceptually illustrate how management choices during early phases of restoration projects can be used to steer the trajectories of wetland restoration (Garcia et al., 2016; Jones et al., 2018; Matthews & Spyreas, 2010; Weidlich et al., 2017; Werner et al., 2016). Interestingly, there is a trade-off between rapidly stimulating mono-specific vegetation cover with low land subsidence through a combination of interventions (planting and creating herbivore exclosures) or taking one or no restoration action and waiting for more diverse plant communities to naturally develop within a decade with higher soil subsidence.

4.1 | Vegetation development

The dominance of reed due to planting rhizomes agrees with the initial assessments of Temmink et al. (2022), who found planting and protecting reed against herbivores to accelerate initial establishment. However, our 6-year study newly shows that these initial priority effects leave their long-term legacy on the plant community assembly, with reed remaining dominant for at least 6 years

and not being outcompeted by other vegetation, such as cattail or willows. This means that excluding herbivores for 1 or 2 years may be sufficient to ensure a high vegetation cover on new bare wetland soils for years, as grazing pressure is lower on fully developed reed patches than on establishing young shoots (Reijers et al., 2019). After an initial establishment phase and reaching a sufficiently high stem density and shoot length, vegetation may eventually overcome herbivory pressure (Reijers et al., 2019). This has also been observed in submerged vegetation that was grazed by waterbirds (van Zuidam et al., 2022).

When reed was not planted and protected from herbivory, the community developed slower and its taxonomical assembly was different. The area was initially dominated by cattail (*Typha latifolia*), both in the presence and absence of herbivores. This is because cattail can easily disperse and germinate within a range of wetland conditions and is less affected by grazing than reed (Meng et al., 2016; Voslamber & Vulink, 2010). However, after its initial dominance, cattail cover declined over time and was replaced by reed in the drier southern basin and by submerged macrophytes (e.g. *Potamogeton pusillus* and *Zannichellia palustris*) in the wetter northern basin (Figures S3 and S4). Cattail cover declined more strongly in the drier basin (Figure S3), most likely because cattail growth suffered from drier conditions, which reduced its competitive advantage relative to reed. This competitive advantage of reed may be the result of clonal expansion (Duhovnikoff & Hazelton, 2014) or due to its high tolerance and adaptability to a range of factors, such as water depth (Vretare et al., 2001).

We show that vegetation cover after 6 years was similar between actively managed and naturally developed treatments, but a monospecific reed composition was achieved by combining the two restoration approaches. The most intensely managed treatment—no herbivory, planted reed—had the least diverse plant community, while the other three treatments (i.e. one restoration action or none) had more similar communities (Figure 3, Figure S2). Jones et al. (2018) found that active restoration was not associated with a more complete or faster recovery in a wide range of terrestrial and wetland ecosystems, which aligns with our data on vegetation cover. As such, letting ecosystems develop on their own may be the most (cost) effective restoration strategy, but this depends on the goal or ecosystem dynamics. By contrast, in ecosystems with alternative stable states, such as vegetated coastal wetlands, bogs, coral or bivalve reefs, or arid drylands, natural development may take decades or longer and requires often infrequent conditions to recover (window of opportunity, Balke et al., 2014). As such, active restoration here is often required to kickstart vegetation or bivalve establishment (Silliman et al., 2015; Temmink et al., 2020).

4.2 | Soil elevation

During wetland restoration, the elevation of the soil relative to the water table is crucial for a wide range of ecosystem

characteristics. For example, higher soil elevation results in shallower water, which warms more rapidly during daytime and provides a different habitat than deeper waters (Jin et al., 2024). In restoration or the construction of new wetlands, the regulation of water level is typically incremental to the further development of the food web along the shoreline. Thus, predicting soil subsidence in relation to wetland restoration measures is key to the success of many projects.

In our plots, the soil elevation decreased over time, but notably the subsidence was strongly dependent on the vegetation present. Specifically, plots with the highest 6-year average vegetation cover, typically dominated by reed (i.e. in the 'no herbivory, planted reed' treatment), had the lowest change in soil elevation compared to plots with the lowest 6-year average vegetation cover, predominantly dominated by submerged macrophytes. This impact of vegetation has important implications for the development of novel wetland ecosystems that need to resist erosion and are often initiated as carbon sinks (Tak et al., 2023) and depend on soil elevation for their ecological development. This is because initial environmental conditions regulate species establishment through environmental filtering (Casanova & Brock, 2000), which thus in turn strongly impact soil subsidence and the resilience of a wetland to resist sea-level rise (Schuerch et al., 2018). Novel soils subside through various mechanisms: physical compaction and consolidation of clays, which in turn interact with evapotranspiration (transfer of water from soil to the atmosphere, which leads to compaction and consolidation, Temmink et al., 2021 and literature therein). By contrast, soil build-up occurs through the accumulation of newly formed biomass and entrapment of (organic) matter (Barciela-Rial et al., 2023; Bouma et al., 2009; Saaltink et al., 2019).

The lower change in soil subsidence in highly vegetated plots that were dominated by reeds most likely occurred through the following mechanisms: (1) fast vegetation establishment resulted in rapid accumulation of organic material by in situ production and entrapment of sediment and externally produced organic matter (Kudo & Ito, 1988; Reijers et al., 2019; Figures S9 and S10), (2) biological armouring of the soil through extensive rooting of reed and cattail prevented erosion and thus the loss of accumulated organic matter and sediment (Maxwell et al., 2017; Figure S9), and (3) fetch-mediated build-up of waves resulted in erosion in permanently inundated areas and subsequent export of soft sediment to the lake, resulting in elevation decrease, where inundated areas tend to become even deeper (Bengtsson et al., 1990, Figure S5). Interestingly, at the landscape level, the variation in soil elevation and resulting water level creates a mosaic of habitats for plants, fish and birds, and is the foundation of a coupled terrestrial and aquatic food web (van Leeuwen et al., 2023, Figure S3). More broadly, the build-up of soil through organic matter production and entrapment of organic matter and/or sediment by wetland vegetation, such as reed, cordgrasses, mangroves, and seagrasses can mitigate the negative effects of sea-level rise (SLR) (Kirwan & Megonigal, 2013; Morris et al., 2002; Schuerch et al., 2018). When the rate of soil accretion is lower than sea level rise (or SLR-induced higher water levels in inland

wetlands), such vegetated systems pose the risk of drowning (Kirwan & Megonigal, 2013; Morris et al., 2002; Schuerch et al., 2018), and thus a rapid establishment of soil-building vegetation through active restoration may reduce the chance of drowning in the face of global change.

5 | CONCLUSIONS

We show that active restoration by combining two interventions, excluding herbivores and planting, can result in the establishment of target vegetation after 1 year, while a more passive approach (either one or no restoration action) yields a more diverse vegetation with similar cover over 6 years. We further show that soil elevation change is strongly controlled by the rapid establishment of a high vegetation cover, which is only achieved through both restoration actions (i.e. excluding geese and planting). However, the cost and time investment that go hand in hand with active restoration determine the large-scale applicability of this approach, which warrants further scrutiny. Thus, with a greater understanding of the biotic and abiotic factors influencing vegetation and soil development in wetland ecosystems, including the identification of trade-offs between management options, comes a greater chance of ensuring the success of wetland restoration projects. Such trade-offs are a recurring theme in ecology, particularly between natural regeneration or active restoration (Uriarte & Chazdon, 2016), environmental quality and production goals for forests (Hua et al., 2022), or between short-term measures like erosion prevention and the long-term recovery processes seen in reclaimed coal mines (Holl, 2002).

To reach climate goals and bend the curve of biodiversity decline, societies have to restore ecosystems at massive scales (Fluet-Chouinard et al., 2023). This is highlighted in the UN Decade on Ecosystem Restoration, Montreal Biodiversity agreement and the EU Nature Restoration Law. Successful restoration hinges on an elaborate understanding of how management choices affect vegetation development and how this in turn determines the development of abiotic conditions (e.g. subsidence, nutrient and energy flows), biotic conditions (e.g. interactions with higher trophic levels) and ecosystem services (e.g. recreational value). In many wetland ecosystems, continued soil subsidence will increase water levels, which can further alter species compositions, potentially undoing the work of planting and leading to unstudied long-term effects on habitat development. All these effects may be mediated by the quality of the established emergent macrophyte vegetation, in terms of increased density, height and patch size that is needed to withstand the impact of herbivory.

AUTHOR CONTRIBUTIONS

Elisabeth S. Bakker, Leon P. M. Lamers, Han Olff designed the experiment. Rachel Alderson, Casper H. A. van Leeuwen, Elisabeth S. Bakker, Kerstin Bouma, Han Olff, Valérie C. Reijers, Stefan T. J.

Weideveld, Bjorn J. M. Robroek, Hui Jin, Leon P. M. Lamers and Ralph J. M. Temmink were involved in carrying out the field experiment. Rachel Alderson, Casper H. A. van Leeuwen and Ralph J. M. Temmink analysed the data. Rachel Alderson and Ralph J. M. Temmink wrote the first draft of the manuscript, and all authors contributed to the subsequent drafts.

ACKNOWLEDGEMENTS

The authors would like to thank Marloes van den Akker, Yvonne Kahlert, the Fieldwork Company, Peter Cruijssen, Koen Princen and the volunteers for helping to set up and monitor the experiment. We acknowledge the Gieskes-Strijbis Fund for financing the project, and Natuurmonumenten for their facilitation of research on the Marker Wadden. Hui Jin was supported by the Postdoctoral Fellowship Program (Grade C) of the China Postdoctoral Science Foundation (Grant No. GZC20240601).

CONFLICT OF INTEREST STATEMENT

None of the authors have a conflict of interest.

DATA AVAILABILITY STATEMENT

All data are available through Yoda, a research data management service by Utrecht University <https://public.yoda.uu.nl/geo/UU01/2T4ZAA.html>: (Alderson et al., 2025).

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SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

Table S1. Temperature and precipitation of the studied site.

Table S2. *F*-values and significance levels for all treatments and their interaction.

Figure S1. The linear regression gradient of vegetation cover (%), the inverse of the Simpson's Diversity Index, reed shoot density (# m⁻²) and maximum reed height (cm) within each plot over 6 years.

Figure S2. The impacts of active reed planting and herbivory on the species cover (%) from year one to year six.

Figure S3. The impacts of active reed planting and herbivory on species cover (%) from year one to year six on the northern and southern basins.

Figure S4. The water level (cm) on the Marker Wadden archipelago in year five and year six.

Figure S5. The elevation (m) of the Marker Wadden archipelago within treatment plots from year one to year six.

Figure S6. The relationship between average vegetation cover, change in elevation, water level, treatment and basin over six years.

Figure S7. The impact of total vegetation cover (%) and reed and cattail cover (%) on soil elevation (m) from year one to year six.

Figure S8. The organic matter content (%) of the Marker Wadden archipelago in year five and year six.

Figure S9. The impacts of reed planting and herbivory on maximum organic matter (%) in year five and year six.

Figure S10. The impact of total vegetation cover (%) and reed and cattail cover (%) on organic matter content (%) in year five and year six.

How to cite this article: Alderson, R., van Leeuwen, C. H. A., Bakker, E. S., Bouma, K., Olff, H., Reijers, V. C., Weideveld, S. T. J., Robroek, B. J. M., Jin, H., Lamers, L. P. M., & Temmink, R. J. M. (2025). Active wetland restoration kickstarts vegetation establishment, but natural development promotes greater plant diversity. *Journal of Applied Ecology*, 00, 1–11. <https://doi.org/10.1111/1365-2664.70021>