Ecological Engineering 222 (2026) 107819

Contents lists available at ScienceDirect

Ecological Engineering

journal homepage: www.elsevier.com/locate/ecoleng

# Multi-year water level drawdown and wildlife grazing drive wetland vegetation succession

Kerstin Bouma [a,b,c,d,*], Gabriela Carrasco Oliva [e], Mats I. Douma [b], Perry Cornelissen [f,g], Mennobart R. van Eerden [h], Ralph J.M. Temmink [e], Bart A. Nolet [g,i], Elisabeth S. Bakker [a,b]

[a] Department of Aquatic Ecology, Netherlands Institute of Ecology (NIOO-KNAW), Droevendaalsesteeg 10, 6708 PB Wageningen, the Netherlands
[b] Wildlife Ecology and Conservation Group, Wageningen University (WUR), Droevendaalsesteeg 2, 6708 PB Wageningen, the Netherlands
[c] Department of Ecology, Radboud Institute for Biological and Environmental Sciences, Radboud University, Heyendaalseweg 135, 6525 AJ Nijmegen, the Netherlands
[d] Center for Macroecology, Evolution & Climate, GLOBE Institute, University of Copenhagen, Universitetsparken 15, 2100 Copenhagen, Denmark
[e] Copernicus Institute of Sustainable Development, Utrecht University, Princetonlaan 8a, 3584, CB, Utrecht, the Netherlands
[f] State Forestry Service, Smallepad 5, 3811 MG Amersfoort, the Netherlands
[g] Department of Theoretical and Computational Ecology, Institute of Biodiversity and Ecosystem Dynamics (IBED), University of Amsterdam, Sciencepark 904, 1098 XH Amsterdam, the Netherlands
[h] Eemu Ecologisch Advies, Golfpark 133, 8241 AC Lelystad, the Netherlands.
[i] Department of Animal Ecology, Netherlands Institute of Ecology (NIOO-KNAW), Droevendaalsesteeg 10, 6708 PB Wageningen, the Netherlands

ARTICLE INFO

*Keywords:*
Vegetation development
*Phragmites australis*
Red deer
Geese
Grazing
Wetland
Water level drawdown

ABSTRACT

In wetlands, multi-annual water level drawdowns and herbivory can induce cyclic vegetation succession. While water level drawdowns can be used in wetland management to increase the area of reed vegetation, an important habitat for wetland birds, herbivory may interfere with this process. Here, we studied the combined effects of a human-induced water level drawdown, i.e. the intentional temporarily and large scale lowering of the water level, and herbivores on wetland vegetation development.

In the Oostvaardersplassen wetland, we used satellite imagery to assess vegetation development with and without water level drawdown and with and without red deer presence (introduced in 1992). An herbivore exclosure experiment (2022–2024) across an elevational gradient tested the effect of grazing on vegetation development during a drawdown.

Satellite imagery showed an expansion of reed cover by 560 ha in the period without red deer (1987–1991) and by 420 ha with red deer (2020–2024), only in the area with drawdowns. The exclosure experiment highlighted an interaction between herbivory and water depth: The presence of red deer at drier locations had minor effects on reed expansion, whereas reed expansion was strongly inhibited at wet locations with presence of geese.

Our findings provide large-scale quantitative evidence of the interaction between a water level drawdown and herbivory on the restoration of reed-dominated wetlands. We show the effectiveness of a water level drawdown, when dry conditions can be maintained for several consecutive years, as a restoration tool to promote reed development and the potential to steer the impact of herbivores during restoration.

## 1. Introduction

The global decline in biodiversity across ecosystems (WWF, 2022) and the large-scale loss of wetlands across the globe (Davidson, 2014; Fluet-Chouinard et al., 2023), calls for urgent and large-scale conservation and restoration. In wetlands, biodiversity typically declines as succession advances and vegetation becomes homogeneous (Farley et al., 2022). Here, stochastic disturbances can set succession back to a pioneer phase and induce a cyclic pattern by allowing succession to advance in between disturbances (i.e. cyclic vegetation succession) (Mori, 2011; Wilcox, 2004). In wetlands, water level can be such a disturbance and an important driver of vegetation dynamics (Liu et al., 2020). Large-scale variations in water level, including a complete water level drawdown, can induce cyclicity in successional patterns in

* Corresponding author at: Center for Macroecology, Evolution & Climate, GLOBE Institute, University of Copenhagen, Universitetsparken 15, 2100 Copenhagen, Denmark.

*E-mail address:* kerstin.bouma@sund.ku.dk (K. Bouma).

https://doi.org/10.1016/j.ecoleng.2025.107819
Received 24 June 2025; Received in revised form 23 September 2025; Accepted 24 September 2025
Available online 1 October 2025

wetlands by initiating secondary succession (Poorter et al., 2024; Stroh et al., 2008). In managed and degraded wetlands, water level is often controlled and kept constant, and this lack of disturbance can lead to continuous linear vegetation succession and results in less heterogeneity (Kong et al., 2017; Zheng et al., 2021a; Zheng et al., 2021b).

In such cases, cyclic water level manipulation, including a human-induced water level drawdown, can be a tool for wetland restoration and management by enhancing vegetation heterogeneity and by creating essential breeding, foraging and resting habitat for bird species (Farley et al., 2022; Liu et al., 2020; Żmihorski et al., 2016). However, the presence of herbivores may interact with the vegetation development in response to such a water level drawdown and thereby impact the suitability of the habitat for wetland birds.

Vertebrate herbivores, such as ungulates and large water bird, can affect vegetation succession through grazing and trampling (Bakker et al., 2016; Marin et al., 2020; Vulink and Van Eerden, 1998). These herbivore-induced disturbances can, similar to a drawdown, result in cyclic vegetation succession, thereby increasing temporal and spatial heterogeneity in vegetation composition and structure (Daleo et al., 2014; Olff et al., 1999). By contrast, herbivory can negatively affect the establishment of key vegetation, such as reed (*Phragmites australis*) that serves as vital bird breeding ground in European wetlands (Alderson et al., 2025; Bakker et al., 2018; Beemster et al., 2010; Gigante et al., 2013; Morganti et al., 2019; Temmink et al., 2022). Herbivores can affect vegetation succession and the establishment of reed vegetation, and these effects may interact with water level drawdowns. However, it is still unclear how they interact and what the overall outcome of this combined abiotic (multi-annual drawdown) and biotic (herbivory) disturbance will be.

In this study, we investigated the combined effects of a human-induced water level drawdown and herbivores on the vegetation development. We used satellite imagery in combination with a field exclosure experiment in the eutrophic clay wetland Oostvaardersplassen to study the combined effect. Water level drawdown was applied in two periods (1987–1991 and 2020–2024), in the western section, while the eastern section remained wet. Red deer were only introduced after the first period; during the second period we used exclosures to create patches without large herbivores We hypothesized that (H1) reed development increases following a drawdown; (H2) reed development will be slower during a drawdown in the presence of deer grazing, and that (H3) sediment elevation interacts with grazing to drive vegetation development.

## 2. Materials & methods

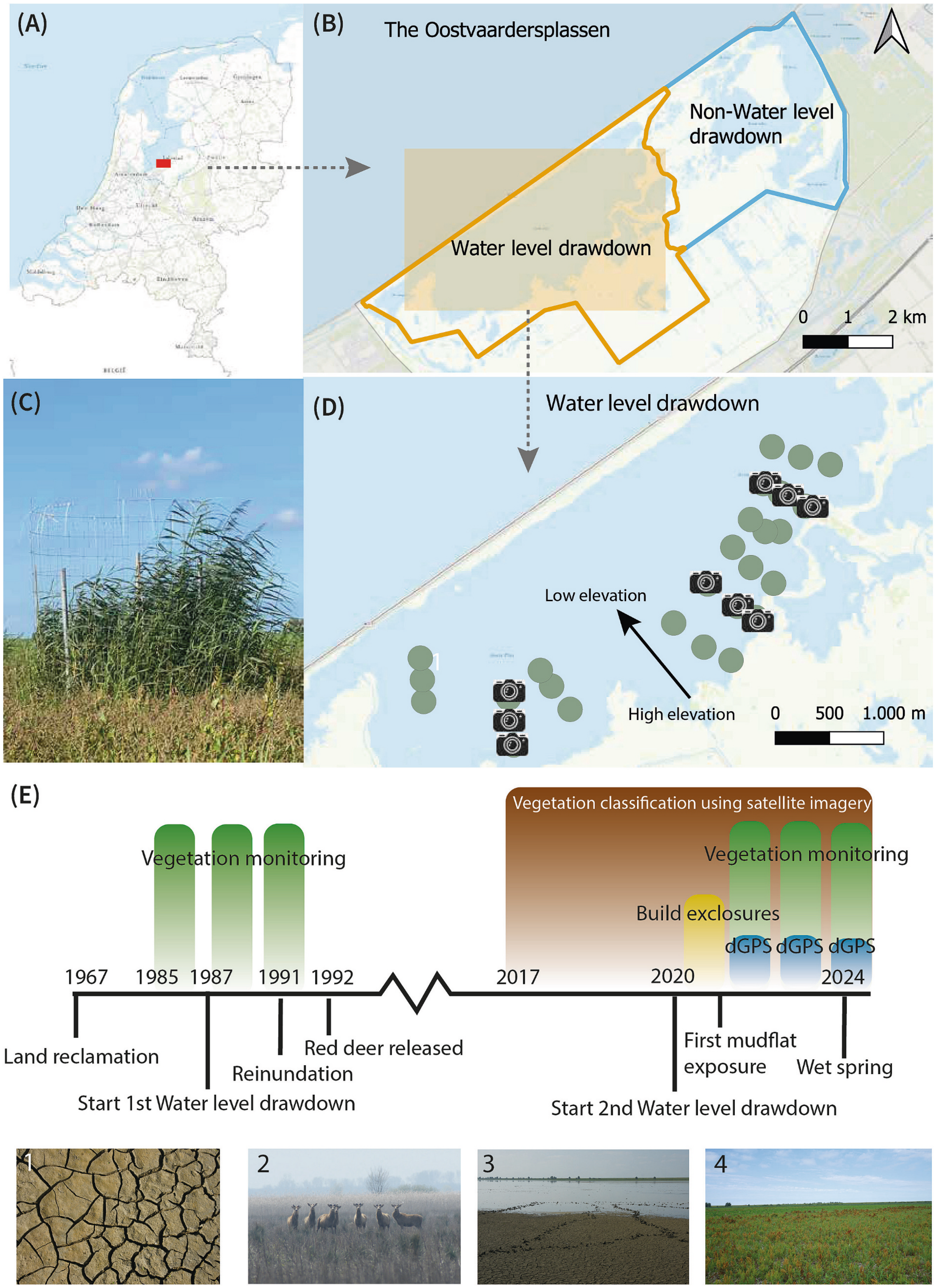
### 2.1. Study site

The Oostvaardersplassen is a eutrophic wetland in the Netherlands (52°27′N 5°19′E) (Fig. 1A). It is in a former part of the Zuiderzee estuary, which was closed off from the North Sea in 1932 and gradually turned into a freshwater lake due to input from the river IJssel (Van Leeuwen et al., 2021). In 1968, land was reclaimed, mainly for agriculture purposes. The lowest and wettest part of the polder (around 5600 ha), destined for industrial activities, was left unmanaged during the first years after reclamation. This part developed into a marsh and attracted many rare and characteristic wetland bird species. This natural development prompted a shift in management strategy, leading to its designation as a protected nature reserve (Cornelissen et al., 2014; Jans and Drost, 1995). The reserve consists of a reed-dominated marsh (*c.* 3600 ha) and a border zone with wet and dry grasslands (*c.* 2000 ha). In this paper, we focussed on the reed-dominated marsh of the reserve (Fig. 1B).

The Oostvaardersplassen is located in a polder and isolated from the Dutch river systems. The water level is controlled by the water board using a pumping station. The water level is kept at a relatively constant level throughout the year for the benefit of agriculture, industry, and housing. As the surface level of the marsh is higher than its surroundings, there is no inflow from surface water. Adjacent to the west side of the polder and the marsh is lake Markermeer, which is separated from the marsh by the Oostvaardersdijk. The water level of the lake is about 4 m above that of the marsh. Percolation from the lake through this dike to the marsh is thought to be minimal due to the fine clay particles that limit water infiltration. Because of its higher surface level, an embankment was made around the marsh to keep the water in. The water level in the marsh is controlled by a weir. Through this embankment, water percolates to the lower area surrounding the marsh. The amount of seepage through the dike and embankment is unknown. Between 1992 and 2024, the annual precipitation was about 800 mm/year and the annual reference evapotranspiration about 200 mm/year (source KNMI). All together, during periods without a water level drawdown, water level fluctuations between winter and summer were around 20 cm. To create a diverse landscape in the border zone consisting of grasslands, heck cattle (*Bos taurus*) and Konik horses (*Equus ferus caballus*) were introduced in the 1980s (Ejrnæs et al., 2024). In 1992, also red deer (*Cervus elaphus*) were introduced, with 42 individuals being released in the grassland area. Up to 2018, red deer numbers were controlled by food supply, severity of the winter and inter- and intra-specific competition, as they live in a fenced area without large predators (Cornelissen et al., 2014). As a result, the number of red deer increased to more than 2500 in 2017. In 2018, the management of the large herbivores changed in response to a decrease in bird biodiversity in the border zone and animal welfare concerns. The population of red deer was gradually reduced to 750 in 2024 through population control. During the drawdown, it was estimated that more than 90 % of the red deer population utilized the marsh area (pers. comm. P. Cornelissen).

Due to the relatively small water level fluctuations (**Fig. S1** for water level data from 1980 to 2024) and high grazing intensity because of tens of thousands of moulting greylag geese (Van Eerden et al., 1997; Vulink et al., 2010; Vulink and Van Eerden, 1998; Zijlstra et al., 1991), the reed extent and heterogeneity of the marsh vegetation decreased in the first decade after reclamation (Jans and Drost, 1995; Van Den Wyngaert et al., 2003; Van Eerden et al., 1997). In 1987, a water level drawdown was conducted in the western section of the wetland area to restore reed vegetation, which lasted until 1991, after which the area was inundated again (see **Appendix S1**). In the eastern section, which is hydrologically separated, no drawdown was undertaken, and the water level remained unaltered, to allow waterbirds to reside in the eastern part, while the western part underwent a multi-annual drawdown. Water level data was monitored on three different locations, one in the western drawdown section and two in the eastern non-drawdown section (in two separate lakes: Hoekplas and Keersluisplas). From 1980 till 2000, water level data was manually monitored twice a month using a monitoring well with a known reference height (m NAP). From 2000 onwards, data loggers were installed in the same monitoring wells and data was collected daily. In the period 2005–2015, data loggers in the drawdown section and the Hoekplas (non-drawdown section) were malfunctioning. Data was still automatically collected in the Keersluisplas in the non-drawdown section and there were some additional manual measurements. Keersluisplas was still hydrologically connected to the Hoekplas and therefore these measurements give a representation of the degree of water level fluctuations between summer and winter in this period.

Other than the difference in water level management, the western and the eastern section are similar regarding vegetation composition (before drawdown) and the presence of high nutrient concentrations in the clay sediment (Bouma et al., 2024). The Oostvaardersplassen organic clay consists mostly of microfossils, biological remains, organic colloid/tissue clothed silt (quartz mainly), with the presence of less than 10 % clay minerals, such as illite and chlorite (Cheng et al., 2004). Yet, sediment elevation is lower in the western section due to the drawdown in the 1990s, which caused subsidence of the sediment. Yearly monitoring of sediment height using a dGPS informed us about land subsidence during the current drawdown. 30 years after the last water level




(caption on next page)

**Fig. 1.** (A) Overview of the Netherlands and (B) Oostvaardersplassen nature reserve with delineated in orange the (western) drawdown section (drawdown from 1987 till 1991 and from 2020 till 2025). Delineated in blue is the (eastern) non-drawdown section. (C) Picture of a reed-dominated exclosure in the summer of 2023, surrounded by pioneer vegetation. (D) Locations of the 27 exclosures and paired control plots in the drawdown section. Camera icons indicate 9 of the 27 exclosures that are equipped with a camera trap. The arrow illustrates the sediment height gradient from high to low elevation. The yellowish colour illustrates the reed and willow vegetation before drawdown. (E) Overview of the monitoring during the first and second water level drawdown. The names indicate the methods used for monitoring (vegetation monitoring (green), vegetation classification using satellite imagery (brown), dGPS measurements (blue)). Additionally, the start of the field experiment, building of exclosures, is shown in yellow. The timeline with important events in the Oostvaardersplassen wetland is shown at the bottom of the line. The pictures illustrate some of the most important events (1 = start 1st drawdown, 2 = introduction of red deer, 3 = start 2nd drawdown, 4 = response during drawdown). (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

drawdown, the same development was observed, a declined area of reed vegetation, and in 2020 another water level drawdown was induced to achieve the same goal of restoring the reed beds (**Appendix S2**).

## 2.2. Vegetation classification using satellite imagery

### 2.2.1. Vegetation structural types former and present drawdown

To determine the vegetation development during the current drawdown (2020–2024) and compare it to the previous drawdown (1987–1991) when red deer where not present, we used satellite imagery to classify vegetation structures on a large scale (Fig. 1E). Landsat satellite images (30 × 30 m) were obtained from Sentinel Hub EO Browser (Tiff 32-bit, high resolution, WGS 84) for the period 2017 till 2024 (June – September). 2019 is missing due to a lack of suitable images because of cloud cover. Clipped images were analysed in R. To quantify the cover of water, bare soil, *Persicaria lapathifolia*, *Rumex maritimus*, pioneer vegetation, new (developed) reed vegetation, old reed vegetation and woody vegetation, we informed a model (rpart (Therneau et al., 2022)) with ground-truthed vegetation data (2022, 2023 and 2024). Vegetation recordings ($n = 57$) were made across the entire former lake area which emerged upon drawdown (including control plots, see section 2.4). At each location, plant species and their cover were recorded (1 × 1 m). The vegetation recordings were clustered (based on kmeans in R) in distinguishable dominant habitat types (pale persicaria (*Persicaria lapathifolia)*, golden dock (*Rumex maritimus*), pioneer vegetation and new (developed) reed). Additionally, using aerial photographs additional locations (without field data) were assigned to the habitat types of “old reed” and “woody vegetation”. Clustering was done for 2022 and 2023 combined ($k = 5$) and separately for 2024 ($k = 3$), due to inundated conditions that made it not possible to combine these into one clustering. These classes and their locations were used to inform the model based on the different band reflections of the Landsat images that correspond to known habitat types (for decision trees and predictions see Fig. S3-S6). For the years 2017, 2018, 2020, 2021 and the entire eastern section (without specific field monitoring), knowledge on the field conditions and high-resolution aerial photographs (PDOK, https://www.pdok.nl/) were used to assign the correct vegetation types to each location and inform the model (for decision trees and predictions see Fig. S3-S6). Total area cover of each habitat type was calculated from the number of pixels for each habitat type.

## 2.3. Field exclosure experiment

To study the effect of geese and red deer on vegetation development, 27 ungrazed plots were paired with grazed control plots. To exclude red deer and geese, we constructed exclosures (2.0 m high to exclude red deer from grazing over the wire, 1.5 m in diameter to exclude birds from flying in) with PVC rods and steel wire (mesh width of 15 × 15 cm to exclude geese from getting in and red deer from reaching through) in April 2022 (Fig. 1C). Within each exclosure we sampled a plot of 1 × 1 meter to exclude edge effects. While red deer and geese could technically reach somewhat inside the exclosure through the mesh, no signs of grazing on plants inside exclosures were observed during the study period. Each paired control plot was located 10 m south-west of the exclosure and in parallel to the existing old reed border. To include differences in sediment height (elevation measured with a dGPS; Piper, TopCon, **Fig. S2**) and potentially different vegetation types, the exclosures plus paired control plots were spread throughout the area in nine transects of three exclosures each at 20–100 (high elevation), c. 300 (intermediate elevation) and c. 600 m (low elevation) from the reed border (Fig. 1D). At the time of the installation of the exclosures, vegetation was only present in the exclosures and control plots closest to the reed border. Winter inundation of the plots occurred in 2022/2023 with 1.39 ± 1.64 cm water on high elevation, 5.83 ± 4.40 cm on intermediate elevation and 11.74 ± 5.09 cm on low elevation and in 2023/2024 with 1.59 ± 3.01 cm on high elevation, 3.83 ± 6.26 cm on intermediate elevation and 6.31 ± 10.28 cm on low elevation. Although differences between locations were small, we did observe locations that were dry in winter and locations that were continuously inundated. In spring, a standing water level (no matter the depth) will inhibit germination (Merendino and Smith, 1991) and through that germination and species survival. It has been shown that a delay in sediment exposure dates of 1 week (Grace, 1987) may already impact recruitment from the seed bank and eventually vegetation composition. In this study area, the vegetation composition along the environmental gradient seems to be driven by environmental factors such as timing of drawdown (e.g. a combination of water level and microtopography), salinity or nutrient availability (Ter Heerdt et al., 2017). A previous study in our study area has shown that the seed bank composition itself did not differ along the environmental gradient (Bouma et al., 2024).

### 2.3.1. Vegetation monitoring

At each plot, vegetation was monitored during peak standing crop in August 2022, August 2023 and July 2024. To monitor vegetation development a 1 × 1 m quadrant was placed in the centre of the exclosure and the control plot to visually estimate the species cover for each plant species. Total cover could exceed 100 %, because of undergrowth. In each plot, height of reed was recorded for three individual stems.

## 2.4. Herbivore species detection and quantification

Wildlife cameras (Bushnell Core no Glow) were employed continuously from August 2022 till August 2024 (**Fig. S7**) on 9 out of the 27 exclosures, covering elevation gradients (high, intermediate, low) in three rows across the area (Fig. 1D). Cameras were visited every 2–3 months to replace batteries and SD-cards. The camera traps were facing towards the old reed vegetation and were located at a height of approximately 150 cm to provide a good view of herbivores visiting the area close to the exclosure. The cameras were triggered by movement and took one picture each time, after which they became insensitive to movement for 10 s. Obtained pictures were loaded into the Agouti environment (Casaer et al., 2019). Agouti automatically groups images into bursts, which is defined as one event in which occurring (groups of) individuals are repeatedly observed (in this case this was defined as pictures taken within 120 s). Each burst was annotated manually with the present species and the count of individuals per species. The cumulative number of red deer or geese (both flying and standing) present at each location for a certain period was divided by the total number of days the camera was deployed in that period. Overall, we analysed 240.602 images that were converted into 32.823 bursts covering the period August 2022 to August 2024. Of these bursts, 6.292 showed an animal on the picture, this included the observation of red deer (52 %) and geese (7 %). The lower number of pictures with geese compared to red deer may be due to flocking of geese which can lead to a sudden peak in observance. Greylag geese (*Anser anser*) were the dominant goose species in the wetland area, followed by white-fronted goose (*Anser albifrons*). Other animals seen in the pictures at low occurrences were starlings (*Sturnus vulgaris*), foxes (*Vulpes vulpes*), yellow wagtail (*Motacilla flava*), reed warblers (*Acrocephalus* spec.) and white-tailed eagle (*Haliaeetus albicilla*).

### 2.5. Data analyses

#### 2.5.1. Satellite imagery

Vegetation recordings for ground-truthing of satellite imagery of 2022, 2023 and 2024 were clustered using kmeans (stats package; (R Core Team, 2023)), resulting in 5 clusters (estimated based on the Elbow Method) and nstart set at 25. The clustered data was used to train the model for recursive partitioning with the function rpart (package rpart; (Therneau et al., 2022)) for the period 2017 till 2024. The complete Landsat satellite images were predicted using the function"predict" (stats package).

#### 2.5.2. Field exclosure experiment

Differences in vegetation composition between exclosure and control plots were assessed per year through non-metric multidimensional scaling (NMDS) with Bray-Curtis distances (vegan package; Oksanen et al., 2022). Subsequently, ADONIS analysis was performed to identify statistical differences between groups (exclosure/control).

We analysed how reed cover (independent variables) was impacted by herbivory (presence/absence), sediment elevation (high, intermediate, low), time (dependent variables) and their interactions with generalised linear mixed models corrected for zero inflation with tweedie family (link = log, glmmTMB package; Brooks et al., 2017). Furthermore, we analysed how pioneer vegetation and total cover (independent variables) were impacted by herbivory (presence/absence), sediment elevation (high, intermediate, low), time (dependent variables) and their interactions with generalised linear mixed models with tweedie family (link = log) (glmmTMB package; Brooks et al., 2017). Cover of cattail and woody vegetation was data-poor and therefore the interactions among the dependent variables were removed from the model. The model was run with a correction for zero inflation and with respectively the negative binomial function and the tweedie (link = log) function.

#### 2.5.3. Herbivore presence

Counts of red deer and geese, obtained from the camera images, were tested for dependence on presence of water (November 2022 – May 2023, October 2023 – August 2024) and sediment elevation (high, intermediate, low) with generalised linear models corrected for zero-inflation with Poisson family distribution (package glmmTMB; Brooks et al., 2017).

Data were analysed in RStudio version 4.0.3 (R Core Team, 2023). All data are shown with their average ± Standard Deviations (SD), and in all hypotheses testing procedures the significance level was pre-set at $\alpha = 0.05$.

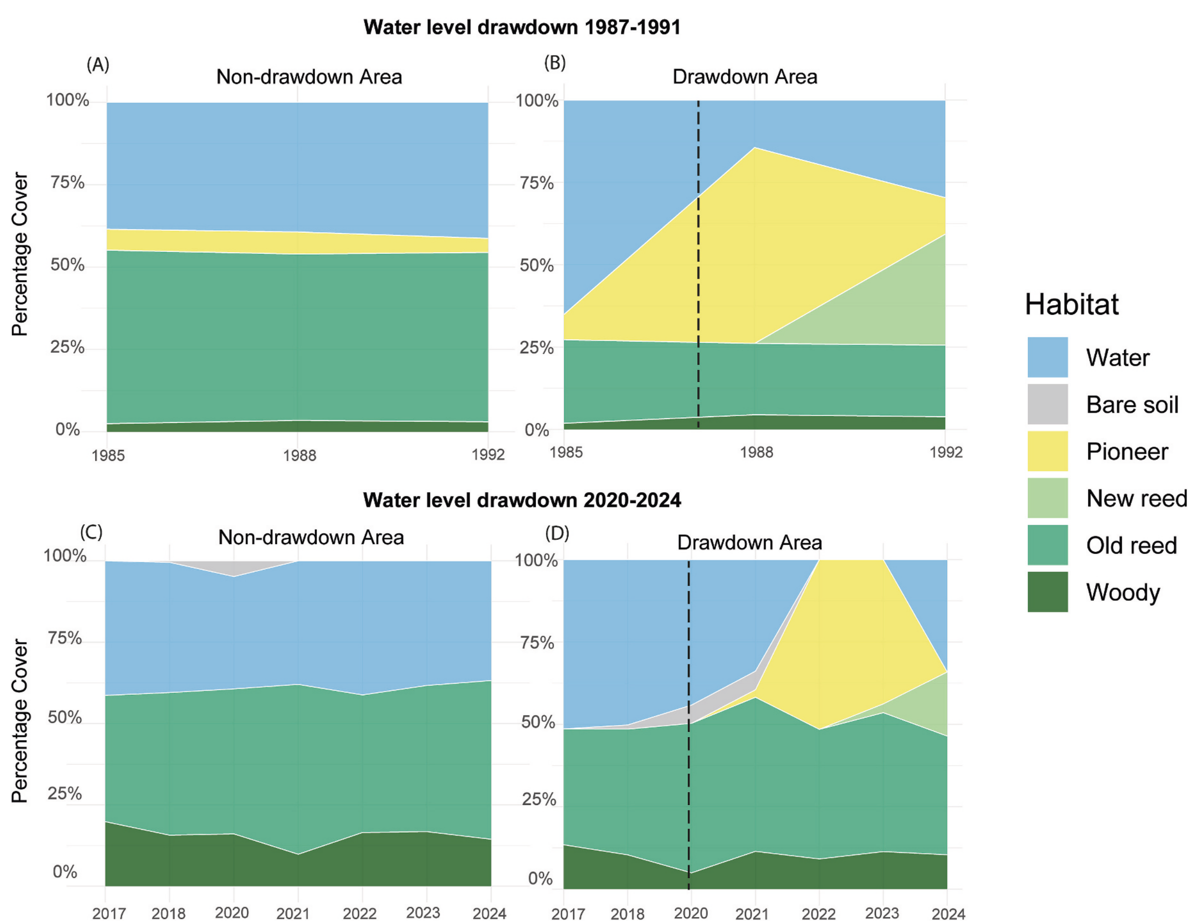



**Fig. 2.** Cover of habitat for the former (A-B; 1987–1991) and the current water level drawdown (C-D; 2020–2024). Each drawdown periods shows the change in habitat for the non-drawdown area (A, C, 1500 ha) and the drawdown area (B,D, 2100 ha). The dashed line indicates the start of the water level drawdown for both time periods. Data for the former drawdown period was obtained from Jans and Drost (1995) and Huijser et al. (1995).

## 3. Results

### 3.1. Vegetation structure and composition development

Satellite imagery showed that before the drawdown in 2020, the Oostvaardersplassen was characterized by open water that was fringed by reed. The reed was accompanied with some woody vegetation (mostly willow, *Salix* spp.) (Figs. 2,3). The two hydrologically separated subareas were similar in this respect. The water level drawdown led to the colonization of 1100 ha by pioneer vegetation during the first year of complete drawdown in 2022 (see **Fig. S8** for a list of plant species). The vegetation was dominated by the pioneer herbs *Persicaria lapathifolia* (150 ha) and *Rumex maritimus* (140 ha). In the second year of the water level drawdown, *Persicaria lapathifolia* cover further expanded to more than 320 ha, while *Rumex maritimus* virtually disappeared (Fig. 3). In 2022 and 2023, respectively 51.5 % and 43.8 % of the area was covered with pioneer vegetation, this resembles the 59.4 % cover of pioneer vegetation during the second year of drawdown in 1988. In 2023, reed started to establish and covered around 60 ha (Figs. 2,3). The wet winter and summer of 2024 resulted in the appearance of shallow water – which was mostly clear with bottom view – and the disappearance of pioneer vegetation. After three years of water level drawdown, reed

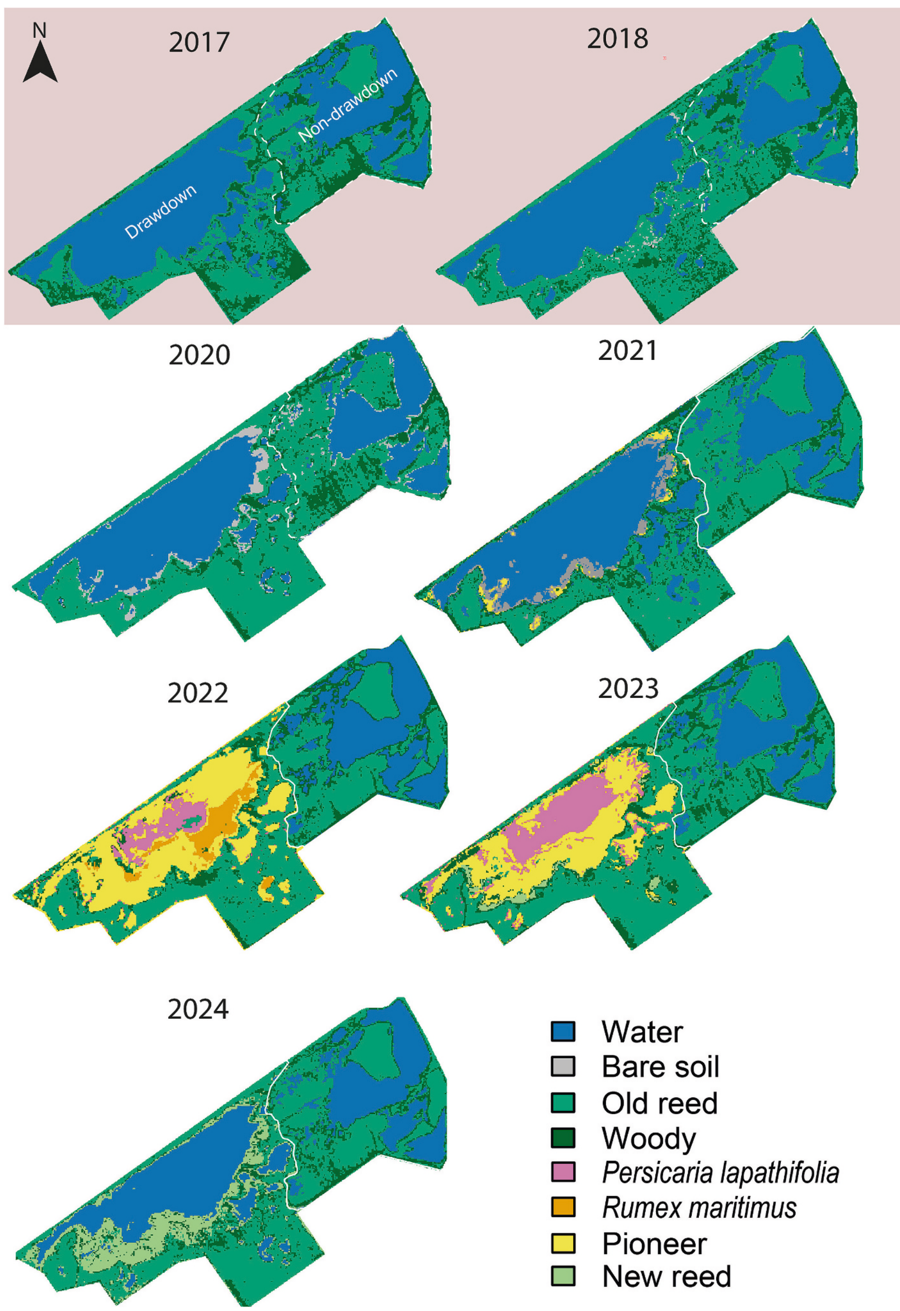



**Fig. 3.** Map of Oostvaardersplassen wetland area from 2017 till 2024 with the coverage of water, bare soil and diverse vegetation types in the drawdown area (west) and non-drawdown areas (east). The white line indicates the separation between the two areas, when dashed the areas were hydrologically connected. The water level drawdown initiated in 2020 (coloured background indicates before the drawdown) in the western part of the Oostvaardersplassen is visible with an initial increase of bare soil at the lake edges (2020–2021), followed by development of pioneer vegetation and in the end expansion of reed (2024). In 2024, the wet spring led to the inundation of the western area until the summer period, limiting the development of pioneer vegetation. In the non-drawdown area (east) the vegetation remains relatively stable. 2019 is missing due to incomplete satellite images and cloud coverage.

vegetation had expanded with a net area of 420 ha closed cover, compared to 560 ha of reed restored during the previous drawdown (1987–1991), covering five growing seasons (Jans and Drost, 1995; Vulink and Van Eerden, 1998).

### 3.2. Field exclosure experiment

#### 3.2.1. Vegetation composition

In the first year of drawdown, bare soil was colonized for 75–100 % by pioneer species irrespective of grazing treatment. In the second year, divergence occurred, and control plots were characterized for c. 70 % by pioneer species, while exclosure plots were characterized by perennial species such as reed (30–40 % cover) and cattail (Fig. 4). In the third year, unintentional inundation of the area due to high precipitation up to July (water level: high elevation = 2.51 ± 5.34 cm, intermediate elevation = 5.23 ± 5.14 cm, low elevation = 7.20 ± 7.49 cm) restricted the development of pioneer vegetation as well as the establishment of new reed at the lower locations with greater distance from the reed border. New reed plants from the previous year were still present in both grazed and ungrazed plots at the higher areas. In the lower laying areas, large differences in cover arose due to grazing by geese, based on camera data (Figs. 5, 6). In addition, plant species composition was impacted by herbivory in the 2nd year of drawdown (2023; May: $F_1 = 6.02$, $p < 0.01$; August: $F_1 = 5.18$, $p = 0.01$) and the 3rd year of drawdown (2024; April: $F_1 = 4.26$, $p < 0.01$; August: $F_1 = 9.32$, $p < 0.01$, **Fig. S9**).

Reed cover was generally higher in exclosure than in control plots ($X^2 = 57.16$, $p < 0.01$) and increased each year ($X^2 = 125.74$, $p < 0.01$). Reed cover was significantly lower at the control plot at the lowest elevation compared to all other combinations (interaction herbivory x sediment elevation; $X^2 = 10.40$, $p < 0.01$) (Fig. 4, **Table S1)**. Cover of pioneer vegetation was lower in 2024 compared to 2022 and 2023 ($X^2 = 71.40$, $p < 0.01$) and in general higher at high elevation compared to intermediate and low ($X^2 = 14.00$, $p < 0.01$). No impact of herbivory on pioneer vegetation cover was observed ($X^2 = 0.00$, $p = 1.00$). Cover of pioneer vegetation was significantly lower in 2024 at the intermediate and low elevation (interaction year x sediment elevation; $X^2 = 21.34$, $p < 0.01$) (Fig. 4, **Table S2)**. Cover of cattail was significantly lower in 2022 compared to 2023 and 2024 ($X^2 = 7.42$, $p = 0.02$). Cattail cover was not impacted by herbivory ($X^2 = 0.20$, $p = 0.65$) or sediment elevation ($X^2 = 0.47$, $p = 0.79$). Woody cover was not impacted by herbivory ($X^2 = 0.01$, $p = 0.94$), year ($X^2 = 1.93$, $p = 0.38$) or sediment elevation ($X^2 = 0.21$, $p = 0.55$). Total cover was higher in exclosure

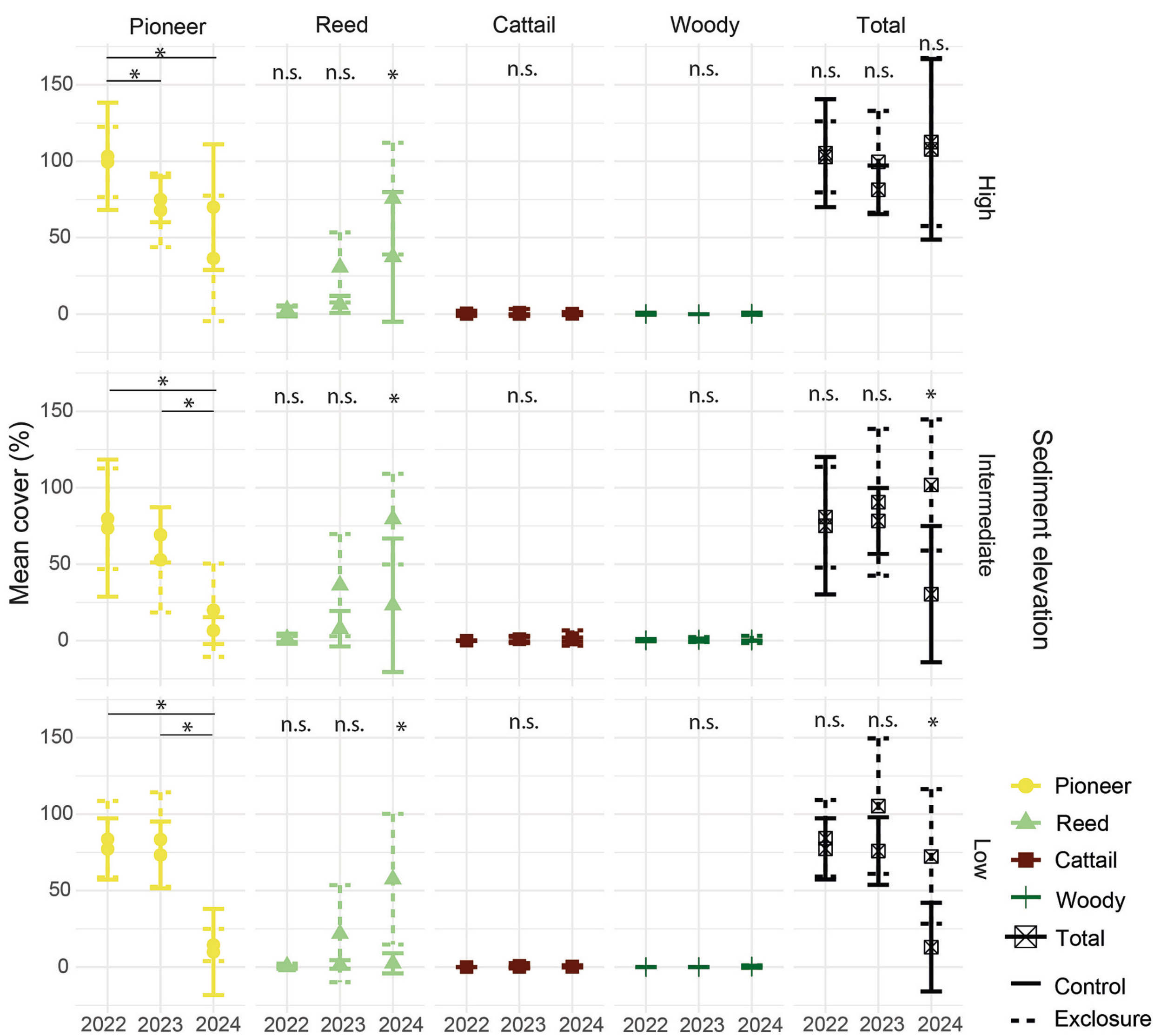



**Fig. 4.** Cover of the main vegetation types (pioneer, reed, cattail, woody) and total cover of control and exclosure plots. The cover is shown for sediment elevation (high, intermediate, low) and measurement times (August 2022, August 2023, July 2024). Dashed lines indicate exclosures and solid lines indicate controls. The mean and the standard deviation are shown in the plots. Significant differences between years are indicated by *.

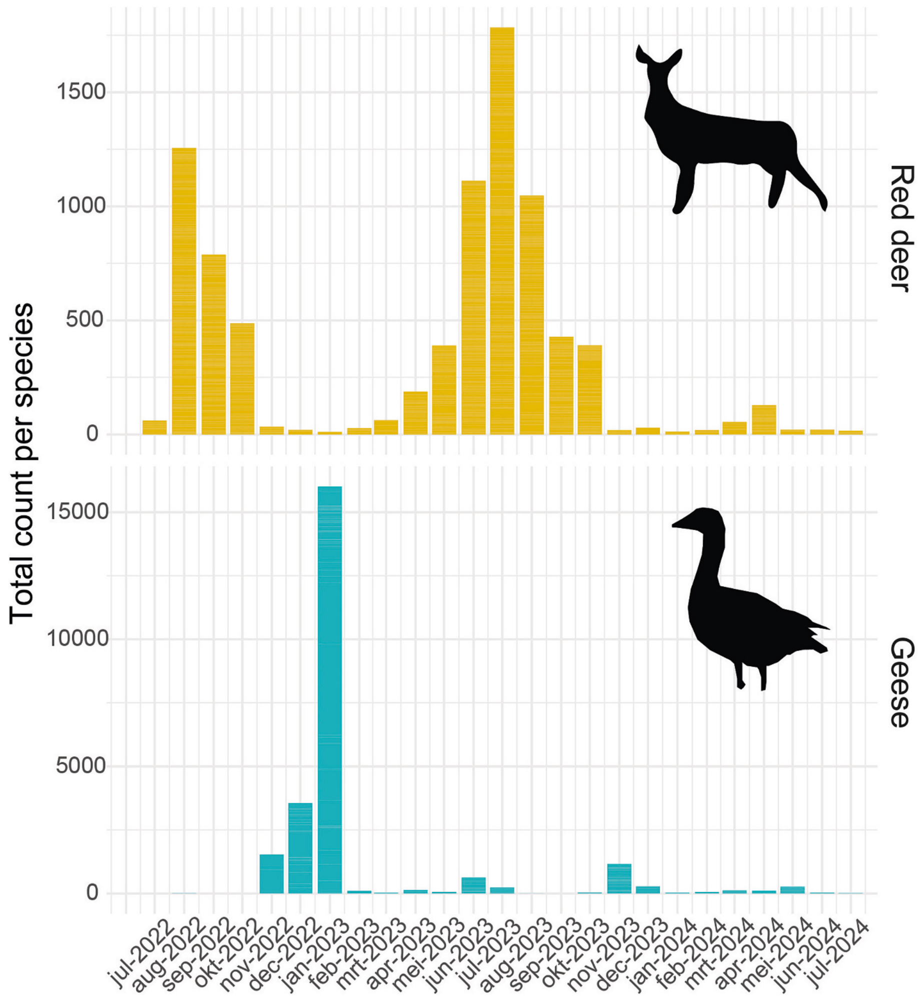



**Fig. 5.** Total count for red deer and geese per month from July 2022 till July 2024. Total count is the sum of the observed individuals for all camera traps per month. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

compared to control plots ($X^2 = 16.306$, $p < 0.01$) and at high elevation compared to low and intermediate ($X^2 = 22.12$, $p < 0.01$). Total cover showed a three-way interaction with herbivory, year and sediment elevation ($X^2 = 18.26$, $p < 0.01$). In 2024, control plots at low and intermediate elevation had less total cover compared to all other plots. Except for the exclosure plots at low elevation, where total cover was equal to total cover in the control plots at intermediate elevation in 2024. (Fig. 4, **Table S3**).

In the first year of drawdown, the maximum height of reed recorded was 81 cm, this increased to 140 cm in August 2023 and to 280 cm in July 2024. Height of reed was affected by an interaction between time, herbivory and sediment height ($X^2 = 18.92$, $p < 0.01$, **Fig. S10**). At low elevation, herbivory reduced height of reed 2–3-fold. At intermediate elevation, height was quite similar in control and exclosure plots in 2022, 1.5 times higher in exclosures in 2023, and not different in 2024. At the highest elevation, reed height was twice as high in exclosures compared to controls in 2023, but in 2022 and 2024 similar between the two.

### 3.3. *Temporal and spatial abundance of red deer and geese*

In total, we had 3.286 images with red deer and 412 with geese (both *Anser anser* and *Anser albifrons*). This resulted in a total count of 8.407 red deer and 24.418 geese (Fig. 5). During the first year of monitoring (July 2022 till June 2023), 4.437 red deer were observed and 22.069 geese. The subsequent year (July 2023 till July 2024), red deer numbers were similar with 3.970, while geese numbers dropped to 2.349. We do not know what is causing this drop in detected geese numbers and whether this is driven by population shifts or climatic variation between years. In general, red deer were mostly observed during dry months (April – October) and geese were observed during wet winter months (November – January). The high amount of precipitation during spring 2024 resulted in the presence of geese and the decrease in red deer presence (Figs. 5, 6).

Total counts of red deer per month were determined by presence of water ($X^2 = 4360.07$, $p < 0.01$), sediment elevation ($X^2 = 159.80$, $p < 0.01$) and their interaction ($X^2 = 52.03$, $p < 0.01$) (**Table S4**). Red deer were most observed on camera pictures when no water was present and tended to stay on high elevation, closer to the reed border (Fig. 6). Although their presence decreased when water was present, they still favoured the higher locations near the reed border. Total counts of geese per month were also determined by presence of water ($X^2 = 1796.08$, $p < 0.01$), sediment elevation ($X^2 = 6592.18$, $p < 0.01$) and their interaction ($X^2 = 232.69$, $p < 0.01$) (**Table S4**). However, geese preferred low and intermediate elevations, further from the reed border, specifically during inundated periods, such as winter and the wet spring of 2024 (Fig. 6). High elevations had the lowest occurrence of geese both with and without the presence of water.

## 4. Discussion

The study aimed to test the combination of a multi-year water level

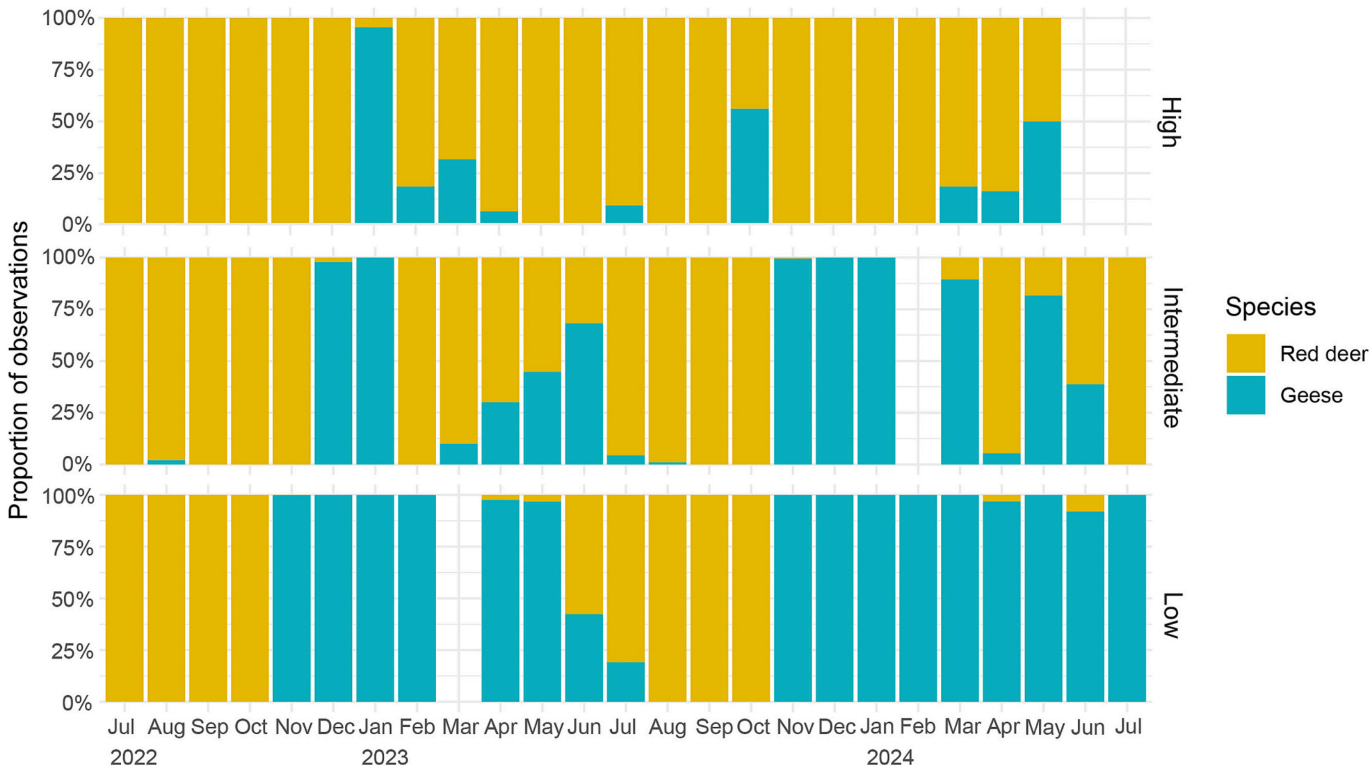



**Fig. 6.** The distribution of the observations of herbivore presence over time and elevation. Proportion of red deer or geese per month from July 2022 till July 2024 for different sediment elevation categories (Low, Intermediate, High). (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

drawdown and herbivore grazing on vegetation development. We focussed on target species reed, which is the foundation of a biodiverse wetland in Europe. Our findings support H1 and H3, by showing that during a water level drawdown reed vegetation strongly expands and vegetation development, and specifically reed development, is more affected by grazing at lower elevational locations. However, our results partially refute H2, by showing that red deer had less impact than expected. Specifically, geese seem to have a stronger effect on vegetation development, in particular by supressing reed, than red deer. Our study took place during three consecutive growing seasons of which two were fully dry. Inundation occurred during winter and during spring and early summer of 2024 due to excessive rainfall, allowing us to study the interaction between sediment elevation (i.e. water depth) and grazing. Our results show that water depth (i.e. sediment elevation) and herbivory determine wetland vegetation composition and the direction of vegetation succession.

### 4.1. Relation sediment elevation and vegetation development

Our study shows that a water level drawdown resets vegetation succession. Initially, bare soil was colonized by pioneer vegetation and subsequently by perennial vegetation, such as reeds. Sediment elevation is a strong determinant of germination success, through its relationship with moisture content and standing water level. Our results indicate that the target vegetation during restoration, reed, showed sensitivity to the presence of water resulting in more reed abundance (no data on germination or sprouting success are available) in drier locations. This sensitivity is corroborated by other studies that show that reed does not germinate below water (Baldwin et al., 2010; Gorai et al., 2006). Additionally, vegetative propagation of reed is impacted by water depth, resulting in longer time to sprout and decreased survival (Tang et al., 2022).

The pattern found for reed vegetation (lower cover at lower elevations) was not consistent across plant species (**Fig. S11**). Species such as *juncus effusus* and *juncus bufonius* seem to increase at lower elevations. This variation in response to sediment elevation leads to varied plant species compositions across an elevational gradient determined through timing and duration of drying (ter Heerdt, 2016; Hidding et al., 2014). Additionally, it is known that bottom substrate heterogeneity can significantly enhance vegetation establishment and diversity in wetlands. Microtopographic variation, including differences of only 1–3 cm in elevation, can increase both species richness and evenness in experimental wetland communities (Vivian-Smith, 1997). By creating environmental gradients, there is suitable habitat for a wider range of species, for example by creating a range of soil moisture conditions (Doherty and Zedler, 2015). The abiotic conditions along this gradient exert a strong environmental filter on the present species pool, which is a process seen in a wide variety of ecosystems, such as prairie pothole wetlands, drylands, kettle holes and riverine systems (Daniel et al., 2019; Le Bagousse-Pinguet et al., 2017; Lozada-Gobilard et al., 2019; Sarneel et al., 2019).

### 4.2. Interaction with grazing

In addition to steering vegetation composition, water level also steered herbivore presence. The spatial and temporal variation in water level resulted in complementary grazing pressure by geese (lower elevations, wet periods) and red deer (higher elevations, dry periods) in space and time. Geese are known to have a profound impact on vegetation, and specifically reed, establishment during wetland restoration in the presence of water (Alderson et al., 2025; Jobe et al., 2022; Temmink et al., 2022). On the other hand, red deer avoid the most wet areas (Romportl et al., 2017) and prefer to forage on grasses, forbs, leaves, shrubs and young shoots (Iacolina et al., 2020; Obidziński et al., 2013).

This grazer-dependent impact on the development of vegetation and specifically reed became clear from our field exclosure experiment. The impact of geese initially leads to reduction of cover of vegetation to almost zero, as observed in our exclosures and corroborated by literature (Sarneel et al., 2014; Temmink et al., 2022). Red deer do not seem to fully reduce cover to zero but rather forage on specific species thereby impacting the vegetation composition in the exclosure plots. Also, other studies mention the impact of red deer on vegetation composition and in creating mosaic landscapes (Müller et al., 2017; Riesch et al., 2020). However, in the first years of the exclosure experiment and drawdown, the impact of red deer on cover of specific species, such as reed, was more pronounced. This led to the faster growth of reed in the exclosures than in the control plots, yet in the longer term, reed cover did not differ much anymore. The differences between the two herbivores may be explained by trait-specific impacts. Geese are known to uproot plants to forage on their root and rhizomes, this is more detrimental to the plant itself then only removing the top of the plant (red deer) (pers. obs. In the field). The impact of red deer transcends the grazing impact, due to its large body weight also physical disturbance of vegetation may play a role in changing the vegetation composition (Danell et al., 2006). The trampling by red deer, creates open places with a specific microclimate that could facilitate germination (Eichberg and Donath, 2018; Ludvíková et al., 2014).So, while geese continuously reset vegetation succession by removing the whole plant, red deer are less destructive and remove plant cover on a smaller scale, probably mostly through physical disturbance.

The impact of red deer on reed vegetation was mostly visible during the first year of drawdown, when the area was very dry, reed plants were young and highly palatable (Loonen et al., 1991) and deer numbers were relatively high. The impact of geese on reed could more clearly be linked to the presence of water. During the wet spring of 2024, there was high cover of reed vegetation in the exclosures but no cover of reed vegetation outside the exclosures at lower elevations where geese are relatively abundant. This difference between exclosure and control was not seen at higher elevations, where geese were often absent. As such, seasonal inundations especially during the growing season will lead to a lower establishment of reed vegetation, mainly due to geese presence, and will interact with the effectiveness of a water level drawdown. However, just having seasonal fluctuations and no water level drawdown, as is the case in the eastern section, does not lead to establishment of reed. Furthermore, other studies have shown that reed needs multiple years to establish during a drawdown (Graveland, 1998; Tóth, 2016). Our findings indicate the necessity to maintain a low water level during wetland restoration to be able to allow establishment of target vegetation.

### 4.3. Conclusions

In conclusion, we show that by steering the water level target vegetation can expand even in the presence of grazers. This implies that protecting target vegetation against grazing during early stages of restoration is not always required (Reis et al., 2021; Villar, 2023; Xu et al., 2025). It is important to allow several years without inundation for the vegetation to increase in resilience to grazing, this increase in resilience is observed in different systems such as brackish marsh systems (Reijers et al., 2019) and during restoration of submerged macrophytes (van Zuidam et al., 2022). After inundation, presence of ungulates and herbivorous birds may increase heterogeneity of the wetland (Riesch et al., 2020).

Our study highlights the importance of combining abiotic environmental filtering and biotic interactions when explaining plant species composition (Kraft et al., 2015). In the long-term, herbivory and water level fluctuations, including a drawdown, will induce a pattern of cyclic succession in reed wetlands. Cyclic succession is observed in a wide array of ecosystems: In savannah and grassland ecosystems, fire and grazing create cyclicity (Van Langevelde et al., 2003), in kelp forests, storms reset succession (Reed et al., 2011) and in river estuaries, the moving of ice initiates vegetation succession (Lind and Nilsson, 2015). Although, the concept of cyclic vegetation succession is already well established, its application in restoration approaches across ecosystems is not often considered. The results of this study show that through large-scale manipulation of the water level it is possible to apply the concept of cyclic succession in both natural and human-engineered ecosystems.

### 4.4. Policy implications

We argue that by using water level as a tool, reed establishment can be facilitated on a large scale. This prevents costly and labour-intensive interventions, such as seeding or planting and large-scale exclosure building or placing wire above the vegetation to reduce goose presence. Since water level manipulation is one of the most common management interventions (Gray et al., 2013), infrastructure for creating a dynamic water level is often already present, for example levees. This makes the shift to a more dynamic water level relatively easy and low in extra costs. Ideally, wetlands are managed as a complex of various successional stages and hydroperiods in close proximity (Bouma, 2025; Gray et al., 2013). This does need further fine-scale infrastructure to be able to have different water level management in different wetland areas. Lastly, the importance of wetlands for breeding and migrating birds, further shows the need for large-scale global wetland restoration. Birds are known to respond quickly to changing water level conditions and the subsequent response of vegetation, and will further benefit from the heterogeneity created in space and time through the use of cyclic water level dynamics (Weller, 1999; Ma et al., 2010; Farley et al., 2022).

## CRediT authorship contribution statement

**Kerstin Bouma:** Writing – review & editing, Writing – original draft, Visualization, Methodology, Investigation, Formal analysis, Data curation, Conceptualization. **Gabriela Carrasco Oliva:** Writing – review & editing, Investigation, Data curation. **Mats I. Douma:** Writing – review & editing, Investigation, Data curation. **Perry Cornelissen:** Writing – review & editing, Methodology. **Mennobart R. van Eerden:** Writing – review & editing, Methodology, Investigation. **Ralph J.M. Temmink:** Writing – review & editing, Supervision. **Bart A. Nolet:** Writing – review & editing, Supervision. **Elisabeth S. Bakker:** Writing – review & editing, Writing – original draft, Visualization, Supervision, Project administration, Methodology, Investigation, Funding acquisition.

## Declaration of competing interest

The authors declare the following financial interests/personal relationships which may be considered as potential competing interests:

Elisabeth S. Bakker reports financial support was provided by Dutch Forest and Nature reserve owners association (VBNE). If there are other authors, they declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

## Acknowledgements

We would like to thank Britt van Zelst, Dennis Waasdorp, Dianneke van Wijk, Dirk van Winden, Emma Polman, Erik Reichmann, Hugo Langezaal, Lars Ursem, Merel, Nacho Villar, Nico Helmsing, Niels Verouden, Rens Koper, Rosan van Halsema, Rosalba Hendriks, Ruben Bos, Taylor Sliedrecht, Thomas Brouwers, Vera van Santvoort, Vincent van Bodegraven and Wiebe Lekkerkerk. We acknowledge the Dutch Forest and Nature reserve owners' association (VBNE) and the OBN knowledge network for financing the project and the State Forestry Service for facilitating the fieldwork.

## Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.ecoleng.2025.107819.

## Data availability

Data is available on DataDryad (http://datadryad.org/): DOI: 10.5061/dryad.rxwdbrvpp

## References


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. J. Appl. Ecol. https://doi.org/10.1111/1365-2664.70021.

Bakker, E.S., Pagès, J.F., Arthur, R., Alcoverro, T., 2016. Assessing the role of large herbivores in the structuring and functioning of freshwater and marine angiosperm ecosystems. Ecography 39, 162–179. https://doi.org/10.1111/ecog.01651.

Bakker, E.S., Veen, C.G.F., Ter Heerdt, G.J.N., Huig, N., Sarneel, J.M., 2018. High grazing pressure of geese threatens conservation and restoration of reed belts. Front. Plant Sci. 871, 1–12. https://doi.org/10.3389/fpls.2018.01649.

Baldwin, A.H., Kettenring, K.M., Whigham, D.F., 2010. Seed banks of Phragmites australis-dominated brackish wetlands: Relationships to seed viability, inundation, and land cover. Aquat. Bot. 93, 163–169. https://doi.org/10.1016/j.aquabot.2010.06.001.

Beemster, N., Troost, E., Platteeuw, M., 2010. Early successional stages of Reed Phragmites australis vegetations and its importance for the Bearded Reedling Panurus biarmicus in Oostvaardersplassen, the Netherlands. Ardea 98, 339–354. https://doi.org/10.5253/078.098.0308.

Bouma, K., 2025. Cyclic water level dynamics determine wetland functioning: Restoring or introducing wetland dynamics to improve habitat heterogeneity and food availability for wetland birds [internal PhD, WU, Wageningen University]. Wageningen University. Doi: 10.18174/680464.

Bouma, K., Bakker, E.S., Wilborts, M., Robroek, B.J.M., Lamers, L.L., Cornelissen, P., van Eerden, M.R., Temmink, R.J.M., 2024. Water level drawdown induces a legacy effect on the seed bank and retains sediment chemistry in a eutrophic clay wetland. Sci. Total Environ. 929. https://doi.org/10.1016/j.scitotenv.2024.172531.

Brooks, M.E., Kristensen, K., Van Benthem, K.J., Magnusson, A., Berg, C.W., Nielsen, A., Skaug, H.J., Machler, M., Bolker, B.M., 2017. glmmTMB balances speed and flexibility among packages for zero-inflated generalized linear mixed modeling. R J 9, 378–400.

Casaer, J., Milotic, T., Liefting, Y., Desmet, P., Jansen, P., 2019. Agouti: a platform for processing and archiving of camera trap images. Biodiver. Inform. Sci. Stand. 3. https://doi.org/10.3897/biss.3.46690.

Cheng, X., Janssen, H., Barends, F.B., denHaan E, J., 2004. A combination of ESEM, EDX and XRD studies on the fabric of Dutch organic clay from Oostvaardersplassen (Netherlands) and its geotechnical implications. Appl. Clay Sci. 25 (3–4), 179–185.

Cornelissen, P., Bokdam, J., Sykora, K., Berendse, F., 2014. Effects of large herbivores on wood pasture dynamics in a European wetland system. Basic Appl. Ecol. 15, 396–406. https://doi.org/10.1016/j.baae.2014.06.006.

Daleo, P., Alberti, J., Pascual, J., Canepuccia, A., Iribarne, O., 2014. Herbivory affects salt marsh succession dynamics by suppressing the recovery of dominant species. Oecologia 175, 335–343. https://doi.org/10.1007/s00442-014-2903-0.

Danell, K., Bergström, R., Duncan, P., Pastor, J., 2006. Large Herbivore Ecology, Ecosystem Dynamics and Conservation, Vol. 11. Cambridge University Press.

Daniel, J., Gleason, J.E., Cottenie, K., Rooney, R.C., 2019. Stochastic and deterministic processes drive wetland community assembly across a gradient of environmental filtering. Oikos 128, 1158–1169. https://doi.org/10.1111/oik.05987.

Davidson, N.C., 2014. How much wetland has the world lost? Long-term and recent trends in global wetland area. Mar. Freshw. Res. 65, 934–941. https://doi.org/10.1071/MF14173.

Doherty, J.M., Zedler, J.B., 2015. Increasing substrate heterogeneity as a bet-hedging strategy for restoring wetland vegetation. Restor. Ecol. 23 (1), 15–25.

Eichberg, C., Donath, T.W., 2018. Sheep trampling on surface-lying seeds improves seedling recruitment in open sand ecosystems. Restor. Ecol. 26, S211–S219. https://doi.org/10.1111/rec.12650.

Ejrnæs, D.D., Olivier, B., Bakker, E.S., Cornelissen, P., Ejrnæs, R., Smit, C., Svenning, J.C., 2024. Vegetation dynamics following three decades of trophic rewilding in the Mesic grasslands of Oostvaardersplassen. Appl. Veg. Sci. 27. https://doi.org/10.1111/avsc.12805.

Farley, E.B., Schummer, M.L., Leopold, D.J., Coluccy, J.M., Tozer, D.C., 2022. Influence of water level management on vegetation and bird use of restored wetlands in the Montezuma Wetlands complex. Wildl. Biol. 2022. https://doi.org/10.1002/wlb3.01016.

Fluet-Chouinard, E., Stocker, B.D., Zhang, Z., Malhotra, A., Melton, J.R., Poulter, B., Kaplan, J.O., Goldewijk, K.K., Siebert, S., Minayeva, T., Hugelius, G., Joosten, H., Barthelmes, A., Prigent, C., Aires, F., Hoyt, A.M., Davidson, N., Finlayson, C.M., Lehner, B., Jackson, R.B., McIntyre, P.B., 2023. Extensive global wetland loss over the past three centuries. Nature 614, 281–286. https://doi.org/10.1038/s41586-022-05572-6.

Gigante, D., Landucci, F., Venanzoni, R., 2013. The reed die-back syndrome and its implications for floristic and vegetational traits of Phragmitetum australis. Plant Sociol. 50, 3–16. https://doi.org/10.7338/pls2013501/01.

Gorai, M., Vadel, A.M., Neffati, M., 2006. Seed germination characteristics of *Phragmites australis* communis: effects of temperature and salinity. Belg. J. Bot. 374 (1), 727–773.

Grace, J.B., 1987. The impact of preemption on the zonation of two Typha species along lakeshores. Ecol. Monogr. 57 (4), 283–303.

Graveland, J.A.A.P., 1998. Reed die-back, water level management and the decline of the Great Reed Warbler Acrocephalus arundinaceus in The Netherlands. ARDEA-WAGENINGEN- 86, 187–201.

Gray, M.J., Hagy, H.M., Nyman, J.A., Stafford, J.D., 2013. Management of wetlands for wildlife. In: Wetland techniques: volume 3: applications and management. Springer Netherlands, Dordrecht, pp. 121–180.

ter Heerdt, G., 2016. Establishment of different riparian plant communities from the same soil seed bank.

Hidding, B., Sarneel, J.M., Bakker, E.S., 2014. Flooding tolerance and horizontal expansion of wetland plants: Facilitation by floating mats? Aquat. Bot. 113, 83–89.

Huijser, M.P., Drost, H.J., Roling, Y.J.B., 1995. Vegetatieontwikkeling en cyclisch waterpeilbeheer in de Oostvaardersplassen. De Levende Natuur 96 (6), 213–222.

Iacolina, L., Lukassen, M.B., Fløjgaard, C., Buttenschøn, R., Nielsen, J.L., Pertoldi, C., 2020. eDNA and metabarcoding for rewilding projects monitoring, a dietary approach. Mamm. Biol. 100, 411–418. https://doi.org/10.1007/s42991-020-00032-y.

Jans, L., Drost, H.J., 1995. De Oostvaardersplassen - 25 jaar vegetatie-onderzoek.

Jobe, J., Krafft, C., Milton, M., Gedan, K., 2022. Herbivory by geese inhibits tidal freshwater wetland restoration success. Diversity (Basel) 14. https://doi.org/10.3390/d14040278.

Kong, X., He, Q., Yang, B., He, W., Xu, F., Janssen, A.B.G., Kuiper, J.J., van Gerven, L.P.A., Qin, N., Jiang, Y., Liu, W., Yang, C., Bai, Z., Zhang, M., Kong, F., Janse, J.H., Mooij, W.M., 2017. Hydrological regulation drives regime shifts: evidence from paleolimnology and ecosystem modeling of a large shallow Chinese lake. Glob. Chang. Biol. 23, 737–754. https://doi.org/10.1111/gcb.13416.

Kraft, N.J.B., Adler, P.B., Godoy, O., James, E.C., Fuller, S., Levine, J.M., 2015. Community assembly, coexistence and the environmental filtering metaphor. Funct. Ecol. 29, 592–599. https://doi.org/10.1111/1365-2435.12345.

Le Bagousse-Pinguet, Y., Gross, N., Maestre, F.T., Maire, V., de Bello, F., Fonseca, C.R., Kattge, J., Valencia, E., Leps, J., Liancourt, P., 2017. Testing the environmental filtering concept in global drylands. J. Ecol. 105, 1058–1069. https://doi.org/10.1111/1365-2745.12735.

Lind, L., Nilsson, C., 2015. Vegetation patterns in small boreal streams relate to ice and winter floods. J. Ecol. 103, 431–440. https://doi.org/10.1111/1365-2745.12355.

Liu, Q., Liu, J., Liu, H., Liang, L., Cai, Y., Wang, X., 2020. Vegetation dynamics under water-level fluctuations : Implications for wetland restoration. J. Hydrol. (Amst) 581, 124418. https://doi.org/10.1016/j.jhydrol.2019.124418.

Loonen, M.J.J.E., Zijlstrai, M., Van Eerdeni, M.R., 1991. Timing of Wing Moult in Greylag Geese (*Anser anser*) in Relation to the Availability of their Food Plants.

Lozada-Gobilard, S., Stang, S., Pirhofer-Walzl, K., Kalettka, T., Heinken, T., Schröder, B., Eccard, J., Joshi, J., 2019. Environmental filtering predicts plant-community trait distribution and diversity: Kettle holes as models of meta-community systems. Ecol. Evol. 9, 1898–1910. https://doi.org/10.1002/ece3.4883.

Ludvíková, V., Pavlů, V.V., Gaisler, J., Hejcman, M., Pavlů, L., 2014. Long term defoliation by cattle grazing with and without trampling differently affects soil penetration resistance and plant species composition in Agrostis capillaris grassland. Agric. Ecosyst. Environ. 197, 204–211. https://doi.org/10.1016/j.agee.2014.07.017.

Ma, Z., Cai, Y., Li, B., Chen, J., 2010. Managing wetland habitats for waterbirds: an international perspective. Wetlands 30 (1), 15–27.

Marin, V.C., Fernández, V.A., Dacar, M.A., Gutiérrez, D.G., Fergnani, D., Pereira, J.A., 2020. Diet of the marsh deer in the Paraná River Delta, Argentina—a vulnerable species in an intensive forestry landscape. Eur. J. Wildl. Res. 66. https://doi.org/10.1007/s10344-019-1358-3.

Merendino, M.T., Smith, L.M., 1991. Influence of drawdown date and reflood depth on wetland vegetation establishment. Wildl. Soc. Bull. (1973-2006) 19 (2), 143–150.

Morganti, M., Manica, M., Bogliani, G., Gustin, M., Luoni, F., Trotti, P., Perin, V., Brambilla, M., 2019. Multi-species habitat models highlight the key importance of flooded reedbeds for inland wetland birds: Implications for management and conservation. Avian. Res. 10. https://doi.org/10.1186/s40657-019-0154-9.

Mori, A.S., 2011. Ecosystem management based on natural disturbances: hierarchical context and non-equilibrium paradigm. J. Appl. Ecol. 48 (2), 280–292.

Müller, A., Dahm, M., Bøcher, P.K., Root-Bernstein, M., Svenning, J.C., 2017. Large herbivores in novel ecosystems-Habitat selection by red deer (Cervus elaphus) in a former brown-coal mining area. PLoS One 12 (5), e0177431.

Obidziński, A., Kiełtyk, P., Borkowski, J., Bolibok, L., Remuszko, K., 2013. Autumn-winter diet overlap of fallow, red, and roe deer in forest ecosystems, Southern Poland. Cent. Eur. J. Biol. 8, 8–17. https://doi.org/10.2478/s11535-012-0108-2.

Oksanen, J., Simpson, G., Blanchet, F., Kindt, R., Legendre, P., Minchin, P., O'Hara, R., Solymos, P., Stevens, M., Szoecs, E., Wagner, H., Barbour, M., Bedward, M., Bolker, B., Borcard, D., Carvalho, G., Chirico, M., De Caceres, M., Durand, S., Evangelista, H., FitzJohn, R., Friendly, M., Furneaux, B., Hannigan, G., Hill, M., Lahti, L., McGlinn, D., Ouellette, M., Ribeiro Cunha, E., Smith, T., Stier, A., Ter Braak, C., Weedon, J., 2022. Vegan: Community Ecology Package.

Olff, H., De Leeuw, J., Bakker, J.B., Platerink, R.J., van Wijnen, H.J., 1999. Vegetation succession and herbivory in a salt marsh changes induced by sea level rise and silt deposition. J. Ecol. 85, 799–814.

Poorter, L., van der Sande, M.T., Amissah, L., Bongers, F., Hordijk, I., Kok, J., Laurance, S.G.W., Martínez-Ramos, M., Matsuo, T., Meave, J.A., Muñoz, R., Peña-Claros, M., van Breugel, M., Herault, B., Jakovac, C.C., Lebrija-Trejos, E., Norden, N., Lohbeck, M., 2024. A comprehensive framework for vegetation succession. Ecosphere 15. https://doi.org/10.1002/ecs2.4794.

R Core Team, 2023. R: A Language and Environment for Statistical Computing.

Reed, D.C., Rassweiler, A., Carr, M.H., Cavanaugh, K.C., Malone, D.P., Siegel, D.A., Siegel, D.A., 2011. Wave disturbance overwhelms top-down and bottom-up control of primary production in California kelp forests source. Ecology 92 (11), 2108–2116.

Reijers, V.C., Cruijsen, P.M.J.M., Hoetjes, S.C.S., van den Akker, M., Heusinkveld, J.H.T., van de Koppel, J., Lamers, L.P.M., Olff, H., van der Heide, T., 2019. Loss of spatial structure after temporary herbivore absence in a high-productivity reed marsh. J. Appl. Ecol. 56, 1817–1826. https://doi.org/10.1111/1365-2664.13394.

Reis, L.K., Junior, G.A.D., Battaglia, L.L., Garcia, L.C., 2021. Can transplanting seedlings with protection against herbivory be a cost-effective restoration strategy for seasonally flooded environments? For. Ecol. Manag. 483, 118742.

Riesch, F., Tonn, B., Stroh, H.G., Meißner, M., Balkenhol, N., Isselstein, J., 2020. Grazing by wild red deer maintains characteristic vegetation of semi-natural open habitats: evidence from a three-year exclusion experiment. Appl. Veg. Sci. 23, 522–538. https://doi.org/10.1111/avsc.12505.

Romportl, D., Bláhová, A., Andreas, M., Chumanová, E., Anděra, M., Červený, J., 2017. Current distribution and habitat preferences of red deer and eurasian elk in the Czech Republic. Eur. J. Environ. Sci. 7, 50–62. https://doi.org/10.14712/23361964.2017.5.

Sarneel, J.M., Huig, N., Veen, G.F., Rip, W., Bakker, E.S., 2014. Herbivores enforce sharp boundaries between terrestrial and aquatic ecosystems. Ecosystems 17, 1426–1438. https://doi.org/10.1007/s10021-014-9805-1.

Sarneel, J.M., Hefting, M.M., Kowalchuk, G.A., Nilsson, C., Van der Velden, M., Visser, E. J.W., Voesenek, L.A.C.J., Jansson, R., 2019. Alternative transient states and slow plant community responses after changed flooding regimes. Glob. Chang. Biol. 25, 1358–1367. https://doi.org/10.1111/gcb.14569.

Stroh, C.L., De Steven, D., Guntenspergen, G.R., 2008. Effect of climate fluctuations on long-term vegetation dynamic in Carolina Bay wetlands. Wetlands 28, 17–27.

Tang, H., Bai, J., Yu, D., Lou, Y., 2022. Estimation of temperature and flooding depth thresholds for Phragmites australis rhizome bud sprouting. Weed Res. 62, 287–295. https://doi.org/10.1111/wre.12537.

Temmink, R.J.M., Van den Akker, M., Van Leeuwen, C.H.A., Thöle, Y., Olff, H., Reijers, V.C., Weideveld, S.T.J., Robroek, B.J.M., Lamers, L.P.M., Bakker, E.S., 2022. Herbivore exclusion and active planting stimulate reed marsh development on a newly constructed archipelago. Ecol. Eng. 175, 106474. https://doi.org/10.1016/j.ecoleng.2021.106474.

Ter Heerdt, Veen, C.G., Van der Putten, Bakker, J.P., 2017. Effects of temperature, moisture and soil type on seedling emergence and mortality of riparian plant species. Aquat. Bot. 136, 82–94.

Therneau, T., Atkinson, B., Ripley, B., 2022. rpart: Recursive Partitioning and Regression Trees. R package version 4.1.19.

Tóth, V.R., 2016. Reed stands during different water level periods: physico-chemical properties of the sediment and growth of Phragmites australis of Lake Balaton. Hydrobiologia 778 (1), 193–207.

Van Den Wyngaert, I.J.J., Wienk, L.D., Sollie, S., Bobbink, R., Verhoeven, J.T.A., 2003. Long-term effects of yearly grazing by moulting Greylag geese (*Anser anser*) on reed (*Phragmites australis*) growth and nutrient dynamics. Aquat. Bot. 75, 229–248. https://doi.org/10.1016/S0304-3770(02)00178-X.

Van Eerden, M.R., Loonen, M., Zijlstra, M., 1997. Moulting Greylag Geese Anser anser defoliating a reed marsh Phragmites australis: Seasonal constraints versus long-term commensalism between plants and herbivores. In: MR Van Eerden Patchwork. Patch Use, Habitat Exploitation and Carrying Capacity for Water Birds in Dutch Freshwater Wetlands. University of Groningen, pp. 241–264. PhD Thesis.

Van Langevelde, F., Van De Vijver, C.A.D.M., Kumar, L., Van De Koppel, J., De Ridder, N., Van Andel, J., Skidmore, A.K., Hearne, J.W., Stroosnijder, L., Bond, W.J., Prins, H.H.T., Rietkerk, M., 2003. Effects of fire and herbivory on the stability of savanna ecosystems. Ecology 84, 337–350. https://doi.org/10.1890/0012-9658(2003)084[0337:EOFAHO]2.0.CO;2.

Van Leeuwen, C.H.A., Temmink, R.J.M., Jin, H., Kahlert, Y., Robroek, B.J.M., Berg, M.P., Lamers, L.P.M., van den Akker, M., Posthoorn, R., Boosten, A., Olff, H., Bakker, E.S., 2021. Enhancing ecological integrity while preserving ecosystem services: Constructing soft-sediment islands in a shallow lake. Ecol. Solut. Evid. 2. https://doi.org/10.1002/2688-8319.12098.

Villar, N., 2023. Trophic cascades help restore vegetation. Science (1979) 382, 516–517. https://doi.org/10.1126/science.adl0578.

Vivian-Smith, G., 1997. Microtopographic heterogeneity and floristic diversity in experimental wetland communities. J. Ecol. 71–82.

Vulink, J.T., Van Eerden, M.R., 1998. Hydrological conditions and herbivory as key operators for ecosystem development in Dutch artificial wetlands. Graz. Conserv. Manage. 217–252. https://doi.org/10.1007/978-94-011-4391-2_7.

Vulink, J.T., Van Eerden, M.R., Drent, R.H., 2010. Abundance of migratory and wintering geese in relation to vegetation succession in man-made wetlands: the effects of grazing regimes. Ardea 98, 319–327. https://doi.org/10.5253/078.098.0306.

Weller, M.W., 1999. Wetland Birds: Habitat Resources and Conservation Implications. Cambridge University Press.

Wilcox, D.A., 2004. Implications of hydrologic variability on the succession of plants in Great Lakes wetlands. Aquat. Ecosyst. Health Manag. 7 (2), 223–231.

WWF, 2022. Living Planet Report 2022 – Building a Nature Positive Society. WWF, Gland, Switzerland.

Xu, C., Silliman, B.R., Chen, J., Li, X., Thomsen, M.S., Zhang, Q., Lee, J., Lefcheck, J.S., Daleo, P., Hughes, B.B., Jones, H.P., Wang, R., Wang, S., Smith, C.S., Xi, X., Altieri, A.H., Van De Koppel, J., Palmer, T.M., Liu, L., Wu, J., Li, B., He, Q., 2025. Herbivory Limits Success of Vegetation Restoration Globally.

Zheng, J., Arif, M., Zhang, S., Yuan, Z., Zhang, L., Dong, Z., Tan, X., Charles, W., Li, C., 2021b. The convergence of species composition along the drawdown zone of the Three Gorges Dam Reservoir, China: implications for restoration. Environ. Sci. Pollut. Res. 28 (31), 42609–42621.

Zheng, J., Arif, M., Zhang, S., Yuan, Z., Zhang, L., Li, J., Ding, D., Li, C., 2021a. Dam inundation simplifies the plant community composition. Sci. Total Environ. 801, 149827.

Zijlstra, M., Loonen, M.J.J.E., Van Eerden, M.R., Dubbeldam, W., 1991. The Oostvaardersplassen as a key moulting site for Greylag geese Anser anser in western Europe. Wildfowl 42, 45–52.

Żmihorski, M., Pärt, T., Gustafson, T., Berg, Å., 2016. Effects of water level and grassland management on alpha and beta diversity of birds in restored wetlands. J. App. Ecol. 53 (2), 587–595.

van Zuidam, B.G., Bakker, E.S., van Geest, G.J., Peeters, E.T.H.M., 2022. Submerged vegetation colonizes behind artificial wave shelter after a 10-year time-lag and persists under high grazing pressure by waterbirds. Aquat. Bot. 181. https://doi.org/10.1016/j.aquabot.2022.103541.