

Master's Thesis – Master Sustainable Development

**Active Rewilding in a Novel Ecosystem: Investigating the Impact of Deer
Herbivory and Water Level Management on Wetland Vegetation
Development**

The case of Oostvaardersplassen park, The Netherlands.



Image Source: Kerstin Bouma, 2023.

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“Cardumen de ambientalas por siempre, atravesando océanos y el universo”

Abstract

Wetlands play a crucial role in providing ecosystem services that contribute to the achievement of the Sustainable Development Goals (SDGs). However, human activities have led to widespread degradation of wetlands over the past three centuries, increasing efforts for wetland restoration.

In some cases, restoring wetlands to their original ecosystem state may no longer be feasible. As a result, new restoration paradigms have emerged as alternative approaches to enhance ecosystem services and resilience, such as rewilding. Active rewilding actions, including the emulation of dry periods to create stochastic disturbances, and the introduction of "ecosystem engineers" for trophic restoration, are currently employed in Oostvaardersplassen park, The Netherlands. A recent induced drawdown, initiated in 2020, aimed to regenerate vegetation by following the natural wetlands cycle. However, this restoration effort faces challenges from red deer (*Cervus elaphus*) herbivory, which might limit vegetation development.

To address this issue, this study investigated the effects of red deer herbivory and artificial water level management on vegetation development during the early stage of ecological succession. The research involved an exclusion experiment in the wetland area of Oostvaardersplassen park. By exploring the co-occurrence of these rewilding measures, the study aimed to fill knowledge gaps regarding the impact of red deer herbivory on wetland vegetation following a drawdown. Particular attention was given to the development of the common reed (*Phragmites australis*) species, as reedbeds serve as vital habitats for numerous species.

On the one hand, the study's findings demonstrated that deer herbivory had adverse effects on reed presence, coverage, and height. On the other hand, in the short-term, herbivory exclusion led to an increase in vegetation coverage. However, other vegetation diversity variables were not significantly affected by herbivory. Additionally, water level fluctuations resulted in different vegetation communities over time, and higher water levels had a negative impact on vegetation development. This research reveals the negative impact of deer herbivory on reed development and highlights potential limitations to overall vegetation growth when herbivory pressure persists. The insights gained from this study are valuable in shaping wetland restoration and management strategies, ultimately contributing to the preservation and enhancement of wetland ecosystem services. To ensure the progression of this ecosystem towards a boom phase, implementing preventive measures to reduce deer impact will be crucial. By doing so, wetland restoration efforts can effectively steer the development of a diverse and resilient ecosystem that benefits both biodiversity and the fulfillment of wetland-related SDGs.

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1. Introduction

Freshwater wetlands have long been damaged because of anthropogenic activities over the past three centuries (Fluet-Chouinard et al., 2023). A recent study conducted by Fluet-Chouinard and colleagues (2023) estimated that a total of 3.4 million square kilometers of wetland surface has been lost since 1700 worldwide, equating to a loss of 21% of the global freshwater wetland surface area. The causes of wetland destruction vary across different regions, with agriculture, urbanization, forestry, pasture, and peat extraction being the most notable factors. The reduction in wetland surface area is coupled with socioecological consequences, leading to a decline in crucial ecosystem services such as nutrient cycling, water purification, and carbon storage (Temmink et al., 2022; Constanza et al., 2014; de Groot et al., 2012; Xu et al., 2020). Hence, directly impacting human well-being. Additionally, wetlands play a vital role in advancing sustainability goals (SDGs) by providing valuable ecosystem services (Ferreira et al., 2023; Ramsar Convention Secretariat, 2018). They act as large carbon sinks, helping combat climate change (SDG 13), and are essential for addressing the biodiversity crisis, as they harbor up to 40% of the world's biodiversity (SDG 15) (Zhang et al., 2020; Ramsar Convention Secretariat, 2018). Even though wetland losses have been leveled off in Europe, it is of special concern that approximately 50% of wetlands in the region have already vanished between 1700 and 2020 (Fluet-Chouinard et al., 2023). To offset the declining trend in wetlands and regain surface losses they have already experienced, well-managed restoration efforts aimed at restoring ecosystem services are urgently needed (UNEP, n.d.; United Nations, 2015).

Restoration science is a growing research topic, highlighting the increasing social interest in this subject (Suding, 2011). Likewise, international policies are putting an effort to counteract ecological damage with the definition of the current decade as the “restoration decade” by United Nations, as well as the European Union aims to restore damaged ecosystems by 2050 (European Commission, 2022). In this regard, clear pathways are needed to accomplish this goal. Within the restoration framework, different paradigms underlie restoration projects (Suding, 2011). For instance, classical restoration paradigms seek to restore an ecosystem to a previous state based on its historical conditions or an analogue ecosystem (Jackson & Hobbs, 2009). However, achieving such an approximation is often challenging due to limitations in knowledge about pre-disturbance ecosystem conditions, or the fact that restoring an ecosystem to its pre-human state becomes nearly impossible once it has undergone a threshold and shifted into a new stable state (Hobbs et al., 2009; Rohr, et al., 2018; Suding & Hobbs, 2009). In this latter case, resetting the ecological state would be highly costly but with no guarantee of success (Jackson & Hobbs, 2009; Rohr, et al., 2018; Suding, 2011). However, novel restoration strategies have emerged that do not involve returning to the historic stable state. Instead, they focus on enhancing the functioning and resilience of degraded land, despite its historical ecosystem composition (Hobbs et al., 2009). This forward-looking paradigm could even lead to developing a nonhistorical resilient ecosystem, capable of withstanding future disturbances and providing diverse ecosystem services (Hobbs et al., 2009; Suding, 2011). This approach is of great significance for the future supply of ecosystem services, especially considering the current scenario of land scarcity and the increasing need for land reclamation for restoration, which has been severely eroded, making the resetting of the ecological conditions unfeasible (Gwenzi et al., 2021).

Rewilding offers a means to facilitate the development and progression of the ecosystem towards restoring ecological functioning (Perino et al., 2019). The aim of rewilding is rooted in forward-looking paradigms as its final goal is not focused on reaching prehuman disturbance conditions (Toit & Petorrelli, 2019). Instead, at the core of rewilding initiatives lies the concept of restoring ecosystems wilderness, which refers to establish the autonomy of natural processes and promoting self-regulation and ecological resilience in the long-term (Perino et al., 2019). It can follow a passive or active restoration pathway, either by allowing the ecosystem to spontaneously undergo ecological succession or by actively guiding the ecosystem through strategic choices (Perino et al., 2019; Suding, 2011). One crucial aspect of rewilding is trophic restoration, which means enhancing trophic complexity by reintroducing absent species that play vital ecological roles, ultimately shaping the desired ecosystem. This approach often involves introducing (non-native) species as functional replacements for missing native species (Perino et al., 2019). Rewilding actions widely utilize certain animals, such as herbivores as ecosystem engineers. They are broadly recognized as ecosystem engineers due to their remarkable capacity to modify vegetation structure, species richness, and composition through their consumption behavior, resulting in a top-down effect (Bakker & Svenning, 2018). By altering the vegetation, which serves as the foundation of the trophic chain, grazers initiate cascading effects on higher trophic levels, potentially leading to an ecosystem shift (Cornelissen et al., 2014b).

Another important aspect of rewilding is allowing stochastic disturbances within the system (Perino et al., 2019). In other words, natural disturbances are intentionally introduced to enhance spatial and temporal heterogeneity in the ecosystem, hence leading to further ecosystem complexity. In the case of wetlands, they are ecosystems shaped by water. Water level fluctuations naturally disturb the system and trigger vegetational ecological succession, which has a significant impact on the ecosystem services they can ultimately provide (Temmink, et al. 2022a; Vroom et al., 2020). In the case of freshwater wetlands, drought disturbances occur cyclically (van der Valk & Davis 1978). During dry years of the cycle these ecosystems experience an increase in the abundance of annual plants and other species that are less tolerant to flooding (van der Valk & Davis, 1976). However, during wetter conditions, the annual plants are gradually replaced by perennial plants. If water levels remain stable, a transition to a less productive open water ecosystem occurs over the long-term, until the next dry period initiates the cyclic vegetation change once again (Liu et al., 2005; Lu et al., 2010; van der Valk & Davis 1978). Wetlands are classified as "boom" and "bust" systems, as they experience high productivity periods (boom) when biodiversity flourishes, followed by bottleneck periods (bust). Both states are strictly related to water level fluctuations (Beemster et al., 2010; Bino et al., 2015; Lemke et al., 2017). In short, a drought disturbance is necessary for vegetation establishment, supporting the system's boom phase upon the return of water (figure 1). The occurrence of stochastic dry events exposes mudflats and creates favorable conditions for germination from the seed bank, growth of annual plants that produce abundant seeds to replenish the seed bank, as well as perennial plants that generate tubers (van der Valk et al., 1992). Therefore, the oscillation between boom-and-bust phases in wetlands is closely tied to the development of vegetation following a drought and an important dynamic to take into account for rewilding.

In the context of novel ecosystems and creating entirely new human-made wetlands, deliberate interventions are necessary to guide the artificial system towards the desired 'boom' phase. These interventions aim to emulate water level fluctuations and establish trophic interactions. Water level

management techniques, such as artificial drawdowns and the introduction of selected herbivores as ecosystem engineers, are combined rewilding strategies that are gaining popularity (Coops et al., 2004; Farley et al., 2021; Smit et al., 2015). As wetlands functionality depends on vegetation (Hobbs et al., 2006; Temmink et al., 2022b), the primary objective in the early stages of establishing a new ecosystem is to revegetate. Promoting in this way, its ecological functionality through a bottom-up approach. In wetland ecosystems, reed vegetation (*Phragmites australis*) is commonly targeted for restoration efforts due to its ecological importance. Reed provides habitat diversity, shelter, nesting, and food resources for several species (Beemster et al., 2010; Šťastný & Riegert, 2021; Voslamber and Vulink, 2010). Therefore, restoring reed vegetation serves as a crucial step towards establishing a thriving wetland ecosystem.

The Oostvaardersplassen (OVP) is part of the National Park Nieuwland, in The Netherlands. It is an example of a rewilding project of a nonhistorical or novel ecosystem, with active management. This active management involves occasional drawdown, by emulating stochastic disturbances, and the introduction of large herbivores to improve trophic complexity. OVP was the result of land reclamation from the ocean in 1968 and nowadays represents an important conservation area within Europe as it houses a wide bunch of threatened bird species, among others.

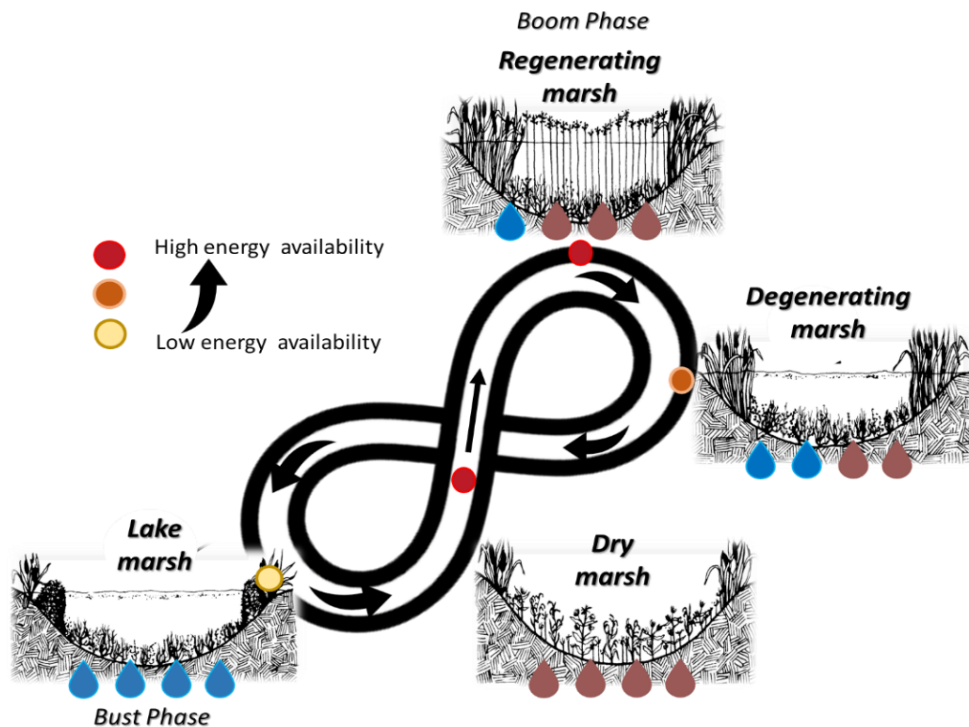


Figure 1. Wetlands' cycle (van der Valk & Davis 1978). This image depicts the different stages of a wetland. This cycle is constantly undergoing in nature which is represented by the infinite figure. The transition of wetlands from one state to another depends on the level of water due to weather conditions. "Dry marsh" is the state of a wetland during a dry period. At this state, mudflats are exposed, facilitating the germination of seeds from the seed bank. Further vegetation development increases energy availability for further trophic levels in the food webs. The subsequent "regeneration state" is when emergent vegetation dominates the habitat. They provide habitat, shelter, and food resources, resulting in a biodiversity enhancement (boom phase). As the cycle progresses, the system transitions to a "degenerating state" characterized by a decline in

emergent plant coverage. Ultimately, it reaches a "lake state" where the absence of emergent vegetation and the dominance of submerged vegetation limits biodiversity (bust phase). Drops represent the percentage of open water in the system.

1.1. Problem definition

The primary short-term objective of the OVP park managers is to enhance productivity in the wetland area. Consequently, a biodiversity and especially bird populations increase is expected by means of habitat, shelter and food provision (Beemster et al., 2010; Farley et al., 2021). This is all by promoting habitat complexity, allowing the growth of reed vegetation, and limiting the sole extent of open water. To achieve this, park managers implemented an artificial drawdown to facilitate the expansion of the reed beds. Additionally, the introduction of red deer (*Cervus elaphus*) in 1992 as ecosystem engineers has been carried out. However, the absence of regulatory influence from top predators in the park allows deer populations to reach high densities, which can potentially have negative impacts on other species groups (Smit et al., 2015, Cornelissen et al., 2014a; 2014b).

On the one hand, while some studies have evaluated the performance of reed and vegetation establishment following a drawdown, many have focused solely on assessing seed and tuber production (Greer et al., 2007; Kross et al., 2008), or have overlooked herbivory pressure (Farley et al., 2021). On the other hand, in cases when herbivory has been considered, research has mainly addressed the impact of geese grazing on vegetation establishment (Coops et al., 2004; Temmink et al., 2022b), or deer herbivory has been investigated in other landscape types (e.g., Barrett & Stiling, 2006, Cornelissen et al., 2014a; 2014b; Smit et al., 2015; Vulink et al., 2000). Namely, the impact of herbivory by red deer on wetland vegetation response following an artificial drawdown remains poorly understood but might have a large impact on the success of these rewilding efforts.

To overcome this knowledge gap, this research aims to investigate the impacts of red deer herbivory and artificial water level management on vegetation development during the first period of ecological succession. It involved an enclosure field experiment in the Oostvaardersplassen park, where herbivory was prevented within a fenced area. The findings will address knowledge gaps about the co-occurrence of these rewilding measures and offer insights for management strategies.

1.2. Research Questions

To address the research gap identified in the previous section the main research question to be answered is:

How do rewilding actions such as red deer (*Cervus elaphus*) herbivory and an ongoing artificial drawdown influence vegetation development in an early successional state, in a freshwater human-constructed and managed wetland ecosystem?

And the following research sub-questions:

- **Sub-question 1:** How does red deer herbivory influence vegetation composition, species richness, and abundance during the first stage of ecological succession triggered by the drawdown?
- **Sub-question 2:** How does red deer herbivory affect the presence, height, and coverage of common reed (*Phragmites australis*) during the first stage of ecological succession triggered by the drawdown?
- **Sub-question 3:** How does water level affect vegetation diversity and common reed (*Phragmites australis*) development during the first stage of ecological succession triggered by the drawdown?
- **Sub-question 4:** How do water level and distance towards the vegetation border influence the presence of red Deer on the wetland area across time?

1.3. Theory section

1.3.1. Herbivory influence on vegetation development

Biotic factors, such as herbivory, have played a significant role in shaping terrestrial ecosystems throughout history (WallisdeVries et al., 1998). Herbivory can have positive, neutral (e.g., Humel et al., 2028; Reijers et al., 2019; Ripa et al., 2023), or negative effects on vegetation of several ecosystems (e.g., Cornelissen et al., 2014a; 2014b). On one hand, it may benefit plants diversity by reducing light competition and promoting species richness (Hegland et al., 2013; Schutz et al., 2003; van Klink et al., 2016). On the other hand, herbivory pressure can limit vegetation development, depending on the ecosystems' productivity (Bakker et al., 2006), synergic effect with other environmental variables (Liu et al., 2020), herbivore densities (e.g., Cornelissen et al., 2014a; 2014b; Güsewell et al., 2007), and the ecosystem stage of the studied system (Temmink et al., 2022b).

Various herbivores, such as crabs and waterbirds, have been studied, revealing detrimental consequences on wetland growth. Particularly, herbivory effects on common reed (*Phragmites australis*) have shown negative impacts on reed development (e.g., Zhang et al., 2021; Bakker et al., 2018; Temmink et al., 2022b). However, less attention has been given to deer herbivory on wetland vegetation, as deer are not usually present in wetland ecosystems. Conversely, herbivory by ungulates has been widely studied in different ecosystems, particularly in woody landscapes. Deer, for example, hinder woody plant establishment and forest recovery (Barrett & Stiling, 2006; Smit et al., 2015). In the Oostvaardersplassen park in the Netherlands, Smit and colleagues (2015) examined the influence of red deer (*Cervus elaphus*) on woody species establishment. Their findings indicate that herbivory restricts wood-pastured landscapes' growth, necessitating grazing refuges for woody vegetation establishment. Ungulates, in general, significantly impact vegetation growth and species richness across various environments due to their foraging behavior (Borowski et al., 2021; Schütz et al., 2003). Moreover, Bakker and colleagues (2006) found that ecosystem productivity play crucial roles in how grazing affects the system. Large herbivores positively impact species richness in highly productive environments by creating "windows of opportunity for colonization," with bare soil patches for germination and increased light availability (Van Belzen et al., 2022). In less productive

ecosystems, vegetation development might be constrained, possibly due to propagule predation limiting plant growth.

These studies highlight the complex and varied effects of herbivory on vegetation development, emphasizing the importance of considering the ecological context when studying herbivory impacts. The direction of the effects might be very context dependent. For instance, in high-productive ecosystems like Oostvaardersplassen (OVP), herbivory could potentially have a positive effect on vegetation diversity. However, the direction of the herbivory effect remains unknown in this early ecosystem stage, where there is not light competition, and vegetation as well as reedbeds are not fully established.

1.3.2. Red deer herbivory impacts on reed development

In OVP, large herbivores such as cattle and horses have been observed converting reedbeds into grassy vegetation within four years (Cornelissen et al., 2014b; Vulink & Van Eerden, 1998). Deer, also considered large herbivores, have been reported to feed on reed, as their terrestrial nature makes their presence in the wetland area less likely. However, during drawdowns or times of reduced water levels, deer may utilize the habitat. Additionally, even in the presence of water, evidence shows that deer feed on macrophytes, negatively impacting conservation efforts (Takafumi et al., 2015). In the United States, deer grazing has been suggested as a management strategy for *Phragmites australis* (Blossey, 2003). These findings raise the possibility that deer could negatively influence reed development in the wetland area, even when water is present.

Furthermore, seasonality plays an important role in deer feeding behavior, with certain preferred plants available during specific seasons, leading to variations in deer presence depending on resource availability (Geber & Verheyden-Tixier, 2008; Ligi & Randveer, 2012). Additionally, habitat usage is also influenced by hunting pressure. Studies have shown that deer tend to avoid open areas during hunting seasons (Ligi & Randveer, 2012). Therefore, as the wetland area is an open space without tall vegetation and deer population are controlled by hunting within the park (during winter), differences in habitat usage may be observed based on the distance to the current vegetation border. The existing vegetation border has taller vegetation, offering protection against threats. Considering the goal of improving reed vegetation expansion, deer herbivory may have an impact on vegetation development in wetland regeneration initiatives due to its feeding behavior and habitat usage within the wetland area.

1.3.3. Abiotic factor influencing vegetation development

It is well known that limiting factors such as soil humidity, nutrients, or organic matter content could constrain vegetation development due to the lack of enough resources to germinate and grow (Bornette & Puijalón, 2010; ter Heerdt et al., 2017). Different plant species generally have distinct environmental requirements and adaptations that enable them to thrive under specific conditions. Functional traits or physiological mechanisms to counteract environmental stress are essential for plants survival (Kettenring et al., 2009; Pan et al., 2021). Therefore, environmental variables usually determine species occurrence and communities' composition (Coops & van der Velde, 1995; Coops

et al., 2004). Furthermore, water depth has a dominant control on vegetation composition in wetlands by limiting photosynthesis. Deeper water levels reduce light availability and carbon dioxide concentration, as well as create anoxic root environments, altering the nutrient cycles (Gries et al., 1990; Pan et al., 2021). In general, increased water levels lead to decreased vegetation cover and vegetation diversity (Chen et al., 2020; van der Valk and Davis, 1978). This is of special concern under prolonged high-water levels when the open water percentage is high, restricting plant reproduction to clonal strategies and the presence of highly adapted species (Alvarez et al., 2005; Engloner & Major, 2011)

In the case of *Phragmites australis*, it is a perennial herbaceous species, commonly inhabiting wetland ecosystems with a high tolerance for environmental stressors (Srivastava et al., 2013). These characteristics enable reed to successfully colonize and thrive in various habitats along a wide environmental gradient, where other plants often struggle to establish (Kettenring et al., 2009). Reed exhibits two reproduction mechanisms: sexual (seeds germination) and asexual (clonal or vegetative). The prevalence of one mechanism over the other for reedbed expansion depends on the water level deepness and stability (Alvarez et al., 2005). Under high and constant water levels, clonal reproduction is more likely to occur, while seed germination becomes possible under dry conditions, enhancing the genetic biodiversity (Alvarez et al., 2005; Engloner & Major, 2011). However, both mechanisms have been shown to be affected for prolonged stable and deep-water levels (Yu et al., 2012). Another crucial factor influencing reedbed recovery is the distance to the source of seeds and available rhizomes, which impacts the speed of reed growth. Shorter distances, among other factors, facilitate faster vegetation expansion (Applestein et al., 2022; Soomers et al., 2012).

In addition, specific environmental conditions need to be met for reed germination. For instance, a long enough dry period exposing the mudflats or shallow water under 4 cm (optimum) is essential. Reed can germinate in deeper water depth; however, the germination rate is considerably reduced as the water level increases (Yu et al., 2012). The work of ter Heerdt and colleagues (2017) in OVP reveals that after a dry or very dry period, certain species, such as *T. latifolia* or *P. australis*, did not emerge. This study underscores the significance of water availability for reed vegetation establishment and development. Consequently, human-induced drought and natural rainfall variability can lead to reduced reed vegetation development if the environmental conditions become too dry. Due to these stressors, wetlands restoration is not always guaranteed.

1.4. Conceptual framework

The above-mentioned theory was summarized in Figure 2. This conceptual framework illustrates the relationship between the theory and the research questions addressed in this study.

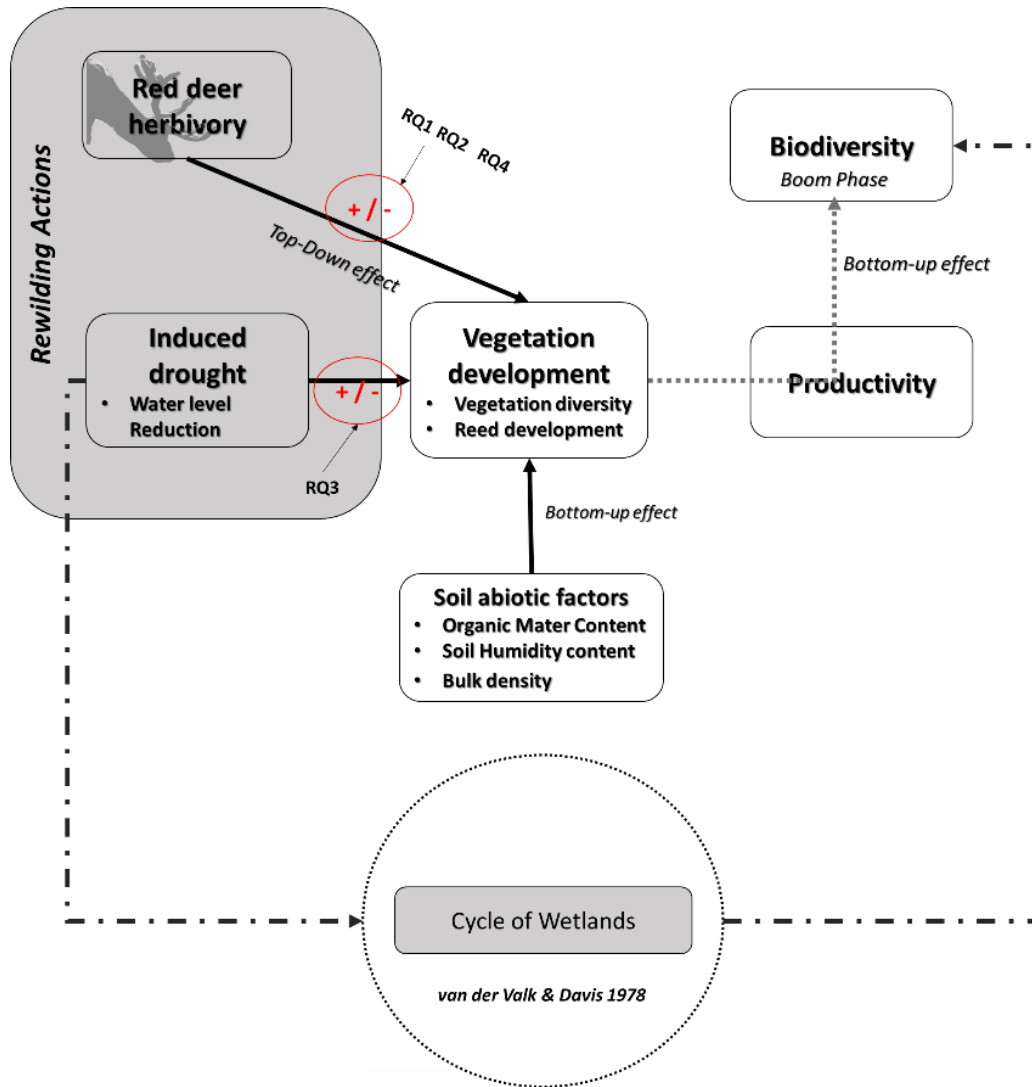


Figure 2. This diagram depicts the conceptual framework of the research, illustrating the theoretical foundation. A human-induced drought is utilized to simulate the dry phase of the wetlands cycle, initiating the cycle from the dry marsh stage (Black dotted line). Water level fluctuations play a crucial role in shaping these states, thus necessitating human management of human-made freshwater wetlands to promote the boom phase. Higher productivity in the system resulting from vegetation enhancement is likely to lead to an increase in biodiversity. However, this area will not be investigated in this research, as represented by the light gray dotted arrow. The success of restoration efforts in increasing species richness can be influenced by environmental and biological variables in a bottom-up perspective. Therefore, understanding the impact of deer herbivory and water level on vegetation and reed development is essential for Oostvaardersplassen managers aiming to enhance habitat diversity.

1.5. Hypothesis

Based on the previous theory framework this research hypothesizes the following:

Hypothesis 1: After a year of the exclusion of red deer, I expect to find a change in the vegetation composition, as well as an increase in species richness, coverage of vegetation and vegetation biodiversity in comparison to plots under herbivory pressure.

Hypothesis 2: After a year of the exclusion of red deer I expect to find an increase in reed presence, height, and coverage in contrast to plots subjected to herbivory.

Hypothesis 3: I expect to find that an increase in water level decreases species richness, coverage of vegetation, and vegetation biodiversity, as well as negatively affect reed development.

Hypothesis 4. During the wetter seasons, deer exhibit a greater presence in more elevated zones compared with the lower zones of the wetland area, while the nearest zone to the vegetation border is the preferable habitat across all seasons in contrast with areas further away from the vegetation border.

2. Methods

2.1. Study Area

This research was conducted in the Oostvaardersplassen (OVP) the Netherlands (52° 26' N, 5° 19' E) (figure 3). The OVP encompass a total area of 5,600 ha of which 3,600 ha is characterized as freshwater wetland. It is one of the first human-made natural parks in Europe. It was established in 1968, due to land reclamation from a marine habitat, called the Zuiderzee, when the South Flevoland polder was created (Wigbels, 1990). The purpose of the reclaimed land was initially for agricultural purpose. However, the area was leaved by its own for a few years when a spontaneously ecological succession started to occur. The area was rapidly colonized by pioneer vegetation and several bird species started to use the novel ecosystem. It was in 1974 when the area was assigned as a protected conservation area and the first conservation actions were taken (Schmeets, 2016). Now, after four decades of management, it is recognized as an important conservation area in Europe with a rich bird diversity, OVP has been nominated for Natura 2000 status (European Commission, n.d; Provincie Flevoland, n.d). OVP can be categorized as a rewilding project of a nonhistorical or novel ecosystem, with active management. This active management involves occasional drawdowns, by emulating stochastic disturbances, and the introduction of large herbivores to improve trophic complexity.

Currently, decreasing trends in bird population have been seen in the wetland area of OVP, indicating the transition towards a less productive ecosystem (Mornout, 2022). In response to this, management strategies to enhance birds' biodiversity have been applied, such as inducing a drawdown. In general, water level in the wetland area of OVP fluctuates according to the weather and occasionally a complete drawdown is actively induced. This water level management is possible due to the existence of dikes around and in the area, and the last induced drought started in 2020 and is still ongoing. This emulated dry period is expected to last until the wetland gets flooded naturally due to weather conditions. A previous drawdown was induced in 1987 which lasted four years (1991) until the system got inundated again. The results of this drawdown were positive for reedbeds extension. Deer was not present in the area and geese was absent due to the lack of water (Coops et al., 2014).

Following rewilding active management, large herbivores were introduced in the park as ecosystem engineers. Red deer (*Cervus elaphus*) was introduced in 1992 after the first drawdown took place in the wetland area (Wallisdevries et al., 1998). Therefore, this drawdown differs significantly from the previous in that herbivory by red deer is present. It is important to highlight that Greylag geese (*Anser anser*) might exert an additional herbivory pressure; however, as the water level is low, geese will not be present in the wetland area. As top predators are still absent from OVP, large herbivores population are managed by humans to avoid animal suffering. This hunting season usually take place by the end of winter (Cornelissen et al., 2014a; 2014b; Smit et al., 2015).

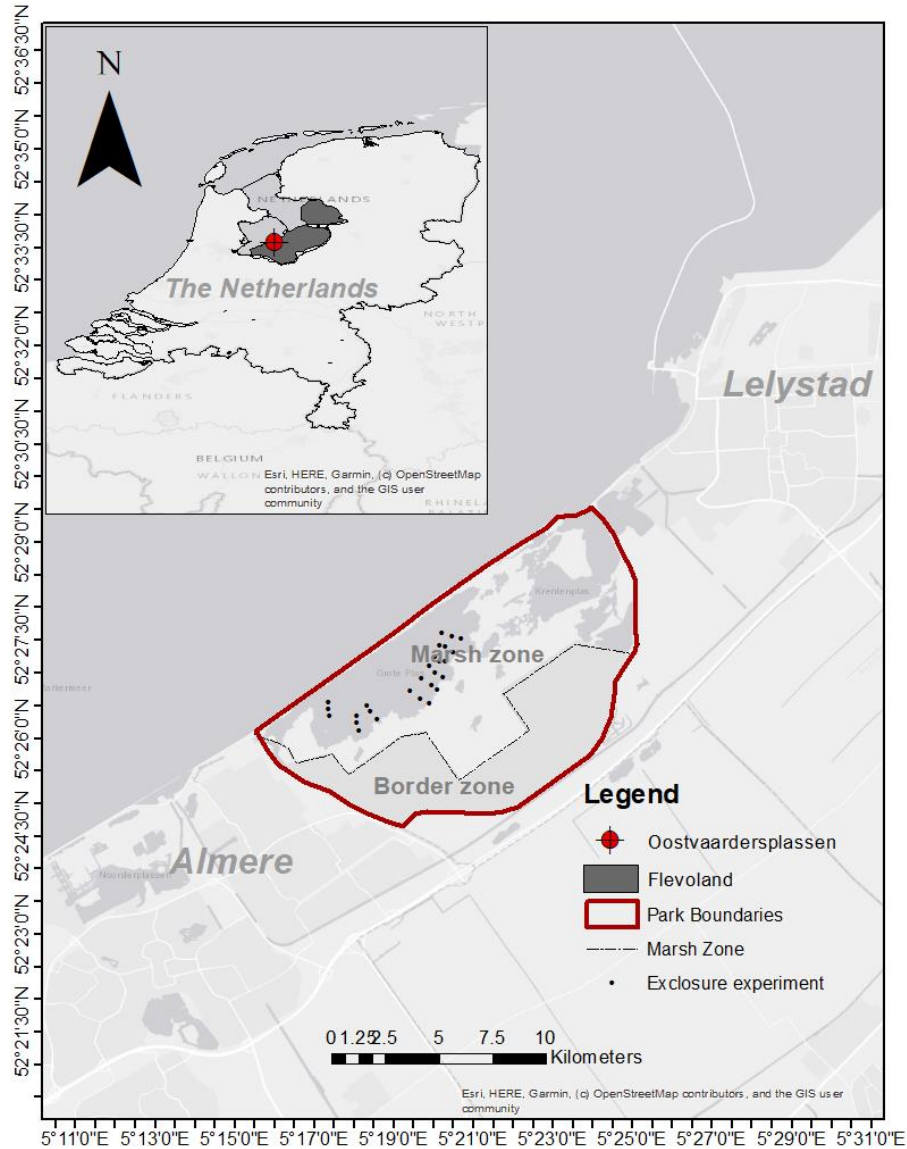


Figure 3. Oostvaardersplassen (OVP) National Park location. The Park is placed in Flevoland province right next to the Markermeer lake.

2.1.1. Soil elevation in OVP

As a result of land reclamation from the ocean, the Oostvaardersplassen (OVP) park is situated below sea level. Furthermore, there are different soil elevations across the area (figure 4). These elevation differences caused variations in water levels and, in addition to other factors such as wind, they also influenced the time it took for the soil to dry after a drawdown. Notably, the north-east area of the park dried out first, followed by the south-west area, and lastly, the central area. The water level was considerably reduced for the first time in September 2021. After that, water level has been shown to fluctuated according to weather and precipitation patterns.

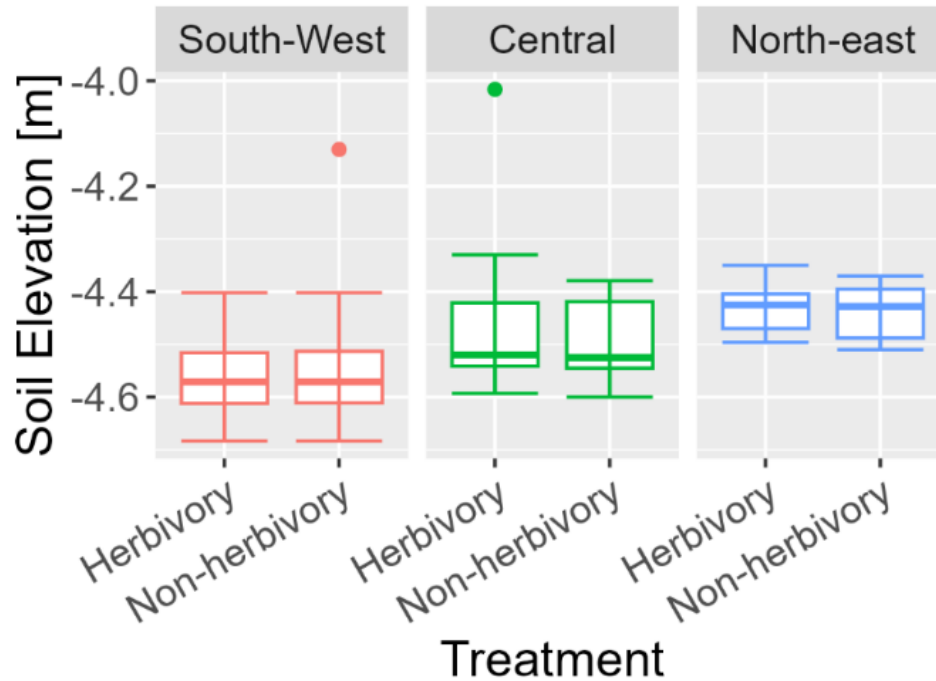


Figure 4. Soil elevation in OVP. Soil elevation differences across the wetland area in OVP influenced the time it took for the soil to dry after the induced dry period. The data are represented by boxplots with their respective error bars. Treatments did not show differences in soil elevation. Some outliers are present, likely due to measurement variations.

2.2. Analytical framework

To answer the main research question and sub-questions, various steps were followed. Hypothesis testing involved the use of data from previous years and fieldwork conducted in 2023. Information from previous years was provided by Netherlands Institute of Ecology (NIOO- KNAW). The data was processed, and statistical analyses were performed. These steps are detailed in the following figure.

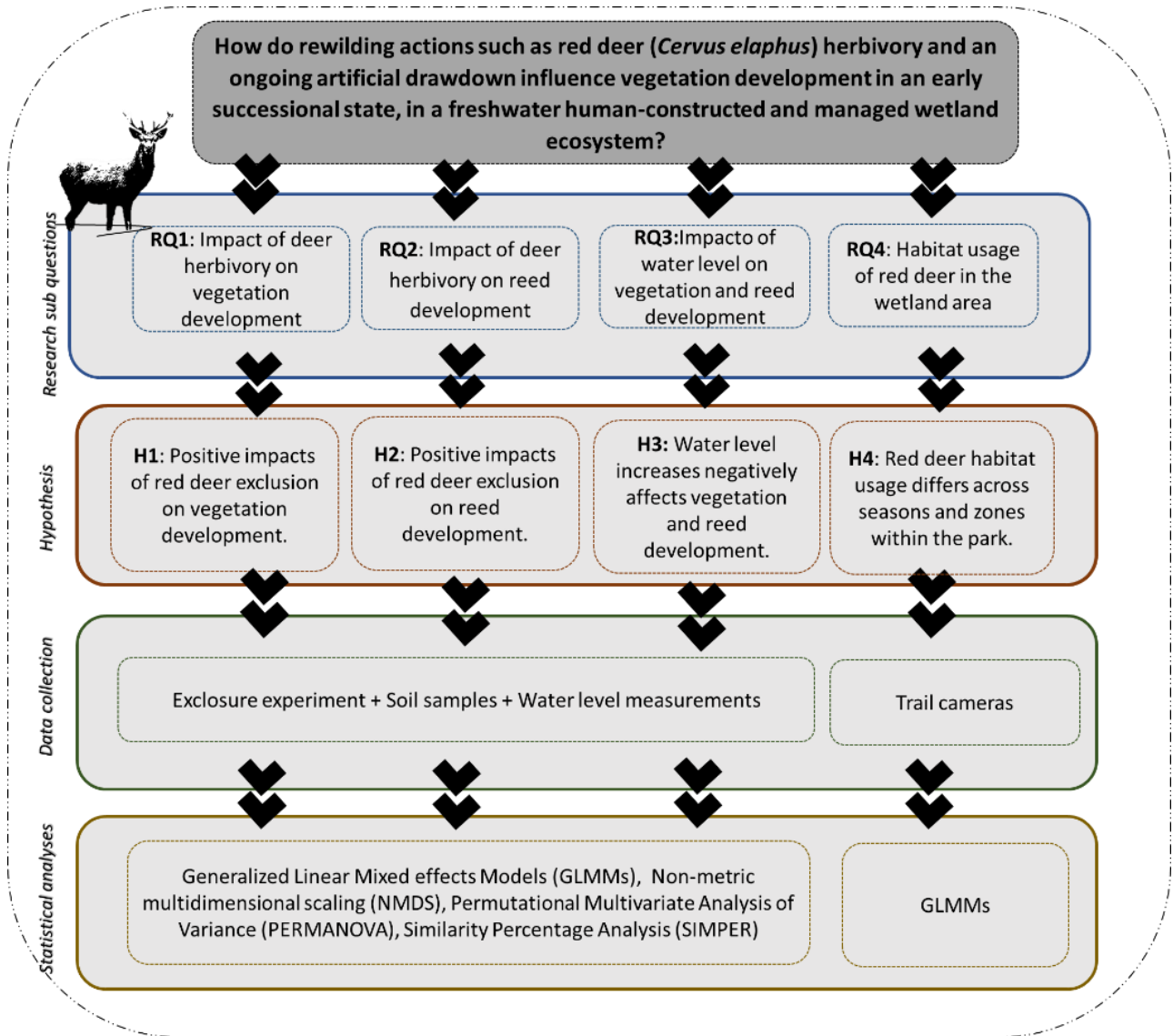


Figure 5. The Research Analytical Framework. Actions to answer the main research question, sub-questions, and hypothesis testing. It also shows the statistical analysis carried out to test the hypothesis.

2.3. Experimental set-up

To investigate the impact of water level and deer herbivory on vegetation development during early succession, a field-based "herbivory experiment" was conducted. This experiment involved excluding herbivores from a specific area. In April 2022, enclosure plots were established in the wetland area of OVP. Twenty-seven replicated sites were selected, both with herbivory (control plots) and with non-herbivory (enclosure plots). To account for the spatial variability within the park, which relates to the water level in the plots and the time taken for the soil to dry after a drawdown due to variations in soil elevation, the sites were divided into three different zones (Figure 6). These zones were classified as "Water Level (WL) Zones" and comprised three categories: "South-West Zone (a)", "Central Zone (b)", and "North-East Zone (c)". Each zone consisted of nine replicates. Additionally,

the wetland area was surrounded by vegetation, and some sample sites were located closer to the existing vegetation border than others. This proximity could affect vegetation development through vegetative reproduction and distance to the source of seeds, providing the nearest sites with a higher chance of vegetative reproduction and faster vegetation colonization. To control for this source of variation, another zone classification was created known as the "Vegetation Border (VB) Zone", consisting of three categories (figure 6). Each VB zone encompassed nine replicates (figure 7).

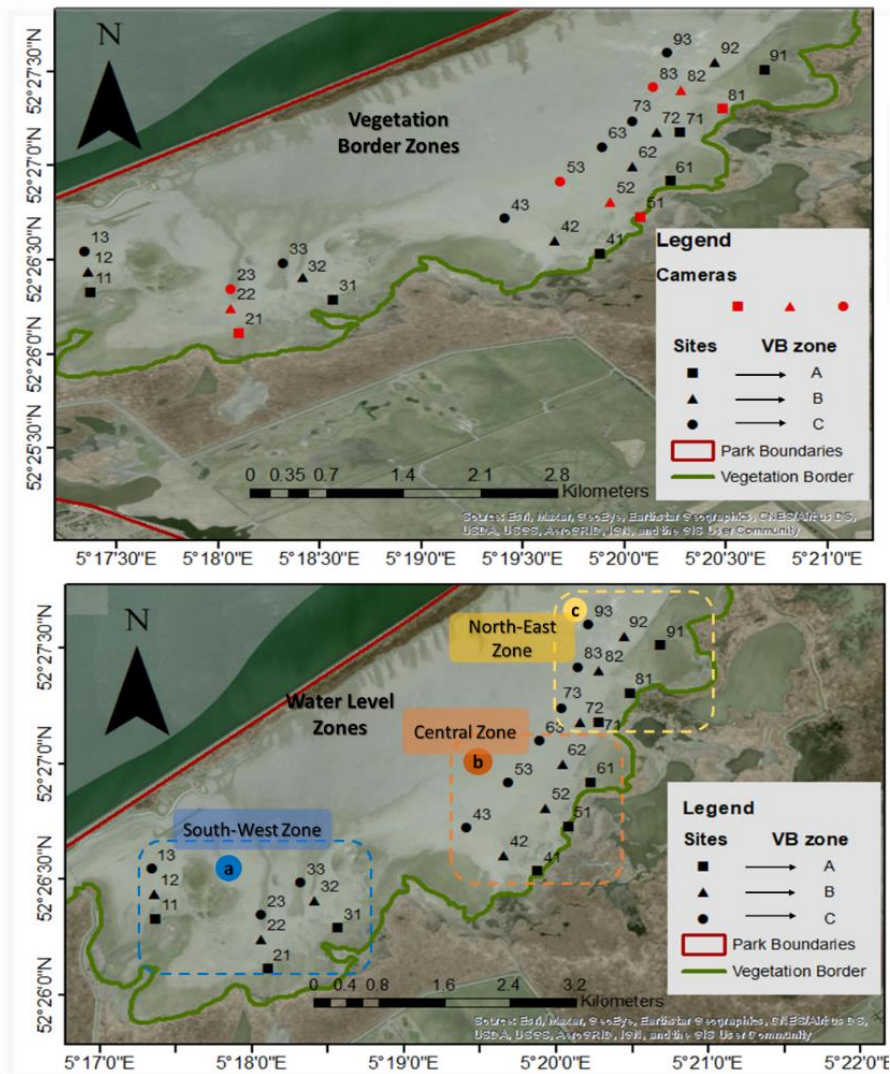


Figure 6. Zones Considered in the Analysis. The "Vegetation Border (VB) Zone" represents the distance to the vegetation border (A, B, and C). The "Water Level (WL) Zone" represents the water level difference within the park (a, b, and c). i) Vegetation Border Zone: the sites represented by the black square are nearer to the VB and belongs to zone A; the black triangle represents sites in zone B, and are situated in a middle distance towards the VB. Lastly, sites represented by a black circle, are the furthest away from the VB. These sites belong to zone C. The sites highlighted in red are the ones where the trial cameras were placed. ii) Water Level Zone: the park is divided in three zones, South-West (a), Central (b) and North-East (c), depending on the water level in the area. In each of these 27 sampling sites in total, there are two plots, a control and an enclosure.

At each sampling site, one enclosure and one control plot were established, approximately 10 meters apart. The enclosures were constructed by covering an area with a diameter of 1.5 meters and a height of 2 meters using a mesh (20 x 15 cm) to prevent deer from entering and grazing in the area. Control plots, where herbivory was allowed, were marked with one wooden pole. During the installation of the enclosures, some vegetation (30% coverage of swamp ragwort (*Senecio congestus*)) was found in plots located closer to the VB (VB zone: A), while the other enclosures were placed on 100% bare soil (VB zone: B and C) (figure 7).

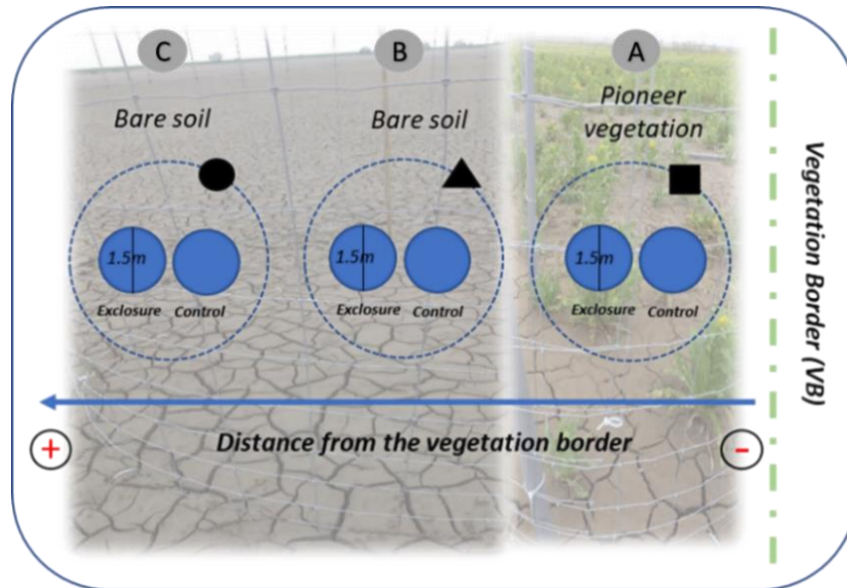


Figure 7. Vegetation Border (VB) Zone. This zone represents three possible distances towards the vegetation border: nearest (vegetation zone A - square), middle (vegetation zone B - triangle), and farthest (vegetation zone C - circle). These three vegetation border zones are located within the wetland area. Within each sampling site (dotted circle), there were two plots: one enclosure and one control. Sites placed in zone A presented 30% coverage of *Senecio congestus* at the time of plot installation. However, in the case of plots in zones B and C, they were placed in completely bare soil.

In addition, nine sites include camera traps (Bushnell core no glow) to detect the presence or absence of deer and other animals in the area. These cameras were installed in the enclosures (within sites 21, 22, 23, 51, 52, 53, 81, 82, and 83) during August 2022 and programmed to snap photographs whenever there was movement (figure 6).

2.4. Data collection and analysis

2.4.1. Herbivory Experiment

We surveyed vegetation in a 1x1 meter plot in all enclosures and controls during late July and August 2022, March 2023 and May 2023. Data collection included recording species composition, vegetation coverage, and the height of the three tallest stems of reeds (measured by a measuring

tape). As data collected during July 2022, was surveyed on the last day of the month, the entire data set was considered as August 2022 to simplify the statistical analysis.

For the vegetation composition measurements, we visually identified all plants in the inventory to species level, except in cases where the identification was uncertain, in which the genus level was reported. We recorded vegetation cover measurements as the percentage of surface covered by specific species. To ensure consistency, the same person visually determined these measurements throughout the study to minimize variations. Vegetation coverage per species was used as a proxy of abundance in Shannon-Index calculations. This allows us to compare the level of biodiversity between samples. We calculated the total vegetation coverage per plot by adding all the species coverage present in a given plot considering different layers of vegetation. We used species composition, Shannon-Index, species richness, and total vegetation coverage as proxies for vegetation development.

From the vegetation coverage data, we determined the presence or absence of reed. A presence/absence matrix was created, where a coverage of 0% indicates the absence of reed in the plot, while a coverage higher than 0% indicates its presence. For the analysis of reed coverage percentage, we only included data where reed was present. In plots with present reed, we calculated the mean height of the reed. However, not all plots had sufficient tall reeds for measurement (>2-3 cm), even when reed was present. As a result, the number of height measurements varied across plots, and the mean reed height was calculated based on the total number of measurements per plot. This approach was taken to avoid a lack of ecological meaning related to zero values. We used reed presence, coverage and height as a proxy for reed development.

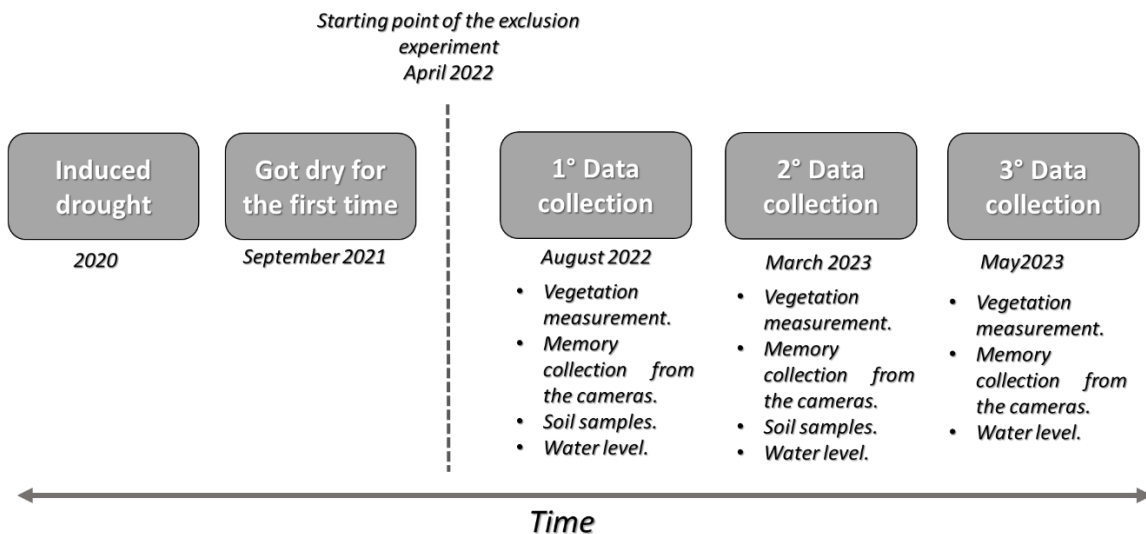


Figure 8. Data Collection. This figure depicts the data collection periods over time since the experiment started. It also indicates when the drawdown started. For this research, September 2021 is considered the starting point of the dry period, as it was the first time when the water level was considerably lowered to 0 cm in some areas within the wetland.

2.4.2. *Abiotic data*

To study water level influence on vegetation diversity and reed development, we measured the above-ground water levels (cm) in all plots at three different time points: August 2022, March 2023, and May 2023. These measurements were randomly taken, and we subsequently calculated the average values for analysis. To account for the influence of soil elevation on water level, we recorded the soil elevation in August 2022. This information was collected using a Differential Global Positioning System (DGPS) (HiPer SR, Topcom, FC-5000, USA), with the samples also being randomly distributed to ensure accuracy. The elevation was measured three times at each point; yielding 9 points per plot. Furthermore, three randomly distributed soil samples in all plots (the topmost 5 cm of the soil, 3.5 cm diameter) using a core soil instrument. The samples were gathered during August 2022 and March 2023. The three replicates were stored in the same bag and labeled with the plot number. Furthermore, soil samples were kept at 4°C until they were analyzed. We analyze the soil moisture and organic matter content later in the laboratory by a method based on gravimetric changes. Firstly, field-collected samples were weighed, and a sub-sample of 20 ml was extracted. The sub-samples were then dried in an oven at 70°C for over 48 hours to remove all water content. We calculate the soil humidity as the weight difference before and after drying, calculated as a percentage of the total weight. Secondly, the loss of ignition (a proxy for organic matter content (OM)) content was determined by aching at 550 °C for 3 hours, removing all organic content and leaving only the soil particles. The remaining weight solely represented the soil particles, allowing calculation of the OM content. Additionally, bulk density of the soil was calculated by dividing the sub-samples' dry weight by their volume (20 ml).

2.4.3. *Trail Cameras*

With the purpose of studying deer habitat usage patterns within the wetland area of OVP, we analyzed the images from the trail cameras. These images were collected on four occasions between August 2022 and May 2023 (Figure 8), covering a total duration of nine months. The captured images underwent artificial intelligence (AI) processing to analyze the habitat usage of deer (Agouti model developed by Wageningen University) (Agouti, n.d.). From the total group of pictures, all images containing deer were detected, and the animal's position in terms of pixel coordinates was recorded. Using R, the images were then cropped based on pixel location and saved as separate sections in a designated folder. Each cropped image was assigned a unique code and information about the date when the picture was taken. Depending on the number of deer present in the original image (Appendix A Image 1), multiple cropped images could be generated. Subsequently, a manual verification process was conducted to ensure the accuracy of the cropped images.

After processing the images, a presence/absence matrix was generated for each camera. It was assumed that if an animal was not captured in any of the photographs taken by the 9 cameras on a given day, it was considered to be absent from the wetland area for that particular day. In summary, the analysis resulted in a table with the camera ID, date, time (hour, minute, and second), and the presence of deer in the cropped images. The same process was applied for pictures where geese were present.

The presence/absence data was grouped by seasons. Subsequently, the presence/absence information was plotted over time to visualize the occurrence of deer throughout the entire

timespan. Additionally, heatmaps were created to depict presence patterns across "Water Level Zones" and "Vegetation Border Zones", aiming to identify any differences in deer presence between these zones that could potentially influence vegetation development. This approach provides a comprehensive understanding of how deer utilize different habitat areas within the park. Additionally, the same methodology was applied to analyze geese data. The objective was to compare the presence patterns of both species and determine whether herbivory could be attributed solely to deer or if geese also exerted significant herbivory pressure on the ecosystem.

2.5. Statistical analyses

The statistical analysis was divided into three sections in order to properly answer the research questions. Particularly, the first section addresses the effects of reed herbivory and water level on vegetation diversity. The second section is focused on the effects of deer herbivory and water level on reed development. The third section is about deer population dynamics within the wetland area of OVP, and the habitat usage of the identified zones in the park (WL and VB zones). All the statistical analysis were performed in R studio version 4.3.0. (R Core Team., 2021).

2.5.1. Vegetation development

a) Sub-questions 1 and 3: Vegetation diversity (species composition, species richness, abundance, and Shannon-index)

To evaluate the influence of herbivory and water level on vegetation diversity across time, we analyzed the species composition, species richness, Shannon-index and total coverage per plot as a proxy.

For comparisons of vegetation community composition between months and between treatments (control: herbivory; Exclosure: non-herbivory), we performed a Non-metric Multidimensional Scaling (NMDS) analysis, using the vegan package in R (Oksanen J. et al., 2022). The coverage data was initially standardized using the Hellinger method, to avoid a strong influence of the abundant or rare species on dissimilarities calculations (Fazekas & Liese, 1996; Legendre & Gallagher, 2001). The Hellinger transformations are effective in downweighing rare species and work well with high-throughput sequencing datasets that contain numerous zero values. Dissimilarities were then calculated using the Bray-Curtis method, which is commonly recommended and preferred for analyzing this type of ecological data (Bray & Curtis, 1957; Legendre & Gallagher, 2001). The NMDS was performed using coverage data for August 2022 and March 2023. Data collected in May of 2023 was excluded from the analysis because of the stress value obtained in the NMDS analysis, which was near to 0, indicating the need of increase the sample size for a better representation of reality. We fit the environmental data collected in the field during August 2022 and March 2023 to the NMDS, by means of envfit function. With this analysis it is possible to visually determine if there were some clusters or groups of species occurring under certain conditions and how the composition of the community changes from one month to another, or between treatments. Significant differences were identified using Permutational Multivariate Analysis of Variance Using Distance Matrices (Bray-Curtis distance) (PERMANOVA) by means of adonis2 function from vegan package (Oksanen J. et al., 2022) with 1000 permutations (Johnson et al., 2017). Furthermore, if there were

significant differences, Tukey's Honest Significant Difference was computed to identify pairwise differences (pairwise adonis). Moreover, we examined which species contributed more to these changes across time, by the Similarity Percentage Analysis (SIMPER) from the vegan package in R. SIMPER operates at the individual level of each species within the groups under comparison, calculating their respective contributions to the overall Bray-Curtis dissimilarities (Clarke, 1993). It identifies the most influential species that drive the variations and patterns observed in the data.

In order to address the research questions and elucidate the influence of herbivory and water level on vegetation development, we conducted generalized linear mixed-effects models (GLMMs) using the glmmTMB package (Brooks et al., 2017) in R. The statistical models were assessed by performing type 3 Wald χ^2 tests using the Anova.glmmTMB command (Lundin et al., 2023). Tukey's Honest Significant Difference was computed to identify pairwise differences using the emmeans package (Lenth, 2021).

We fit two models per each independent variable to keep the models as simple as possible, (i) the first for analyze the effect of herbivory on time (time models), and (ii) the second for analyze the interaction between herbivory and water level (water level models). The GLMMs aimed to model the relationship between the dependent variable (vegetation development) and the fixed effects (herbivory, water level and/or months). The models were assessed for goodness of fit using the DHARMA package (Hartig, 2022). Depending on the variable types (continuous or discrete) (table 1), different error distributions (Gauss, Gamma, Generalized Poisson, Poisson, Binomial) were used for fitting the models. Also, zero inflation modelling was needed in some models (table 2).

We examine the influence of the independent variables and their interaction on species richness total vegetation coverage per plot, and Shannon index (response variables) as a proxy of vegetation development. The Shannon index was calculated using the vegan package in R. In order to better represent biodiversity within plots, we correct the Shannon index by its exponential ($\text{Exp}(H)$) as Jost (2007) indicates. **(i) Time models:** the error distribution of the models to address the effect of herbivory on time were fitted as follows; a) Species richness: Generalized Poisson distribution; b) Square root of total coverage plus one: Gauss distribution; c) Exponential Shannon index: Gamma distribution (with a log link function). **(ii) Water level models:** the models to address the effect of herbivory and water level were fitted with the following error distributions; a) species richness: Poisson distribution; b) Square root of total coverage plus one: Gauss distribution; c) square root of the exponential Shannon index: Gauss distribution.

All response variables were assessed with respect to the fixed effect of herbivory (Herb), time models also included months as a fixed effect, and water level models included water level mean as fixed effect (WLM). Additionally, "water level zones (Zone_WL)", "vegetation border zones (Zone_VB)" and plot ID were included in all the models as random effects to account for potential variation associated with the plot locations within the OVP, and to ensure pair comparisons of repeated measures per plot (3 measurements per plot). The detailed model specifications are provided in table 2.

Dependent Variable	Variable type
Shannon-Index (SH)	Continuous and positive
Species Richness (SR)	Discrete and positive
Total Vegetational Coverage (%)	Continuous proportion
Reed Presence	Binomial (1: present; 0: absent)
Reed Coverage (%)	Continuous proportion (from 0 to 100%)
Reed Height (cm)	Continuous and positive
Deer Presence	Binomial (1: present; 0: absent)
Independent Variables	Variable type
Water Level (cm)	Continuous and positive
Soil Humidity (%)	Continuous proportion (from 0 to 100%)
Soil Organic matter (%)	Continuous proportion (from 0 to 100%)
Bulk Density (%)	Continuous proportion (from 0 to 100%)
Herbivory (Herb)	Binomial (1: herbivory; 0: non-herbivory)
Time (month)	Categorical (July, August, March, and May)
Plot ID	Categorical
Water Level Zone (Zone_WL)	Categorical (a, b, c)
Vegetation Border Zone (Zone_VB)	Categorical (A, B, C)

Table 1. Variables Resume. Overview of dependent and independent variables and variable type used in the present analysis.

b) Sub-questions 2 and 3: Phragmites australis development (presence, height, and coverage)

We conducted a GLMM analysis to investigate the influence of herbivory and water level on reed development following a drawdown. The goodness of fit, post-hoc, and data interpretation procedures were the same as in the previous section. Reed presence, coverage (%), and height (RHM) (cm) were used as estimations of reed development and served as the response variables in the GLMMs. The models included fixed effects such as herbivory, water level mean, and months, while also incorporating random effects such as "water level zones," "vegetation border zones," and plot IDs, similar to the preceding models. For simplicity of the modelling, we developed two types of models for each response variable. (i) time models, with herbivory and months as fixed effects, and (ii) water level models, with herbivory and water level mean as fixed effects. This approach allowed us to gain insights into the effects of herbivory and water level on reed development in a comprehensive manner, providing valuable information for this study.

We fitted the models with different error distribution depending on the type of variable as follows. **(i) Time models:** a) reed presence: Binomial distribution; b) square root of reed coverage: Gauss distribution; c) reed height mean: Gauss distribution. In this model was necessary to include water level mean as a fixed effect and zero inflation to improve the goodness of fit of the model. **(ii) Water level models:** a) reed presence: Binomial distribution; b) reed coverage: Gamma distribution (with a log link function); c) reed height mean: Gauss distribution. In this model months were added as random effects and zero inflation was added into the formula to improve the goodness of fit of the

model. It is worth noting that the reed coverage models were specifically applied to continuous data points that were greater than zero. Zero values were already analyzed in the presence/absence models.

		Time Models					
		Response Variable	Fixed effects	Random effects	Link Function	Error distribution	Zero inflation
Vegetation Development	Biodiversity	Species Richness	Treatment * Month	Zone_VB + Zone_WL + ID	log	Generalized Poisson	No
		sqrt (Total Coverage +1)			identity	Gaussian	No
		Exponential Shannon Index			log	Gamma	No
	Reed development	Presence / absence	Treatment * Month	Zone_VB + Zone_WL + ID	logit	Binomial	No
		sqrt (Reed Coverage)			identity	Gaussian	No
		Mean Height of Reed	Treatment * Month + WLM		identity	Gaussian	Yes
		Water Level Models					
		Response Variable	Fixed effects	Random effects	Link Function	Error distribution	Zero inflation
Vegetation Development	Biodiversity	Species Richness	Treatment * WLM	Zone_VB + Zone_WL + ID	log	Poisson	No
		sqrt (Total Coverage +1)			identity	Gaussian	No
		sqrt (Exponential Shannon Index)			identity	Gaussian	No
	Reed development	Presence / absence	Treatment * WLM	Zone_VB + Zone_WL + ID	logit	Binomial	No
		Reed Coverage			log	Gamma	No
		Mean Height of Reed	Treatment * WLM + Month		identity	Gaussian	Yes

Table 2. Herbivory Models. Summary of the response (predicted) and predictor variables, fitted error distributions, and equation syntax used in the model, by means of *glmmTMB* package. (*) Denotes interaction between the variables. Fixed effects, Treatment: (1: Control (herbivory), 0: Exclosure (non-herbivory)); WLM: water level mean; Month (August 2022, March 2023, and May 2023). Random effects, Vegetation Border Zone (Zone_VB), Water Level Zone (Zone_WL) and plot ID.

2.5.2. Red Deer Habitat Patterns

a) Sub-question 4: Exploratory analysis of red deer habitat usage (deer presence/absence)

We conducted an exploratory analysis using data collected from camera traps to shed light on the habitat usage and presence/absence patterns of deer in the wetland area of OVP over space and time. This analysis involved binary data indicating the presence or absence of deer. To assess the influence of park zones (WL Zone and VB zone) and months on deer presence/absence response, we performed a GLMM analysis. Three models were developed for this purpose.

The first model aimed to examine the presence patterns on the wetland area across seasons (table 3). The second model aimed to address the impact of the 'Water Level (WL) Zone' on deer occurrence. It was fitted with a binomial error distribution, and months and WL zone were included as fixed effects. The 'Vegetation Border (VB) Zone' was considered as a random effect. The second model aimed to explore the influence of the VB Zone on deer presence patterns. In this model, months and VB zone were included as fixed effects, while WL zone was considered as a random effect. Both models were conducted in R using the glmmTMB package (Brooks et al., 2017).

Response Variable	Fixed effects	Random effects	Link Function	Error distribution	Zero inflation
Deer presence / absence	Seasons	Zone_VB + Zone_WL	logit	Binomial	No
Deer presence / absence	Zone_VB * Seasons	Zone_WL	logit	Binomial	No
Deer presence / absence	Zone_WL * Seasons	Zone_VB	logit	Binomial	No

Table 3. Deer models. Summary of the response (predicted) and predictor variables, fitted error distributions, and equation syntax used in deer models, by means of glmmTMB package. (*) Denotes interaction between the variables. Seasons (summer, autumn, winter and spring), Vegetation Border: Zone (Zone_VB) and Water Level Zone: (Zone_WL).

3. Results

To answer the research questions, the results section was divided into three sub-sections. The first examines the influence of red deer herbivory and water level on vegetation development. The second sub-section focuses on the impacts of red deer herbivory and water level on reed development. Lastly, the third section addresses deer population dynamics in the wetland area of OVP.

3.1. Vegetation Development

3.1.1. Sub-questions 1 and 3: Vegetation diversity (species composition, species richness, abundance, and Shannon-index)

a) Vegetation Composition Analysis

Vegetation communities changed over time (figure 9). The vegetation composition observed in August 2022 differed from the species pool present in March 2023 ($F = 137.74$, $p = 0.001$). Herbivory treatments did not show a significant difference in species composition ($F = 0.2194$, $p = 0.9131$). The species that contributed the most to the difference across time were *Rumex maritimus* (RUMA) (21%), *Persicaria maculosa* (PEMA) (8.5%), *Oxybasis rubra* (OXRU), *Ranunculus sceleratus* (RASC) (5%), as well as the vegetation type "old vegetation (OLVE)" (26%). The species *Phragmites australis* (PHAU) did not contribute to the community change between months August 2022 and March 2023.

We found that vegetation composition was affected by soil elevation (WL zones) and sampling periods ($F = 4.769$, $p = 0.006$) (figure 10). Plots surveyed in August 2022 did show a difference across all water level zones ([a-b]: $F = 4.9958$, $p = 0.002$; [a-c]: $F = 8.728$, $p = 0.001$; [b-c]: $F = 6.162$, $p = 0.001$). Conversely, for plots sampled in March 2023, the only zone that remained different was "WL zone c" (the highest elevation) ([a-c]: $F = 4.026$, $p = 0.011$; [b-c]: $F = 4.581$, $p = 0.015$). In the case of "WL zone a" and "WL zone b", their vegetation communities homogenized after seven months from the first sampling period ([a-b]: $F = 0.458$, $p = 0.739$). Additionally, the average plots with *Phragmites australis* differed significantly between "WL zone b" and "WL zone c" ($p = 0.012$), with *Phragmites australis* contributing 5% to the difference between those zones.

The vegetation border zones significantly influenced the species composition, and this effect was also dependent on the sampling period ($F = 3.7225$, $p = 0.017982$) (figure 11). Particularly, in August 2022, the only significant difference in community composition was observed between "VB zone A" and "VB zone C", the nearest and the farthest areas from the existing vegetation border respectively ([A-C]: $F = 4.6429$, $p = 0.001$). However, the two nearest areas, "VB zone A" and "VB zone B," did not differ significantly from each other ([A-B]: $F = 2.1256$, $p = 0.051$), and the middle area, "VB zone B," did not differ significantly from the farthest zone, "VB zone C" ([B-C]: $F = 2.4577$, $p = 0.052$). Eventually, in March 2023, only the nearest area to the vegetation border, "VB zone A," remained different from "VB zone B" and "VB zone C" ([A-B]: $F = 4.7608$, $p = 0.009$; [A-C]: $F = 15.249$, $p = 0.001$). VB Zones B and C, evolved towards the same community after seven months of the first measurement ([B-C]: $F = 2.398$, $p = 0.069$). The species *Phragmites australis* contributed significantly

to dissimilarities among vegetation border zones in March 2023, being more abundant in the nearest area to the vegetation border than in middle and furthest away zones ([A-B]: $P = 0.004$; [A-C]: $P = 0.021$). It is important to notice that the arrow for PHAU (*Phragmites australis*) appears perpendicular to the environmental variable water level mean (WLM), indicating an inverse relationship between them. The blue arrows represent the environmental variables that were considered for this analysis, all of them were significantly influencing vegetation composition. These variables included mean water level, organic matter content (OM), soil humidity (HUM), and bulk density (BD) (WLM: $r^2 = 0.5765$, $p = 0.001$; OM: $r^2 = 0.1528$, $p = 0.002$; HUM: $r^2 = 0.7323$, $p = 0.001$; BD: $r^2 = 0.5736$, $p = 0.001$).

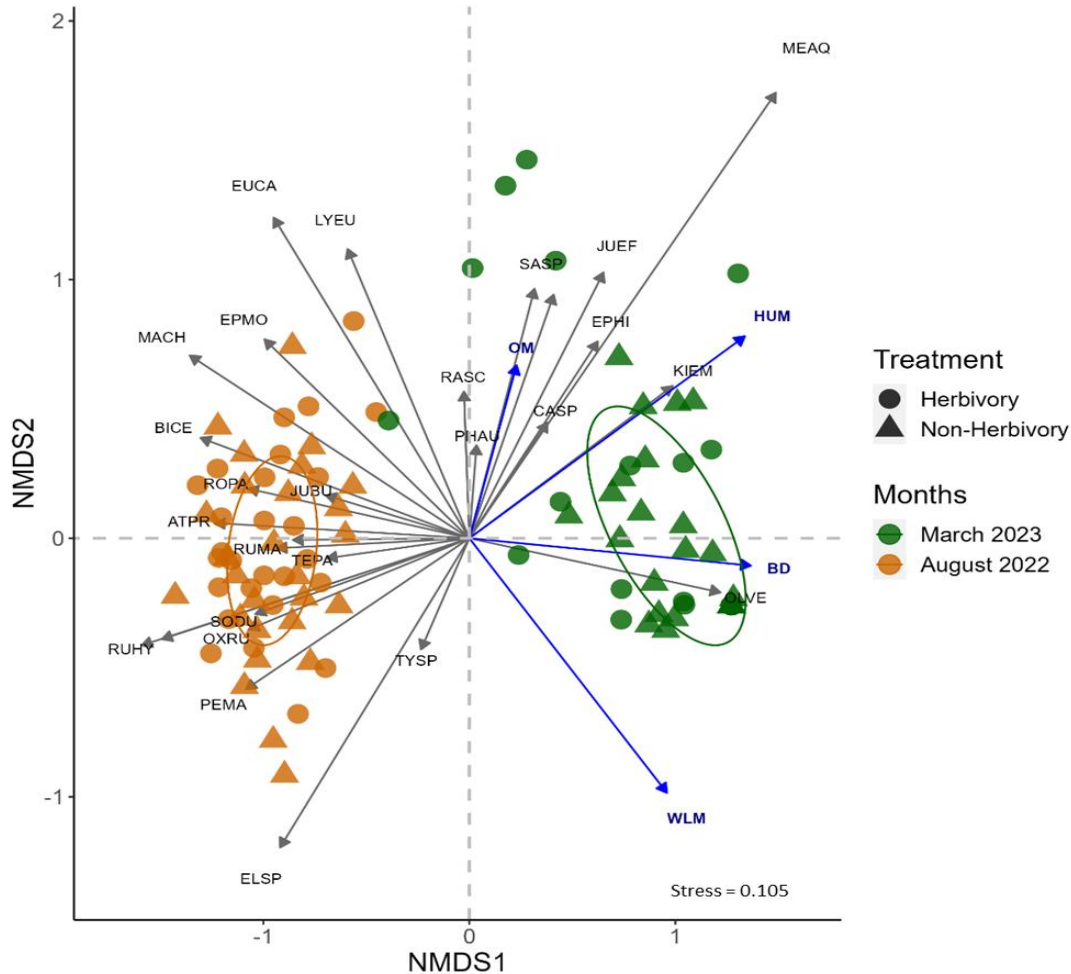


Figure 9. Non-Parametric multidimensional scaling plot of species composition in the wetland area of OVP across time. The NMDS ordination plot shows the vegetation community changes between months. The NMDS ordination analysis was carried out with coverage data as abundance proxy of vegetation species present in the wetland area of OVP. The data was previously Hellinger-transformed, and dissimilarities were calculated using Bray–Curtis’s matrices. Sampling sites are represented by triangles (non-herbivory) and squares (herbivory), and colors represent the month of sampling. Grey rows symbolize plant species, and the blue rows are environmental variables that influence the observed patterns (OM: organic matter content (p -value= 0.002); WLM: water level mean (p -value= 0.001); BD: bulk density (p -value= 0.001); HUM: soil humidity (p -value= 0.001)).

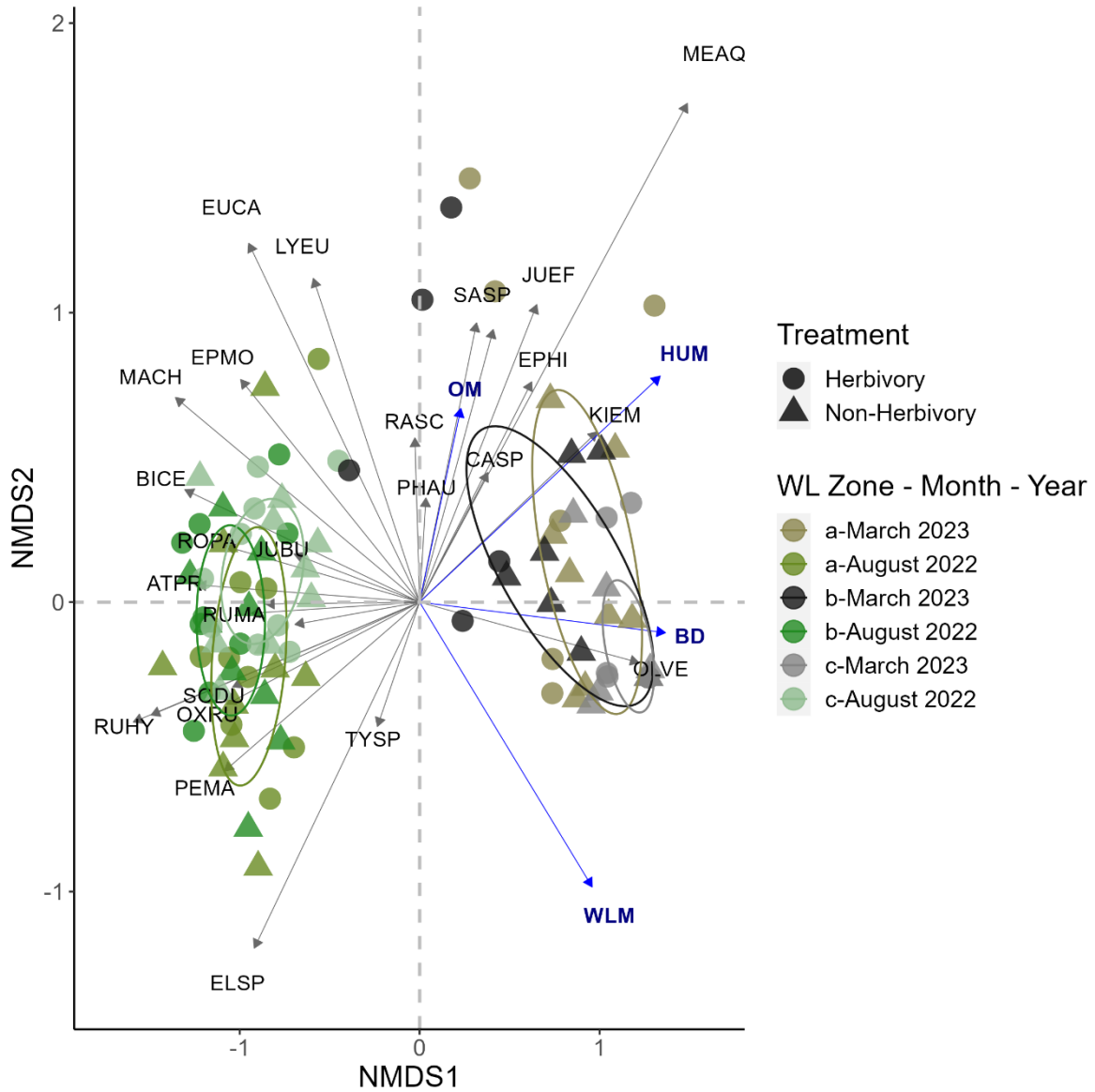


Figure 10. Non-Parametric multidimensional scaling plot of species composition in the wetland area of OVP across time considering water level zones. The NMDS ordination plot shows the vegetation community changes between months taking into account water level zones. The NMDS ordination analysis was carried out with coverage data as abundance proxy of vegetation species present in the wetland area of OVP. The data was previously Hellinger-transformed, and dissimilarities were calculated using Bray–Curtis’s matrices. Sampling sites are represented by triangles (non-herbivory) and squares (herbivory), and colors represent the interaction between month of sampling and water level zones. Grey rows symbolize plant species, and the blue rows are environmental variables that influence the observed patterns (OM: organic matter content (p -value= 0.002); WLM: water level mean (p -value= 0.001); BD: bulk density (p -value= 0.001); HUM: soil humidity (p -value= 0.001)).

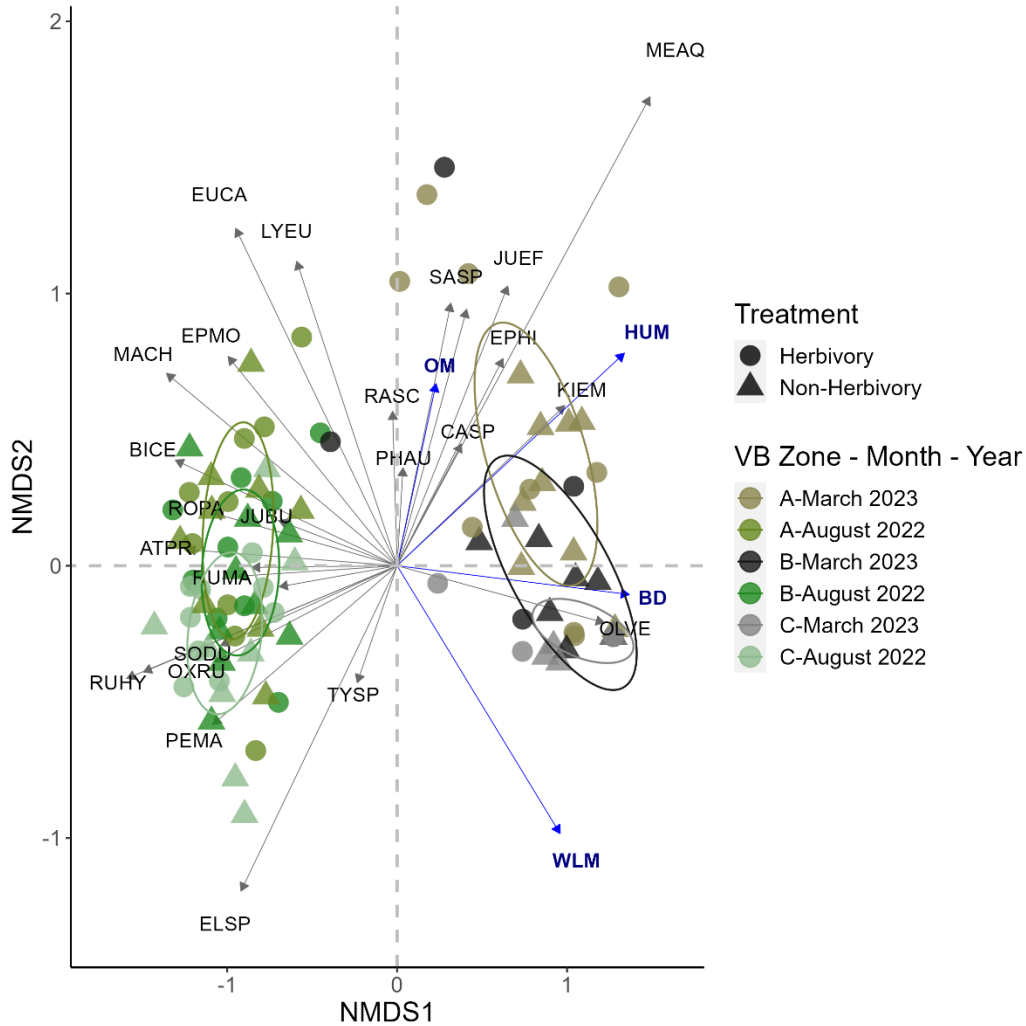


Figure 11. Non-Parametric multidimensional scaling plot of species composition in the wetland area of OVP across time considering vegetation border zones. The NMDS ordination plot shows the vegetation community changes between months taking into account the distance to the vegetation border zone. The NMDS ordination analysis was carried out with coverage data as abundance proxy of vegetation species present in the wetland area of OVP. The data was previously Hellinger-transformed, and dissimilarities were calculated using Bray-Curtis's matrices. Sampling sites are represented by triangles (non-herbivory) and squares (herbivory), and colors represent the interaction between month of sampling and VB zones. Grey rows symbolize plant species, and the blue rows are environmental variables that influence the observed patterns (OM: organic matter content (p -value= 0.002); WLM: water level mean (p -value= 0.001); BD: bulk density (p -value= 0.001); HUM: soil humidity (p -value= 0.001)).

b) *Species richness*

The sampling period (month) and water level influenced species richness. Nevertheless, herbivory treatments did not result in any differences in this response variable (figure 12A). Furthermore, no significant interaction was identified between herbivory treatments with water level ($\chi^2 = 2.38$, $p = 0.123$) nor sampling months ($\chi^2 = 2.611$, $p = 0.27104$). Species richness fluctuated over months ($\chi^2 = 24.089$, $p < .001$). The highest value in species richness was reached in August 2022 (non-herbivory = 4.370 ± 0.329 ; herbivory = 4.555 ± 0.289 ; average \pm SE) and the lowest was in March 2023 (non-herbivory = 2.148 ± 0.415 ; herbivory = 1.592593 ± 0.3746195). After March 2023, species richness increased again however not as much as in August 2022 for both treatments ([May-August]: herb: $p < .001$, non-herb: $p < .001$) (figure 12A). Regarding water level effect, it was found an inverse relationship between water level and species richness ($\chi^2 = 20.994$, $p < .001$). When the water level was 0 cm, species richness reached the highest value, corresponding to 9 species. However, at 3 cm of water level, the maximum number of species was reduced to 7 and to 5 species at 4 cm of water level. With further increases in water level, there was a noticeable reduction in species richness. After reaching 15 cm of water level, no plant species were found, independently of the sampling period and treatment (figure 13A).

c) *Total Coverage of Vegetation*

Total coverage per plot changed across time and was negatively influenced by water level increases (figure 13 B). Furthermore, an interaction effect was found between the exclusion of herbivores and time (figure 12B). No interaction effect was found between herbivory treatments and mean water level ($\chi^2 = 0.579$, $p = 0.447$). The highest total vegetation coverage was found in August 2022 (non-herbivory: $89.7 \pm 5.21\%$; herbivory: $86.2 \pm 7.04\%$), followed by a decrease in March 2023 (non-herbivory: $9.04 \pm 2.27\%$; herbivory: $8.46 \pm 3\%$). After two months of preventing herbivory, total vegetation coverage increased on average by 3 percent in May 2023 (non-herbivory: $39.2 \pm 6.3\%$) than it was in March 2023 for the non-herbivory treatment ($p < 0.001$). Meanwhile, the herbivory treatment in May 2023 remained the same as in the previous measurement in March 2023 for the same treatment ($p = 0.318$). In relation to the water level, it negatively influenced the total vegetation coverage in both treatments, dropping from 162% (maximum value) of total vegetation coverage when the water level was 0 cm to 56% of total vegetation coverage when the water level reached 4 cm. All plots with a water level of more than 15 cm did not present any coverage (figure 13B).

d) *Shannon-Index*

Water level did influence vegetation diversity (figure 13C). However, the exclusion of herbivores did not lead to differences in the exponential Shannon index (figure 12C). Furthermore, there was no interaction between water level and treatments ($\chi^2 = 0.061$, $p = 0.804$) nor between months and treatments ($\chi^2 = 1.531$, $p = 0.465$). Specifically, August 2022 exhibited the highest biodiversity for both treatments (non-herbivory = 2.879 ± 0.19 ; herbivory = 2.825 ± 0.17) compared to March 2023 (Herb: $p < .001$; non-herb: $p < .001$) and May 2023 (Herb: $p = 0.007$; non-herb: $p = 0.003$) (figure 12C). Additionally, the exponential Shannon index was negatively influenced by an increasing water level ($\chi^2 = 15.5014$, $p < .001$). Precisely, the highest Shannon index value ($\exp(H) = 2.68 \pm 0.119$) was observed when water was absent (WLM = 0 cm), and as the water level increased, the exponential

Shannon index decreased sharply. After reaching 8 cm of water level, the exponential Shannon index reached its minimum value ($\exp(H) = 1$) (figure 13C).

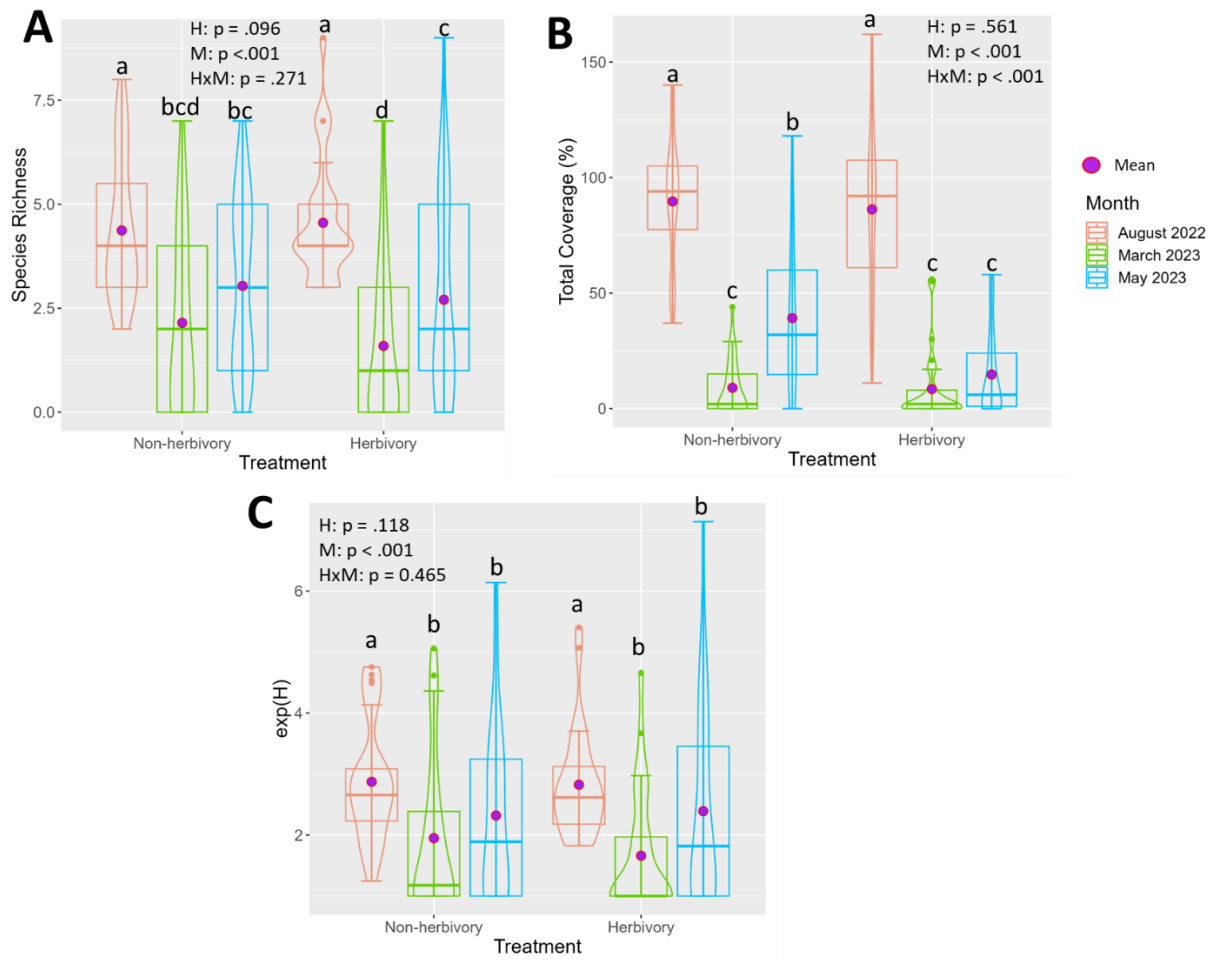


Figure 12. Impact of herbivory treatments across time on vegetation diversity dependent variables. A) species Richness, B) Total Vegetation Coverage (%), and C) Exponential Shannon Diversity Index ($\exp(H)$), for each treatment and time of measurement. The significance, represented by different letters, was obtained from GLMMs and by means of Tukey test post-hoc analysis. This figure depicts the obtained results as boxplot with error bars, and violin plot to visualize the variations on data distribution among measurements. It also includes the mean value of treatments at each sampling period. (H: Herbivory; M: months; H x M: interaction between herbivory and months).

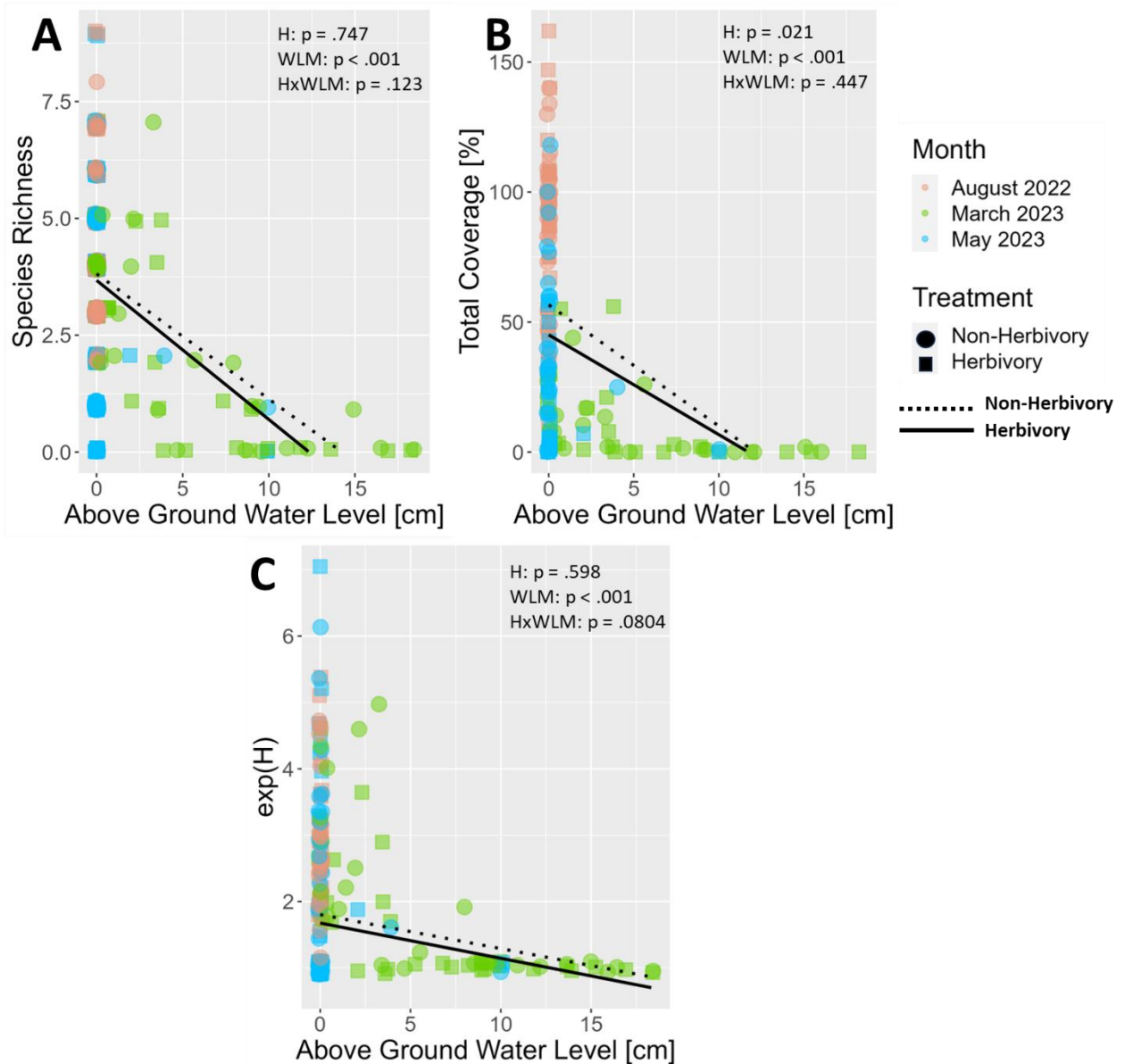


Figure 13. Impact of above ground water level mean (WLM) on vegetation diversity dependent variables, A) Species Richness, B) Total Coverage (%), and C) Exponential Shannon Diversity Index ($\exp(H)$), for each treatment and time of measurement. The figures show the relationship between water level increase and the response variables. Furthermore, the figures also include months distinctions with different colors. The lines were fitted by an exponential decay function using the fitted values for each model (H: Herbivory; WLM: water level mean; H x WLM: interaction between herbivory and water level mean).

3.1.2. Sub-questions 2 and 3 *Phragmites australis* development (presence, height, and abundance)

a) Reed presence

The presence of reed was influenced by herbivory treatments over time (figure 14). During August 2022, reed presence was observed in 33% of the non-herbivory plots and in 25% of the herbivory plots ($p = 0.9757$). In March 2023, the scenario in terms of reed presence did not change compared to August 2022 ([August-March]: Herb: $p = 1$; non-herb: $p = 0.976$). In the following months, there was an increase in the proportion of plots containing reed ($\chi^2 = 16.141$, $p < .001$). By May 2023, reed occurred in around 75% of plots, but only in non-herbivory treatments. This indicates that reed presence was on average approximately 3 times more frequent in non-herbivory plots compared to plots subjected to herbivory ([herb - non-herb] $p = 0.004$). Water level did not show an influence on reed presence ($\chi^2 = 0.7238$, $p = 0.395$), and no interaction was found between herbivory treatments and water level ($\chi^2 = 0.615$, $p = 0.433$) (figure 16A).

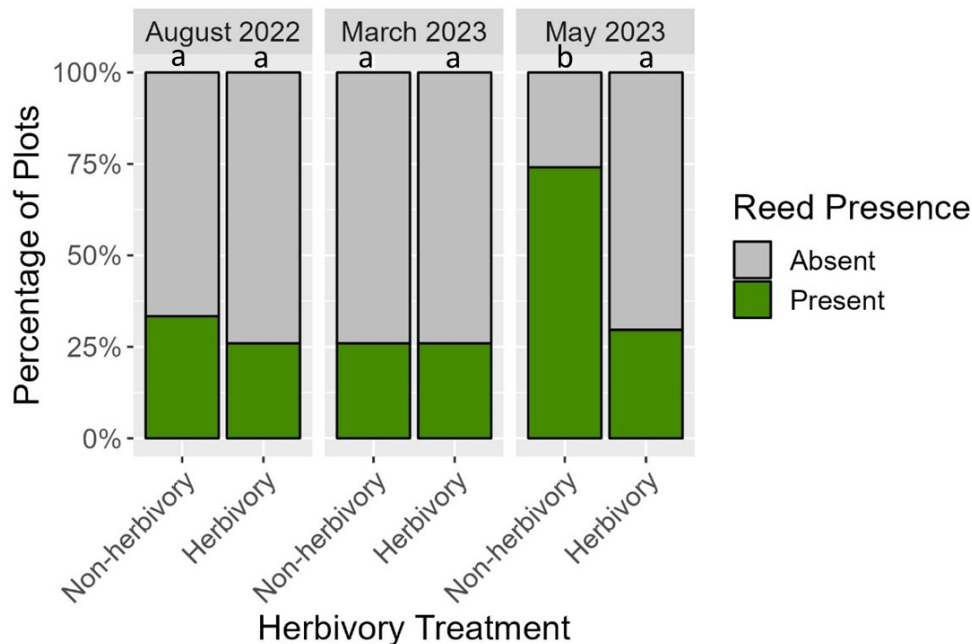


Figure 14. Percentage of plots with reed presence / absence across time. The plot shows the percentage of plots that presented reed across time. Different letters denote significant differences.

b) Coverage of reed

The coverage of reed exhibited variations over time, and the extent of this change was found to be related to the herbivory treatment (figure 15A). The herbivory exclusion resulted in a significantly higher reed coverage after ten months ($\chi^2 = 12.133$, $p = 0.002$). During the first (August 2022: [herb]: $4 \pm 1.57\%$; [non-herb]: $4.33 \pm 0.7\%$), and second sampling periods (March 2023: [herb]: $3.43 \pm 1.21\%$; [non-herb]: $3.43 \pm 0.95\%$), reed showed the same percentage of coverage, without any difference among treatments (Herb: $p = 1$; non-herb: $p = 0.998$). Then, in May 2023 reed coverage suddenly increased reaching $21.5 \pm 3.63\%$ of reed coverage, this was an average 2.43 percent more coverage compared with non-herbivory treatment in the same month (figure 15A). Additionally, mean water level was found to have a significant influence on reed coverage ($\chi^2 = 15.142$, $p < .001$), and no

interaction effect was found between herbivory treatments and water level ($\chi^2 = 0.767$, $p = 0.382$). Increasing mean water level was associated with a reduction on reed coverage across all treatments and sampling periods. After 5 cm of water level above ground the percentage of coverage of reed was reduced (figure 16B).

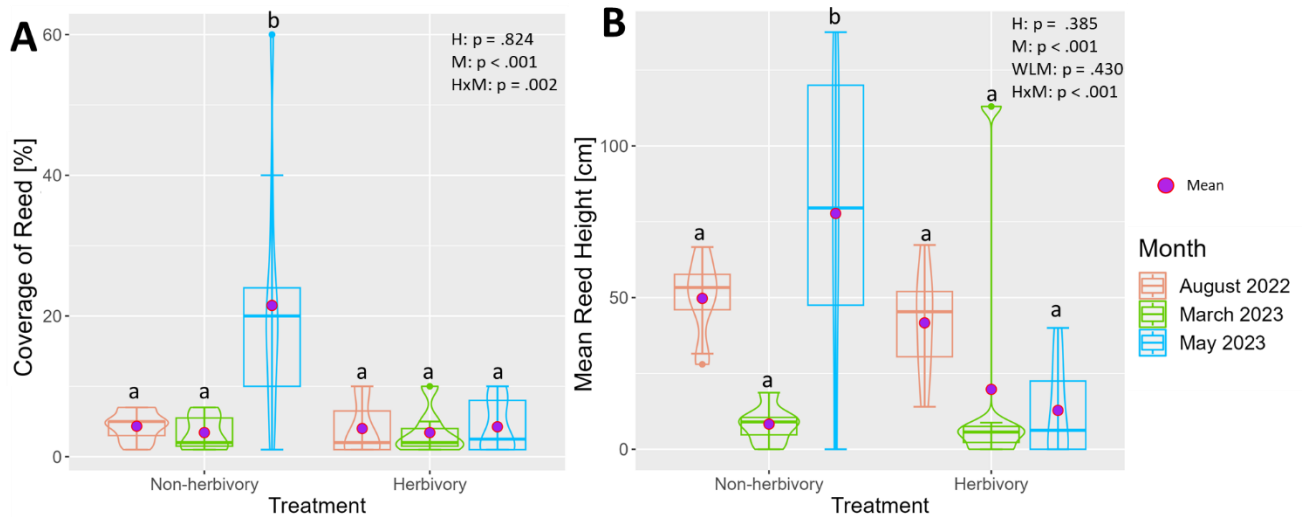


Figure 15. Impact of herbivory treatments across time on reed development dependent variables. A) Reed Coverage (%), and B) Mean Reed Height (cm) for each treatment and time of measurement. The significance, represented by different letters, was obtained from GLMMs and by means of Tukey test post-hoc analysis. This figure depicts the obtained results as boxplot with error bars, and violin plot to visualize the variations on data distribution among measurements. It also includes the mean value of treatments at each sampling period. (H: Herbivory; M: months; WLM: mean water level, H x M: interaction between herbivory and months).

c) Reed height

The height of reed fluctuated across time and the exclusion of herbivores allowed reed to growth (figure 15B). When reed was present, prevention of herbivory for ten months lead to an increase on reed height (non-herb-May: 77.7 ± 10.1 cm). Comparatively, in May 2023, reed height in the non-herbivory treatment (Herb-May: 12.8 ± 5.6 cm) was on average 2.4 cm lower than in the herbivory treatment ($p < .001$). Water level influence reed height depending on the treatment ($\chi^2 = 8.851$, $p = 0.003$). It appears that under herbivory pressure, water level increase may have a positive effect on reed height, compared to the non-herbivory treatment (figure 16C). Conversely, in the absence of herbivory, an increase in water level may result in a decline in reed height. In general, observations concentrated around the median; however, it's worth noting an outlier in the herbivory treatment during March 2023, which deviated from the overall pattern might influence the observed positive trend (figure 15B). Both models were fitted with zero inflation, and the results indicated that the predictors did not have a significant influence on the zero values of the height of reed stems.

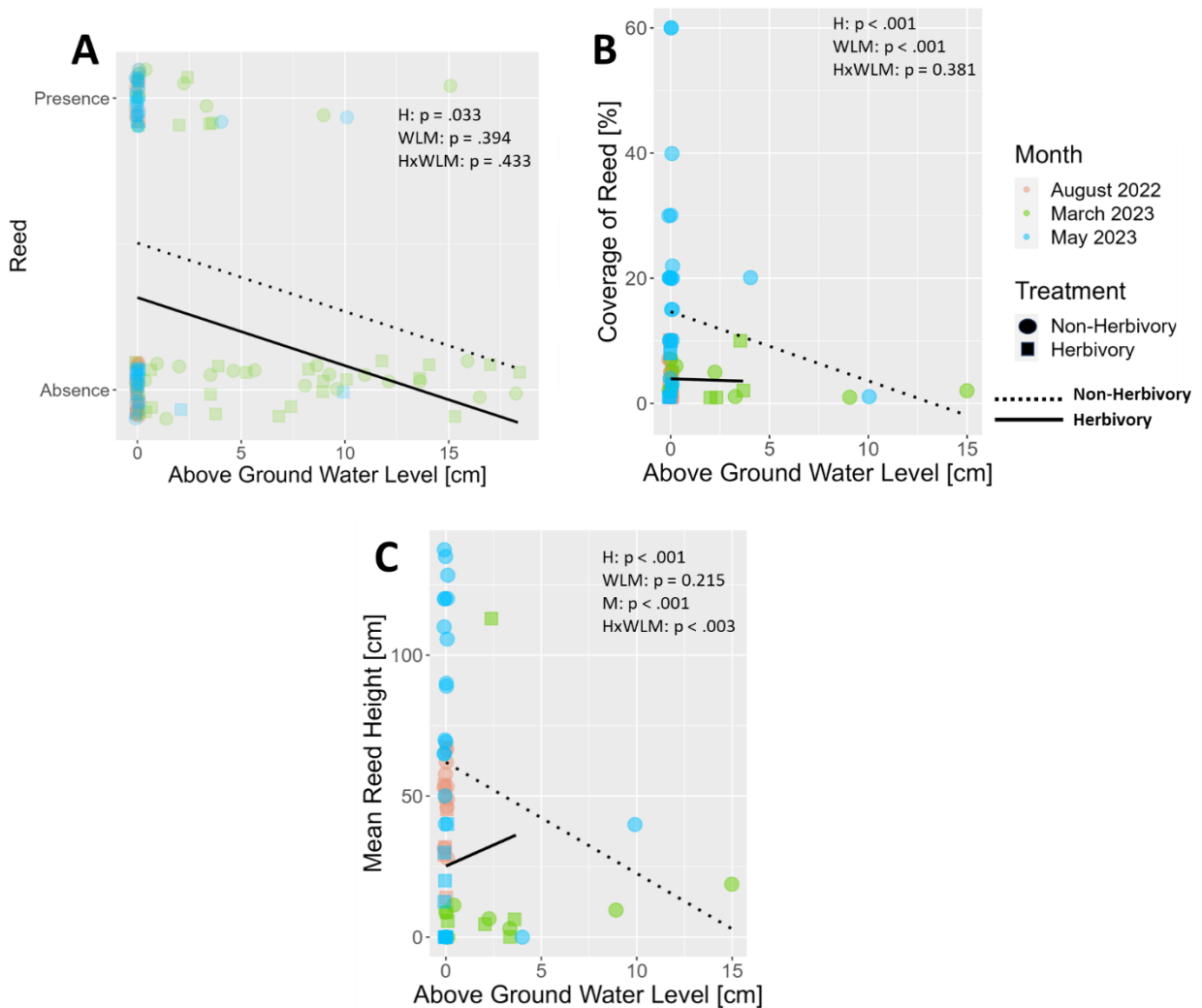


Figure 16. Impact of above ground water level mean (WLM) on reed development dependent variables, A) Reed Presence, B) Coverage of Reed (%), and C) Mean Reed Height (cm), for each treatment and time of measurement. The figures show the relationship between water level increase and the response variables. Furthermore, the figures also include months distinctions with different colors. The lines were fitted by an exponential decay function using the fitted values for each model. (H: Herbivory; WLM: water level mean; M: months; H x WLM: interaction between herbivory and water level mean).

3.2. Red Deer habitat Patterns

3.2.1. Sub-question 4: Exploratory analysis of red deer habitat usage (deer presence/absence)

a) Presence absence analysis

Deer were not completely absent from the wetland area in OVP during any month of the sampling period (figure 17B). This indicates that there was at least one deer present on at least one day of each month. However, there is a clear presence/absence pattern observed over seasons (figure 17A)

($\chi^2 = 218.691$, $p < .001$). During summer deer were continuously present in the wetland area, with sightings on the trail cameras observed on almost every day within that timeframe. Then, deer occurrence decreased during autumn ([summer – autumn]: $p < .001$), and there was even less deer presence during winter ([summer – winter]: $p < .001$). Winter was the seasons with the lowest proportion of sightings. During the following season, spring, deer increase again, reaching the same presence levels than in autumn ([autumn – spring]: $p = 0.694$). In the case of geese presence/absence dynamics, they followed an opposite pattern (figure 17A).

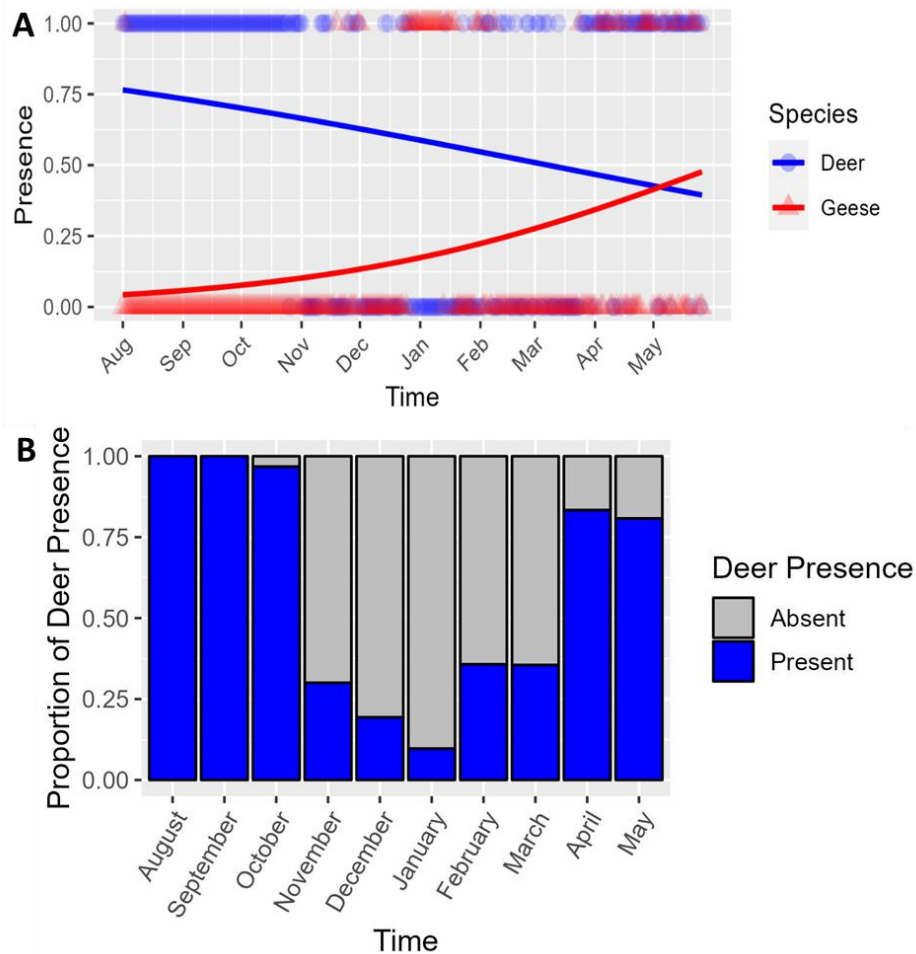


Figure 17. Red Deer Population Dynamics. A) *Deer and Geese Population Dynamics over Time:* This figure compares the presence patterns of deer and geese across time in the wetland area of OVP. B) *Proportion of Deer Sightings per Month:* The figure shows the proportion of days per month when deer were present in the wetland area.

b) *Vegetation Border Zone analysis*

We found that the presence of deer was influenced by the distance to the vegetation border ($\chi^2 = 13.332$, $p < .001$), seasons ($\chi^2 = 96.068$, $p < .001$), and their interaction ($\chi^2 = 35.299$, $p < .001$) (figure 18). Specifically, during autumn, "VB zone A" presented more deer occurrences compared to "VB zone C" ($p = 0.020$). It was on average 0.87 times more likely to find deer in zone A instead of C during autumn. In the case of spring, it was on average 2.1 times and 4.2 times more likely to find deer in

"VB zone A" than in "VB zone B" ($p < .001$) and "VB zone C" ($p < .001$), respectively. Furthermore, VB zones B and C did not differ significantly during spring ($p = 0.205$). Deer presence also showed differences among vegetation border zones during summer, with deer occurring on average 1.1 times more in "VB zone A" than in "VB zone C" ($p < .001$). During summer, "VB zone A" and "VB zone B" did not differ among them ($p = 0.199$) nor "VB zone B" and "VB zone C" ($p = 0.858$). On the contrary, winter did not significantly influence deer presence ([A-B]: $p = 0.277$; [A-C]: $p = 1$, [B-C]: $p = 1$).

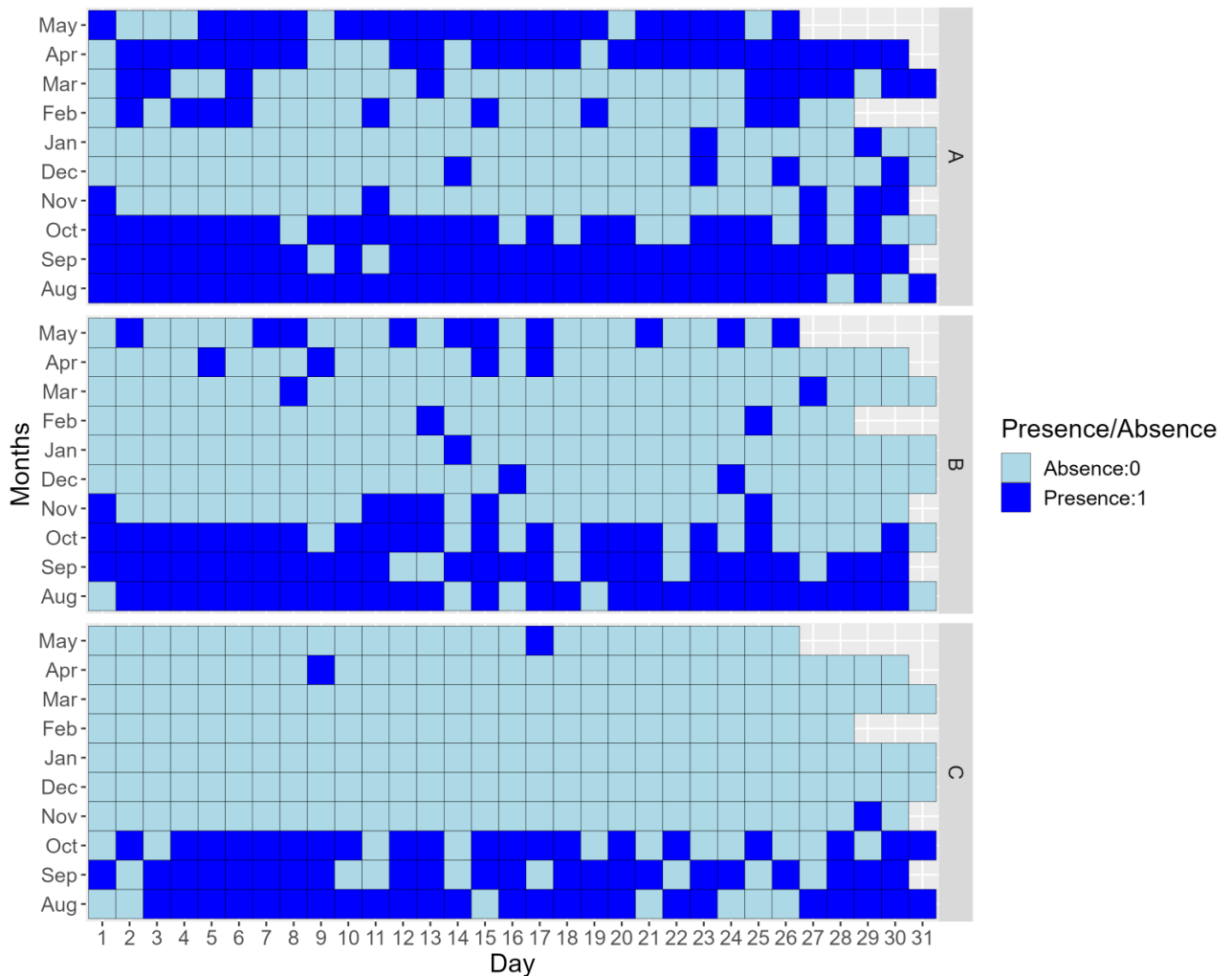


Figure 18. Deer presence heat map across vegetation border zones. The heatmap shows the presence patterns over time, across the different vegetation border zones in the wetland area of OVP.

c) Water Level Zone analysis

We found that water level zones influenced deer presence within the wetland area ($\chi^2 = 25.150$, $p < .001$), as well as seasons ($\chi^2 = 123.130$, $p < .001$) and their interaction ($\chi^2 = 37.178$, $p < .001$) (figure 19). During summer, deer were on average 1.4 and 1.3 times more likely to be found in "WL zone a" compared to "WL zone b" and "WL zone c," respectively ([a-b]: $p < .001$; [a-c]: $p < .001$). Water level zones b and c did not differ among them ($p = 1$). Furthermore, during autumn, the only difference was found between "WL zone a" and "WL zone b". It was on average 0.9 times more probability to

fin deer in “WL zone a” ($p < .001$). Spring and winter did not show any difference in deer occurrence across water level zones (Spring: [a-b] $p = 1$; [a-c] $p = 0.136$; [b-c] $p = 0.381$; winter: [a-b] $p = 0.672$; [a-c] $p = 1$; [b-c] $p = 0.499$).

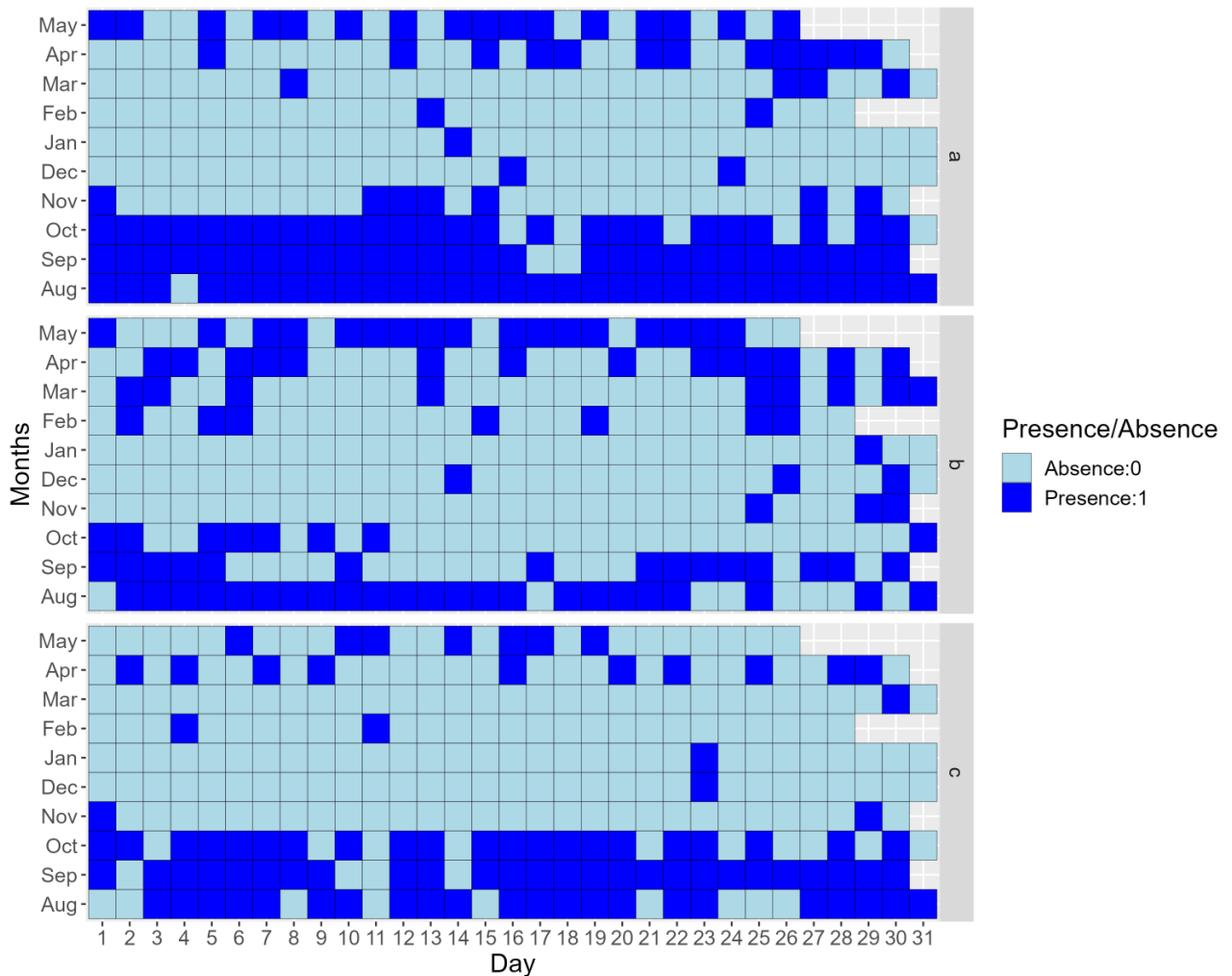


Figure 19. Deer presence heat map across water level zones. The heatmap shows the presence patterns over time, across the different water level zones in the wetland area of OVP.

4. Discussion

Vegetation development in the wetland area was partially influenced by red deer herbivory at this early stage of ecological succession. The artificial drawdown triggered vegetation ecological succession, and the ecosystem showed signs of evolving towards a more *Phragmites australis*-oriented community, although it was still incipient. Water level significantly shaped vegetation, with increasing water levels limiting vegetation and reed coverage, and leading to different communities across water level variations. Specifically, the results of this study demonstrate that, in the short-term, the exclusion of herbivory increased vegetation coverage. However, herbivory did not significantly impact other vegetation diversity variables. After approximately one year of the induced

drought in the wetland, the system constantly evolved and changed, as vegetation development variables fluctuated over time. Moreover, herbivory had a strong negative influence on reed development.

4.1. Time Patterns and Minimal Impact of Deer Herbivory on Wetland Vegetation Development: Potential Negative Effects of Prolonged Herbivory

The findings of this research suggest that herbivory had contrasting effects on different vegetation variables, partially supporting the first hypothesis. Vegetation composition changed across time, but it was not influenced by deer herbivory exclusion. In addition, species richness and Shannon index remained unaffected, but herbivory exclusion had a positive impact on total vegetation coverage.

The change in species composition was not influenced by herbivory exclusion over a thirteen-month period since deer exclusion. However, community composition did change across time, due to the drawdown that reset vegetation succession (e.g., Coops et al., 2004; Ter Heerdt & Drost, 1994; Vulink et al., 2000). Furthermore, vegetation border zones did influence vegetation composition, with areas nearer to the vegetation border having different vegetation communities compared to the furthest away area. This pattern was observed in August 2022 and March 2023, suggesting an effect of vegetation border zones on initial species composition and its development over time. Species with vegetative reproduction, as *Phragmites australis*, found it easier to colonize nearby areas rather than distant ones. After seven months from the first sampling period (March 2023), middle distance (VB zone B) and the longest distant areas (VB zone C) showed similar vegetation composition, while the nearest area (VB zone A) remained different. The species *Phragmites australis* contributed significantly to dissimilarities among vegetation border zones, being more abundant in the nearest area to the vegetation border. Previous research (Temmink et al., 2022b) suggested that reed planting accelerates reed development. The distance to the vegetation border may serve as an analog for active planting, as shorter distances favor reed development due to vegetative reproduction, similar to the effect of active planting.

While environmental variables such as soil organic matter content, humidity, and bulk density showed an influence on community patterns, they were not extensively analyzed in this research. Further evaluation of how these variables influence the occurrence and development of certain species would be interesting. It is important to highlight that OVP is categorized as a highly productive area. Therefore, nutrients are not a limiting factor for plant growth, which could otherwise constrain vegetation development (Verhoeven et al., 1996).

Species richness and the Shannon index were not affected by herbivory during the short timeframe of this research (thirteen months of herbivory exclusion), whereas total vegetation coverage was negatively affected by herbivory. On the one hand, the negative effect on coverage aligns with previous findings where herbivory limited vegetation coverage (Barret & Stiling, 2006). On the other hand, other research has found positive impacts of herbivory on vegetation diversity and species richness; however, those studies focus on stable ecosystems (e.g., Bekker et al., 2006; Hegland et al., 2013; Schutz et al., 2003; van Klink et al., 2016). In these cases, herbivory offers a "window of opportunity" for less competitive species, opening patches of bare soil for establishment and reducing light competition (Bekker et al., 2006). In the wetland area of OVP, a recent drawdown

disturbance had reset the system back to an unstable state, resulting in low light competition and extensive bare soil. At this point, other mechanisms such as facilitation become more important than reducing competition between species (Zhang & Shao, 2013; Zhao et al., 2007).

Our results showed a time pattern in species richness, total vegetation coverage, and the Shannon index. The observed decrease in those variables after August 2022 is likely associated with seasonal changes. August represents summer in the northern hemisphere, a period of peak productivity (Hummel et al., 2018). During winter, vegetation growth was restricted, but a recovery trend for species richness and the Shannon index was observed after the winter season (March 2023 and May 2023), regardless of the treatment. However, deer herbivory hindered vegetation coverage and has the potential to damage vegetation development with prolonged exposure to deer herbivory. Therefore, continuous monitoring of the area is crucial for understanding the post-May 2023 developments.

4.2. Initial Low Presence of Reed and Sudden Improvement of Red Development in Non-Herbivory Plots: The need of Herbivory Refuges

Following a thirteen-month period of red deer exclusion, the areas without herbivory exhibited a significant increase in the presence, height, and coverage of reed compared to the plots subjected to herbivory. This finding confirms the prediction made by the second hypothesis.

The first eleven months after the exclusion experiment (April 2022 - March 2023) showed minimal reed presence, regardless of the treatment. However, in May 2023, reed presence increased sharply but only in the non-herbivory treatment, indicating the importance of preventing herbivory for early-stage reed development. This result aligns with other studies that found herbivory hampers reed development (e.g., Vulink et al. 2000; Bakker et al. 2018). Even after a short exclusion period, the results were significant, with similar patterns observed in reed coverage (abundance) and height, both constrained by herbivory once reed was present.

The aim of the park managers in OVP is to create a wetland landscape dominated by *Phragmites australis* (PHAU). However, in March 2023, the vegetation did not clearly form a PHAU-oriented community. Since dissimilarities in communities across time (August 2022 - March 2023), without any zone distinction, were not driven by *P. australis*. In May 2023, *P. australis* became more present in the area, but limitations in statistical analysis (NMDS stress equal to zero) prevented determining if it was a more PHAU-dominated community. It is recommended to increase the sampling size for future research to avoid shortcomings on statistical analysis.

This research provides evidence of deer consumption affecting reed coverage and height. Previous studies have also found red deer feeding on reed (Cornelissen et al., 2014a; 2014b; Vulink et al., 2000), and deer have been known to cause ecosystem shifts in other ecosystem types (Cornelissen et al., 2014b; Smit et al., 2015). The stage of the ecosystem played a crucial role in defining the direction of herbivory effects, as shown in the vegetation diversity section. Once reed beds are fully vegetated, research indicates no detrimental effects of herbivory (Reijers et al., 2019). However, in the early development stages of reed beds, as observed in this study, herbivory hampers reed growth, consistent with previous findings (Bakker et al., 2018; Liu et al., 2020; Vulink et al., 2000; Zhang et al., 2021). Therefore, the expected effect of deer herbivory was found. To promote reed

development, especially in the early stages of wetland succession, it would be essential to consider grazing refuges (Smit et al., 2015; Barrett & Stiling, 2006).

4.3. Water Level Inhibits Vegetation and Reed Development: A Need of Water Level Thresholds

The evidence partially supports hypothesis four, indicating an inverse relationship between above ground water level and vegetation diversity variables, as well as reed coverage. However, reed presence was not affected by water level increases. In terms of reed height, water level showed contrasting effects depending on the herbivory treatment.

Overall, water level was an important factor explaining changes on vegetation community, as well as the reduction of (i) species richness, (ii) total vegetation coverage (%), (iii) Shannon index, and (iv) reed coverage (%). The finding is partially consistent with prior research, which has shown that deeper water levels have a negative impact on vegetation development (e.g., Alderson 2023; Coops et al., 2004). However, in the specific case of *P. australis* presence, it was found to be unaffected by water level changes. *P. australis* is an aquatic plant tolerant to floodings, allowing reproduction under a range of water levels, even 15 cm of water depth (Meng et al., 2016; Yu et al., 2012). Based on the results, it seems like water level fluctuation in the wetland did not surpass its tolerance. Furthermore, water level had contrasting impacts on reed height, depending on herbivory treatment. In non-herbivory plots with existing reed, water level negatively affected height, while in herbivory plots, it had a positive effect. Unexpectedly, herbivory seemed to suppress a mechanism or variable present in non-herbivory plots, causing the observed differences. One possible explanation might be the availability of light for growth. The presence of deer outside the exclosures resulted in the removal of old vegetation from the previous season, which in turn reduced the stress of light competition. In contrast, within the exclosures, old vegetation accumulated, and when combined with the increasing water level, a synergistic effect of both variables was observed. It is important to note that the smaller sample size might have influenced the positive height trend under herbivory, as it emphasized outliers. However, the negative trend in non-herbivory and the slightly different trend in herbivory plots, for both reed height and coverage, should not be overlooked. This is especially significant considering that the germination of *P. australis* has been shown to be sensitive to light availability (Kettenring & Whigham, 2018).

Water level significantly influenced vegetation communities, as different plant species have varying tolerance levels to water level fluctuations (Coops & Velde, 1995; Griest et al., 1990; Meng et al., 2016). Some plants germination is less successful underwater, such as *Phragmites australis*, which shows a higher likelihood of germination when the above-ground water level does not exceed 2-4 cm (Meng et al., 2016; Yu et al., 2012). The impact of water level zones on the park's species composition was evident, with each zone's drying time playing a crucial role in shaping the species community. After seven months from the first sampling period, the North-East area of the park (VB zone c), being the first to dry up, remained the only community that showed a significant difference. *Phragmites australis* emerged as a key factor in explaining the dissimilarities between the first and last zones to dry up, highlighting the importance of a long enough dry period for reed to reproduce and establish. This is in line with other research where time of inundation accounted for *P. australis* seedling germination (Alvarez et al., 2005; Coops & van Velde, 1995).

Furthermore, the findings indicate that maintaining the water level below a certain threshold is crucial for the expansion of vegetation during wetland recovery (van der Valk and Davis 1978). Once the water level exceeds this threshold, all the vegetation diversity variables were significantly reduced. However, the threshold at which vegetation is affected differs between reed and other vegetation species. For reed, the above ground water level should be kept below 5 cm, as its coverage drastically decline beyond this value. In contrast, other vegetation types have a higher threshold of over 13 cm for limiting their development. To increase vegetation diversity and expand reedbeds, constant monitoring of water levels is necessary, and prompt action should be taken if they exceed the threshold. In the case of OVP, where the focus is on restoring reedbeds, maintaining a lower water level is essential for reed extension compared to other vegetation types.

4.4. Deer Presence Patterns and Management Implications: Deer Influence on Vegetation

Water level and vegetation border zones were found to influence deer presence in the wetland area of OVP. However, the effect was not as expected, deer were mostly absent in the wetland area during winter (wet period). In addition, the nearest zone from the vegetation border was the preferable habitat during spring and not across all seasons as it was hypothesized.

Deer were observed in the wetland areas of OVP during all seasons, and they actively fed on *Phragmites australis*, leading to herbivory pressure. Throughout the entire sampling period, geese were not continuously present, indicating that the herbivory on *Phragmites australis* was primarily caused by deer. Even during months when geese were observed, it was possible to differentiate their consumption behavior from that of deer. Deer predominantly fed on the top parts of tall herbs (stems), while geese fed from the bottom of the plant. This difference in feeding behavior allowed for the identification of the herbivory source, confirming that it was mainly due to deer.

The presence of deer in OVP's wetland area was influenced by water level zones, particularly during the dry summer of 2022. The lowest or north-west zone showed the highest deer occurrence. This preference for the lowest zone was likely due to favorable food resources rather than water level, as in August 2022 the wetland area was already dry (Güsewell et al., 2007). This allowed deer to freely move around the area. Vegetation species compositions varied among water level zones in August 2022, indicating potential differences in food availability (Hummel et al., 2018). Deer were also more likely to be found closer to the vegetation border during spring. In the previous winter season, deer were largely absent, possibly due to increased water levels, food scarcity, and the hunting season that took place in winter (Güsewell et al., 2007; Ligi & Randveer, 2012). Red deer and other deer species have shown changes in habitat usage due to hunting (Ligi & Randveer, 2012). Therefore, after winter, deer returned to the wetland; however, as an open area, it was safer to stay near the existing vegetation border. This winter absence might be considered beneficial, as it reduces pressure on vegetation during challenging winter conditions.

The above-described patterns had management implications. The results are showing that deer habitat usage differ across the wetland area. Therefore, some areas could suffer more herbivory damage and might need to avoid deer presence. This research suggests that preferable vegetation types might be present in the South-west area of the park (lowest elevation). Additionally, the area nearest to the vegetation border is also more inhabited by deer, due to a sense of higher protection

as it was predicted, or maybe it was also because of preferable vegetation availability. Cornelissen and colleagues (2014a), findings suggest that herbivory can be influenced by the species composition in the surrounding neighborhood. If a particular species is surrounded by preferred plant species, it is more likely to be eaten. Conversely, if a species is surrounded by non-preferred plant species, it is more likely to be protected from herbivory. This information highlights the importance of considering the plant community composition when studying and managing herbivory effects on vegetation. Based on the above, deer herbivory impact might not be equally distributed in the wetland area; reed development might be more constrained when it is surrounded by preferable species (, such as in the South-west area of the park or nearer to the vegetation border. This could be of special concern for reed development in the nearest area toward the vegetation border, as vegetation started to recover in spring, and *P. australis* became more abundant.

4.5. Further research

The findings of this research highlight the importance of the next steps, which include conducting vegetation measurements after May 2023. This follow-up study aims to confirm the progression towards a more PHAU-oriented community and to verify the impact of red deer herbivory on vegetation development over longer period. Furthermore, it is crucial to explore the relationship between the different species occurrences in the wetland and the abiotic environmental variables, as these variables have been found to be correlated with species composition. Vegetation has shown to influence abiotic conditions, and at the same time, abiotic conditions affect vegetation, leading to the establishment of feedback mechanisms between them (Temmik et al., 2022a). These relations are important to identify in a novel ecosystem to ensure resilience and self-regulation (Perino et al., 2019).

Even the importance of herbivory densities on herbivory impacts, deer densities were not studied in this research due to the experimental design. The primary aim was to identify deer presence in the wetland area rather than establish deer densities. To calculate densities from images, a specific sampling design would be needed (Becker et al., 2022; Ripa et al., 2023). Establishing deer densities in the wetland area is a next step for the OVP managers, as high deer densities often imply a negative impact on vegetation development, especially considering that deer have already shown preferences in habitat usage within the wetland area. Additionally, as water levels start to increase, the geese population might also increase (Coops et al., 2004), leading to herbivory pressure from two species instead of one. It is still unknown what will happen with deer habitat usage at higher water levels, but it might be a period of coexistence. Future research should take this potential habitat overlap in consideration.

Within the OVP wetland area, vegetation successions are ongoing, and the results showed a trend towards a more PHA-oriented community, aligning with the park managers' objectives. However, vegetation establishment is only the initial step to trigger the boom phase and enhance ecosystem services provision. Therefore, once full reed establishment is achieved, future research should focus on how reedbeds enhancement sets the base for biodiversity improvement at higher trophic levels, and the development of vegetation-abiotic feedbacks, including nutrient cycling and carbon storage. These factors play a crucial role in combating climate change and addressing the current biological conservation crisis.

5. Conclusion

This study sheds light on the development of novel ecosystems and the successful artificial management of a wetland ecosystem. The findings highlight the crucial role of herbivory by deer in vegetation succession in the early ecosystem stage. Red deer negatively impacted reed development and potentially hindering overall vegetation growth with prolonged exposure. However, the implementation of the drawdown rewilding measure at this early ecological succession state has shown promising positive effects on vegetation and reed development. Moving forward, it is imperative to address the issue of deer herbivory in the area when water levels are lowered to ensure the continued success of wetland restoration efforts. Preventive measures aimed at reducing deer impact will be vital in guiding the progression of this ecosystem towards a boom phase.

The duration of the herbivory exclusion experiment and the recent drawdown disturbance have been instrumental in shaping vegetation and reed development outcomes. As such, further research is warranted to explore the long-term implications of herbivory on wetland vegetation dynamics in similar disturbed ecosystems. Understanding the broader applicability of these findings in other ecosystems worldwide will be essential for effective restoration and conservation efforts in the future. Moreover, with the ongoing UN Decade on Restoration, the insights gained from this study hold significant importance in contributing to the global restoration agenda. By incorporating these research findings into conservation and restoration strategies, we can make substantial strides towards achieving sustainable development goals and safeguarding critical ecosystems. In conclusion, the dynamic interplay of ecological processes observed in this study underscores the importance of continued monitoring and adaptive management to foster the successful restoration of novel ecosystems.

6. References

- Agouti. (n.d.). Home. Retrieved July 20, 2023, from <https://www.agouti.eu/>.
- Alvarez, M. G., Tron, F., & Mauchamp, A. (2005). Sexual versus asexual colonization by *Phragmites australis*: 25-year reed dynamics in a Mediterranean marsh, southern France. *Wetlands*, 25(3), 639-647. [https://doi.org/10.1672/0277-5212\(2005\)025\[0639:svacbp\]2.0.co;2](https://doi.org/10.1672/0277-5212(2005)025[0639:svacbp]2.0.co;2)
- Alderson, R. (2023). Long-Term Soil and Vegetation Development on a Forward-Looking Wetland Restoration Project: A Case Study of the Marker Wadden [Master's thesis, Utrecht University].
- Applestein, C., Caughlin, T. T., & Germino, M. J. (2022). Post-fire seed dispersal of a wind-dispersed shrub declined with distance to seed source, yet had high levels of unexplained variation. *AoB PLANTS*, 14(6). <https://doi.org/10.1093/aobpla/plac045>
- Bakker, E. S., & Svenning, J.-C. (2018). Trophic rewilding: impact on ecosystems under global change. *Philosophical Transactions of the Royal Society B: Biological Sciences*, 373(1761), 20170432. <https://doi.org/10.1098/rstb.2017.0432>

Bakker, E. S., Ritchie, M. E., Olf, H., Milchunas, D. G., & Knops, J. M. H. (2006). Herbivore impact on grassland plant diversity depends on habitat productivity and herbivore size. *Ecology Letters*, 9(7), 780–788. <https://doi.org/10.1111/j.1461-0248.2006.00925.x>

Barrett, M. A., & Stiling, P. (2006). Effects of Key deer herbivory on forest communities in the lower Florida Keys. *Biological Conservation*, 129(1), 100-108. <https://doi.org/10.1016/j.biocon.2005.10.026>

Becker, M., Huggard, D. J., Dickie, M., Warbington, C., Schieck, J., Herdman, E., Serrouya, R., & Boutin, S. (2022). Applying and testing a novel method to estimate animal density from motion-triggered cameras. *Ecosphere*, 13(4). <https://doi.org/10.1002/ecs2.4005>

Beemster, N., Troost, E., & Platteeuw, M. (2010). Early successional stages of ReedPhragmites australisVegetations and its importance for the bearded Reedling<i>Panurus biarmicus</i>in Oostvaardersplassen, The Netherlands. *Ardea*, 98(3), 339-354. <https://doi.org/10.5253/078.098.0308>

Bino, G., Kingsford, R. T., & Porter, J. (2015). Prioritizing Wetlands for Waterbirds in a Boom and Bust System: Waterbird Refugia and Breeding in the Murray-Darling Basin. *PLOS ONE*, 10(7), e0132682. <https://doi.org/10.1371/journal.pone.0132682>

Blossey, B. (2003). A framework for evaluating potential ecological effects of implementing biological control of *Phragmites australis*. *Estuaries*, 26(2), 607–617. <https://doi.org/10.1007/bf02823736>

Borowski, Z., Gil, W., Barton, K., Zajączkowski, G., Łukaszewicz, J., Tittenbrun, A., & Radlinski, B. (2021). Density-related effect of red deer browsing on palatable and unpalatable tree species and forest regeneration dynamics. *Forest Ecology and Management*, 496, 119442. <https://doi.org/10.1016/j.foreco.2021.119442>

Bornette, G., & Puijalon, S. (2010). Response of aquatic plants to abiotic factors: A review. *Aquatic Sciences*, 73(1), 1-14. <https://doi.org/10.1007/s00027-010-0162-7>

Bray, J. R., & Curtis, J. T. (1957). An ordination of the upland forest communities of southern Wisconsin. *Ecological Monographs*, 27(4), 325-349. <https://doi.org/10.1086/2842271>

Brooks, M., Kristensen, K., Benthem, K., Magnusson, A., Berg, C., Nielsen, A., Skaug, H., Mächler, M., & Bolker, B. (2017). GlmmTMB balances speed and flexibility among packages for zero-inflated generalized linear mixed modeling. *The R Journal*, 9(2), 378. <https://doi.org/10.32614/rj-2017-066>

Chen, Z., Yuan, X., Roß-Nickoll, M., Hollert, H., & Schäffer, A. (2020). Moderate Inundation stimulates plant community assembly in the drawdown zone of China's Three Gorges reservoir. *Environmental Sciences Europe*, 32(1). <https://doi.org/10.1186/s12302-020-00355-0>

Clarke, K. R. (1993). Non-parametric multivariate analyses of changes in community structure. *Austral Ecology*, 18(1), 117-143. <https://doi.org/10.1111/j.1442-9993.1993.tb00438.x>

Coops, H., & Velde, G. (1995). Seed dispersal, germination and seedling growth of six helophyte species in relation to water-level zonation. *Freshwater Biology*, 34(1), 13-20. <https://doi.org/10.1111/j.1365-2427.1995.tb00418.x>

Coops, H., Vulink, J. T., & Van Nes, E. H. (2004). Managed water levels and the expansion of emergent vegetation along a lakeshore. *Limnologica*, 34(1-2), 57-64. [https://doi.org/10.1016/s0075-9511\(04\)80022-7](https://doi.org/10.1016/s0075-9511(04)80022-7)

Cornelissen, P., Bokdam, J., Sykora, K., & Berendse, F. (2014a). Effects of large herbivores on wood pasture dynamics in a European wetland system. *Basic and Applied Ecology*, 15(5), 396–406. <https://doi.org/10.1016/j.baae.2014.06.006>

Cornelissen, P., Gresnigt, M. C., Vermeulen, R. A., Bokdam, J., & Smit, R. (2014b). Transition of a *Sambucus nigra* L. dominated woody vegetation into grassland by a multi-species herbivore assemblage. *Journal for Nature Conservation*, 22(1), 84–92. <https://doi.org/10.1016/j.jnc.2013.09.004>

Costanza, R., de Groot, R., Sutton, P., van der Ploeg, S., Anderson, S. J., Kubiszewski, I., Farber, S., & Turner, R. K. (2014). Changes in the global value of ecosystem services. *Global Environmental Change*, 26(26), 152–158. <https://doi.org/10.1016/j.gloenvcha.2014.04.002>

de Groot, R., Brander, L., van der Ploeg, S., Costanza, R., Bernard, F., Braat, L., Christie, M., Crossman, N., Ghermandi, A., Hein, L., Hussain, S., Kumar, P., McVittie, A., Portela, R., Rodriguez, L. C., ten Brink, P., & van Beukering, P. (2012). Global estimates of the value of ecosystems and their services in monetary units. *Ecosystem Services*, 1(1), 50–61. <https://doi.org/10.1016/j.ecoser.2012.07.005>

Engloner, A. I., & Major, Á. (2011). Clonal diversity of *Phragmites australis* propagating along water depth gradient. *Aquatic Botany*, 94(4), 172-176. <https://doi.org/10.1016/j.aquabot.2011.02.007>

European Commission. (n.d.). Natura 2000. Retrieved May 15, 2023, from https://ec.europa.eu/environment/nature/natura2000/index_en.htm

European Commission. (2022, June). Nature Restoration Law. Environment. Retrieved March 15, 2023, from https://environment.ec.europa.eu/topics/nature-and-biodiversity/nature-restoration-law_en

Farley, E. B., Schummer, M. L., Leopold, D. J., Coluccy, J. M., & Tozer, D. C. (2021). Influence of water level management on vegetation and bird use of restored wetlands in the Montezuma wetlands complex. *Wildlife Biology*, 2022(2). <https://doi.org/10.1002/wlb3.01016>

Fazekas, I., & Liese, F. (1996). Some properties of the Hellinger transform and its application in classification problems. *Computers & Mathematics with Applications*, 31(8), 107-116. [https://doi.org/10.1016/0898-1221\(96\)00035-1](https://doi.org/10.1016/0898-1221(96)00035-1)

Ferreira, C. S., Kašanin-Grubin, M., Solomun, M. K., Sushkova, S., Minkina, T., Zhao, W., & Kalantari, Z. (2023). Wetlands as nature-based solutions for water management in different environments. *Current Opinion in Environmental Science & Health*, 33, 100476. <https://doi.org/10.1016/j.coesh.2023.100476>

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., ... McIntyre, P. B. (2023). Extensive global

wetland loss over the past three centuries. *Nature*, 614(7947), 281-286. <https://doi.org/10.1038/s41586-022-05572-6>

Gebert, C., & Verheyden-Tixier, H. (2008). Variations of diet composition of red deer (*Cervus elaphus* L.) in Europe. *Mammal Review*, 31(3-4), 189-201. <https://doi.org/10.1111/j.1365-2907.2001.00090.x>

Greer, A. K., Dugger, B. D., Graber, D. A., & Petrie, M. J. (2007). The effects of seasonal flooding on seed availability for spring migrating waterfowl. *Journal of Wildlife Management*, 71(5), 1561-1566. <https://doi.org/10.2193/2006-376>

Gries, C., Kappen, L., & Losch, R. (1990). Mechanism of flood tolerance in reed, *Phragmites australis* (Cav.) Trin. ex Steudel. *New Phytologist*, 114(4), 589-593. <https://doi.org/10.1111/j.1469-8137.1990.tb00429.x>

Güsewell, S., Pohl, M., Gander, A., & Strehler, C. (2007). Temporal changes in grazing intensity and herbage quality within a Swiss fen meadow. *Botanica Helvetica*, 117(1), 57-73. <https://doi.org/10.1007/s00035-007-0798-7>

Provincie Flevoland. (n.d.). Oostvaardersplassen. Retrieved May 15, 2023, from <https://www.flevoland.nl/wat-doen-we/natuur/oostvaardersplassen>

Gwenzi, W. (2021). Rethinking restoration indicators and end-points for post-mining landscapes in light of novel ecosystems. *Geoderma*, 387, 114944. <https://doi.org/10.1016/j.geoderma.2021.114944>

Hartig, F. (2022). DHARMA: Residual Diagnostics for Hierarchical (Multi-Level / Mixed) Regression Models. R package version 0.4.6, <https://CRAN.R-project.org/package=DHARMA>.

Hegland, S. J., Lilleeng, M. S., & Moe, S. R. (2013). Old-growth forest floor richness increases with red deer herbivory intensity. *Forest Ecology and Management*, 310, 267-274. <https://doi.org/10.1016/j.foreco.2013.08.031>

Hobbs, R. J., Arico, S., Aronson, J., Baron, J. S., Bridgewater, P., Cramer, V. A., Epstein, P. R., Ewel, J. J., Klink, C. A., Lugo, A. E., Norton, D., Ojima, D., Richardson, D. M., Sanderson, E. W., Valladares, F., Vilà, M., Zamora, R., & Zobel, M. (2006). Novel ecosystems: Theoretical and management aspects of the new ecological world order. *Global Ecology and Biogeography*, 15(1), 1-7. <https://doi.org/10.1111/j.1466-822x.2006.00212.x>

Hobbs, R. J., Higgs, E., & Harris, J. A. (2009). Novel ecosystems: Implications for conservation and restoration. *Trends in Ecology & Evolution*, 24(11), 599-605. <https://doi.org/10.1016/j.tree.2009.05.012>

Hummel, S. L., Campa, H., Winterstein, S. R., & Dunton, E. M. (2018). Understanding how a keystone herbivore, white-tailed deer impacts wetland vegetation types in southern Michigan. *The American Midland Naturalist*, 179(1), 51-67. <https://doi.org/10.1674/0003-0031-179.1.51>

Jackson, S. T., & Hobbs, R. J. (2009). Ecological restoration in the light of ecological history. *Science*, 325(5940), 567-569. <https://doi.org/10.1126/science.1172977>

- Johnson, R. M., Ramond, J., Gunnigle, E., Seely, M., & Cowan, D. A. (2017). Namib desert edaphic bacterial, fungal and archaeal communities assemble through deterministic processes but are influenced by different abiotic parameters. *Extremophiles*, 21(2), 381-392. <https://doi.org/10.1007/s00792-016-0911-1>
- Jost, L. (2007). Partitioning diversity into independent Alpha and beta components. *Ecology*, 88(10), 2427-2439. <https://doi.org/10.1890/06-1736.1>
- Kettenring, K. M., McCormick, M. K., Baron, H. M., & Whigham, D. F. (2009). *Phragmites australis* (Common Reed) Invasion in the Rhode River Subestuary of the Chesapeake Bay: Disentangling the Effects of Foliar Nutrients, Genetic Diversity, Patch Size, and Seed Viability. *Estuaries and Coasts*, 33(1), 118–126. doi:10.1007/s12237-009-9241-1
- Kettenring, K. M., & Whigham, D. F. (2018). The role of propagule type, resource availability, and seed source in *Phragmites* invasion in Chesapeake Bay wetlands. *Wetlands*, 38(6), 1259-1268. <https://doi.org/10.1007/s13157-018-1034-5>
- Kross, J., Kaminski, R. M., Reinecke, K. J., Penny, E. J., & Pearse, A. T. (2008). Moist-soil seed abundance in managed wetlands in the Mississippi alluvial Valley. *Journal of Wildlife Management*, 72(3), 707-714. <https://doi.org/10.2193/2007-100>
- Legendre, P., & Gallagher, E. D. (2001). Ecologically meaningful transformations for ordination of species data. *Oecologia*, 129(2), 271-280. <https://doi.org/10.1007/s004420100716>
- Lemke, M. J., Hagy, H. M., Dungey, K., Casper, A. F., Lemke, A. M., VanMiddlesworth, T. D., & Kent, A. (2017). Echoes of a flood pulse: short-term effects of record flooding of the Illinois River on floodplain lakes under ecological restoration. *Hydrobiologia*, 804(1), 151–175. <https://doi.org/10.1007/s10750-017-3220-5>
- Lundin, O., Boetzel, F. A., Ward, K. L., & Williams, N. M. (2023). Wildflower plantings have mixed effects on insect herbivores and their natural enemies. *Agriculture, Ecosystems & Environment*, 355, 108587. <https://doi.org/10.1016/j.agee.2023.108587>
- Lenth, R. V. (2021). emmeans: Estimated Marginal Means, aka Least-Squares Means. R package version 1.6.0. URL: <https://CRAN.R-project.org/package=emmeans>
- Ligi, K., & Randveer, T. (2012). Pre-winter diet selection of red deer (*Cervus elaphus* L.) in Estonia. *Baltic Forestry*, 18, 150-155.
- Liu, G., Zhou, J., Li, W., & Cheng, Y. (2005). The seed bank in a subtropical freshwater marsh: implications for wetland restoration. *Aquatic Botany*, 81(1), 1–11. <https://doi.org/10.1016/j.aquabot.2004.07.001>
- Liu, Z., Fagherazzi, S., Ma, X., Xie, C., Li, J., & Cui, B. (2020). Consumer control and abiotic stresses constrain coastal saltmarsh restoration. *Journal of Environmental Management*, 274, 111110. <https://doi.org/10.1016/j.jenvman.2020.111110>
- Lu, Z.-J., Li, L.-F., Jiang, M.-X., Huang, H.-D., & Bao, D.-C. (2010). Can the soil seed bank contribute to revegetation of the drawdown zone in the Three Gorges Reservoir Region? *Plant Ecology*, 209(1), 153–165. <https://doi.org/10.1007/s11258-010-9732-y>

- Meng, H., Wang, X., Tong, S., Lu, X., Hao, M., An, Y., & Zhang, Z. (2016). Seed germination environments of typha latifolia and Phragmites australis in wetland restoration. *Ecological Engineering*, 96, 194-199. <https://doi.org/10.1016/j.ecoleng.2016.03.003>
- Mornout, D. (2022). Ecosystem services of constructed wetlands under stable and fluctuating water levels: The case of Oostvaardersplassen & Marker Wadden (pp. 1–75) [MSc thesis Water Resources Management]. <https://edepot.wur.nl/567790>
- Oksanen, J., Blanchet, F. G., Friendly, M., Kindt, R., Legendre, P., McGlinn, D., Minchin, P. R., O'Hara, R. B., Simpson, G. L., Solymos, P., Stevens, M. H. H., Szoecs, E., & Wagner, H. (2022). vegan: Community Ecology Package. R package version 2.5-7. <https://CRAN.R-project.org/package=vegan>
- Pan, J., Sharif, R., Xu, X., & Chen, X. (2021). Mechanisms of waterlogging tolerance in plants: Research progress and prospects. *Frontiers in Plant Science*, 11. <https://doi.org/10.3389/fpls.2020.627331>
- Perino, A., Pereira, H. M., Navarro, L. M., Fernández, N., Bullock, J. M., Ceausu, S., Cortés-Avizanda, A., van Klink, R., Kuemmerle, T., Lomba, Â., Pe'er, G., Plieninger, T., Benayas, J., Sandom, C., Svenning, J. C., & Wheeler, H. (2019). Rewilding complex ecosystems. *Science*, 364, eaav5570. <https://doi.org/10.1126/science.aav5570>
- Ramsar Convention Secretariat. (2018). Wetlands and the Sustainable Development Goals (SDGs): Reference Manual. Ramsar Convention Secretariat. https://www Ramsar.org/sites/default/files/documents/library/wetlands_sdgs_e_0.pdf
- Reijers, V. C., Cruijsen, P. M., Hoetjes, S. C., Akker, M., Heusinkveld, J. H., Koppel, J., Lamers, L. P., Olff, H., & Heide, T. (2019). Loss of spatial structure after temporary herbivore absence in a high-productivity reed marsh. *Journal of Applied Ecology*, 56(7), 1817–1826. <https://doi.org/10.1111/1365-2664.13394>
- R Core Team. (2021). R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. URL: <https://www.R-project.org/>
- Rohr, J. R., Bernhardt, E. S., Cadotte, M. W., & Clements, W. H. (2018). The ecology and economics of restoration: When, what, where, and how to restore ecosystems. *Ecology and Society*, 23(2). <https://doi.org/10.5751/es-09876-230215estore ecosystems>
- Šťastný, V., & Riegert, J. (2021). Habitat use of breeding birds in Central European reed beds. *Wetlands Ecology and Management*, 29(1), 81–91. <https://doi.org/10.1007/s11273-020-09768-3>
- Schmeets, E. (2016). The Oostvaardersplassen: “Making Space” (for) Wilderness. *MaRBL*, 5. <https://doi.org/10.26481/marble.2015.v5.342>
- Suding, K. N., & Hobbs, R. J. (2009). Threshold models in restoration and conservation: A developing framework. *Trends in Ecology & Evolution*, 24(5), 271-279. <https://doi.org/10.1016/j.tree.2008.11.012>
- Soomers, H., Karssen, D., Soons, M. B., Verweij, P. A., Verhoeven, J. T., & Wassen, M. J. (2012). Wind and water dispersal of wetland plants across fragmented landscapes. *Ecosystems*, 16(3), 434-451. <https://doi.org/10.1007/s10021-012-9619>

Suding, K. N. (2011). Toward an era of restoration in ecology: Successes, failures, and opportunities ahead. *Annual Review of Ecology, Evolution, and Systematics*, 42(1), 465-487. <https://doi.org/10.1146/annurev-ecolsys-102710-145115>

Smit, C., Ruifrok, J. L., Van Klink, R., & Olf, H. (2015). Rewilding with large herbivores: The importance of grazing refuges for sapling establishment and wood-pasture formation. *Biological Conservation*, 182, 134-142. <https://doi.org/10.1016/j.biocon.2014.11.047>

Schütz, M., Risch, A. C., Leuzinger, E., Krüsi, B. O., & Achermann, G. (2003). Impact of herbivory by red deer (*Cervus elaphus* L.) on patterns and processes in subalpine grasslands in the Swiss National Park. *Forest Ecology and Management*, 181(1-2), 177-188. [https://doi.org/10.1016/s0378-1127\(03\)00131-2](https://doi.org/10.1016/s0378-1127(03)00131-2)

Srivastava, J., Kalra, S. J., & Naraian, R. (2013). Environmental perspectives of *Phragmites australis* (Cav.) trin. Ex. Steudel. *Applied Water Science*, 4(3), 193-202. <https://doi.org/10.1007/s13201-013-0142-x>

Takafumi, H., Matsumoto, A., Aotani, K., & Yoshida, T. (2015). The cross-ecosystem impact of deer on an endangered submerged macrophyte, *Ranunculus nipponicus* var. *submersus*. *Global Ecology and Conservation*, 4, 581-588. <https://doi.org/10.1016/j.gecco.2015.10.011>

Temmink, R. J., Lamers, L. P., Angelini, C., Bouma, T. J., Fritz, C., Van de Koppel, J., Lexmond, R., Rietkerk, M., Silliman, B. R., Joosten, H., & Van der Heide, T. (2022a). Recovering wetland biogeomorphic feedbacks to restore the world's biotic carbon hotspots. *Science*, 376(6593). <https://doi.org/10.1126/science.abn1479>

Temmink, R. J., Van den Akker, M., Van Leeuwen, C. H., Thöle, Y., Olf, H., Reijers, V. C., Weideveld, S. T., Robroek, B. J., Lamers, L. P., & Bakker, E. S. (2022b). Herbivore exclusion and active planting stimulate reed marsh development on a newly constructed archipelago. *Ecological Engineering*, 175, 106474. <https://doi.org/10.1016/j.ecoleng.2021.106474>

Ter Heerdt, G. N., & Drost, H. J. (1994). Potential for the development of marsh vegetation from the seed bank after a drawdown. *Biological Conservation*, 67(1), 1-11. [https://doi.org/10.1016/0006-3207\(94\)90002-7](https://doi.org/10.1016/0006-3207(94)90002-7)

Ter Heerdt, G. N. J., Veen, C. G. F., Van der Putten, W. H., & Bakker, J. P. (2017). Effects of temperature, moisture and soil type on seedling emergence and mortality of riparian plant species. *Aquatic Botany*, 136, 82-94. <https://doi.org/10.1016/j.aquabot.2016.09.008>

Toit, J. T., & Pettorelli, N. (2019). The differences between rewilding and restoring an ecologically degraded landscape. *Journal of Applied Ecology*, 56(11), 2467-2471. <https://doi.org/10.1111/1365-2664.13487>

UNEP. (n.d.). UN Decade on Restoration. Retrieved March 15, 2022, from <https://www.decadeonrestoration.org/>

United Nations. (2015). *Transforming our world: the 2030 agenda for sustainable development*. New York: United Nations, Department of Economic and Social Affairs.

- van der Valk, A. G., & Davis, C. B. (1978). The Role of Seed Banks in the Vegetation Dynamics of Prairie Glacial Marshes. *Ecology*, 59(2), 322–335. <https://doi.org/10.2307/1936377>
- van der Valk, A. G., & Davis, C. B. (1976). Changes in the composition, structure, and production of plant communities along a perturbed wetland coenocline. *Vegetatio*, 32(2), 87–96. <https://doi.org/10.1007/bf02111903>
- van der Valk, A. G., Pederson, R. L., & Davis, C. B. (1992). Restoration and creation of freshwater wetlands using seed banks. *Wetlands Ecology and Management*, 1(4), 191–197. <https://doi.org/10.1007/bf00244924>
- van Klink, R., Ruifrok, J. L., & Smit, C. (2016). Rewilding with large herbivores: Direct effects and edge effects of grazing refuges on plant and invertebrate communities. *Agriculture, Ecosystems & Environment*, 234, 81–97. <https://doi.org/10.1016/j.agee.2016.01.050>
- Van Belzen, J., Fivash, G. S., Hu, Z., Bouma, T. J., & Herman, P. M. (2022). A probabilistic framework for windows of opportunity: The role of temporal variability in critical transitions. *Journal of The Royal Society Interface*, 19(190). <https://doi.org/10.1098/rsif.2022.0041>
- Voslamber, B., & Vulink, J. T. (2010). Experimental manipulation of water table and grazing pressure as a tool for developing and maintaining habitat diversity for Waterbirds. *Ardea*, 98(3), 329–338. <https://doi.org/10.5253/078.098.0307>
- Verhoeven, J., Koerselman, W., & Meuleman, A. (1996). Nitrogen- or phosphorus-limited growth in herbaceous, wet vegetation: Relations with atmospheric inputs and management regimes. *Trends in Ecology & Evolution*, 11(12), 494–497. [https://doi.org/10.1016/s0169-5347\(96\)10055-0](https://doi.org/10.1016/s0169-5347(96)10055-0)
- Vroom, R. J., Temmink, R. J., Van Dijk, G., Joosten, H., Lamers, L. P., Smolders, A. J., Krebs, M., Gaudig, G., & Fritz, C. (2020). Nutrient dynamics of sphagnum farming on rewetted bog grassland in NW Germany. *Science of The Total Environment*, 726, 138470. <https://doi.org/10.1016/j.scitotenv.2020.138470>
- Vulink, J. T., & Van Eerden, M. R. (1998). Hydrological conditions and herbivory as key operators for ecosystem development in Dutch artificial wetlands. In *Grazing and conservation management* (pp. 215–248). Springer Netherlands.
- Vulink, J. T., Drost, H. J., & Jans, L. (2000). The influence of different grazing regimes on phragmites- and shrub vegetation in the well-drained zone of a eutrophic wetland. *Applied Vegetation Science*, 3(1), 73–80. <https://doi.org/10.2307/1478920>
- Wigbels, V. L. (1990). *Wetland Management in the Oostvaardersplassen*. Den Haag: Ministerie van Verkeer en Waterstaat.
- Wallisdevries, M. F., Wieren, S. E., & Bakker, J. P. (1998). *Grazing and conservation management*. Springer Netherlands.
- Xu, X., Chen, M., Yang, G., Jiang, B., & Zhang, J. (2020). Wetland ecosystem services research: A critical review. *Global Ecology and Conservation*, 22, e01027. <https://doi.org/10.1016/j.gecco.2020.e01027>

Yu, J., Wang, X., Ning, K., Li, Y., Wu, H., Fu, Y., Zhou, D., Guan, B., & Lin, Q. (2012). Effects of salinity and water depth on germination of *Phragmites australis* in coastal wetland of the Yellow River delta. *CLEAN - Soil, Air, Water*, 40(10), 1154-1158. <https://doi.org/10.1002/clen.201100743>

Zhao, H., Zhou, R., Su, Y., Zhang, H., Zhao, L., & Drake, S. (2007). Shrub facilitation of desert land restoration in the Horqin sand land of Inner Mongolia. *Ecological Engineering*, 31(1), 1-8. <https://doi.org/10.1016/j.ecoleng.2007.04.010>

Zhang, L., & Shao, H. (2013). Direct plant–plant facilitation in coastal wetlands: A review. *Estuarine, Coastal and Shelf Science*, 119, 1-6. <https://doi.org/10.1016/j.ecss.2013.01.002>

Zhang, C., Wen, L., Wang, Y., Liu, C., Zhou, Y., & Lei, G. (2020). Can Constructed Wetlands be Wildlife Refuges? A Review of Their Potential Biodiversity Conservation Value. *Sustainability*, 12(4), 1442. <https://doi.org/10.3390/su12041442>

Zhang, L., Lan, S., Angelini, C., Yi, H., Zhao, L., Chen, L., & Han, G. (2021). Interactive effects of crab herbivory and spring drought on a *Phragmites australis*-dominated salt marsh in the Yellow River Delta. *Science of the Total Environment*, 766, 144254. <https://doi.org/10.1016/j.scitotenv.2020.144254>

Appendix A

Species List		
Number	Scientific name	Code
1	<i>Juncus effusus</i>	JUEF
2	<i>Poa annua</i>	POAN
3	<i>Rorippa palustris</i>	ROPA
4	<i>Ranunculus sceleratus</i>	RASC
5	<i>Epilobium hirsutum</i>	EPHI
6	Old Vegetation	OLVE
7	<i>Salix sp.</i>	SASP
8	<i>Menta aquatica</i>	MEAQ
9	<i>Rumex maritimus</i>	RUMA
10	<i>Typha sp.</i>	TYSP
11	Kieplant	KIEM
12	<i>Tephrosia palustris</i>	TEPA
13	<i>Phragmites australis</i>	PHAU
14	<i>Carduus sp.</i>	CASP
15	<i>Juncus bufonius</i>	JUBU
16	<i>Solanum dulcamara</i>	SODU
17	<i>Atriplex prostrata</i>	ATPR
18	<i>Bidens tripartita</i>	BITR
19	<i>Persicaria maculosa</i>	PEMA
20	<i>Matricaria chamomilla</i>	MACH
21	<i>Oxybasis rubra</i>	OXRU
22	<i>Tephrosia palustris</i>	TEPA
23	<i>Epilobium montanum</i>	EPMO
24	<i>Lycopus europaeus</i>	LYEU
25	<i>Rumex hydrolapathum</i>	RUHY
26	<i>Bidens frondosa</i>	BIFR
27	<i>Alopecurus aequalis</i>	ALAE
28	<i>Eupatorium cannabinum</i>	EUCA
29	<i>Taraxacum officinale</i>	TAOF
30	<i>Veronica anagallis-aquatica</i>	VEAN
31	<i>Limosella aquatica</i>	LIAQ
32	<i>Bidens cernua</i>	BICE
33	<i>Eleocharis sp.</i>	ELSP
34	<i>Sambucus nigra</i>	SANI

Table 1. List of species presented in OVP.

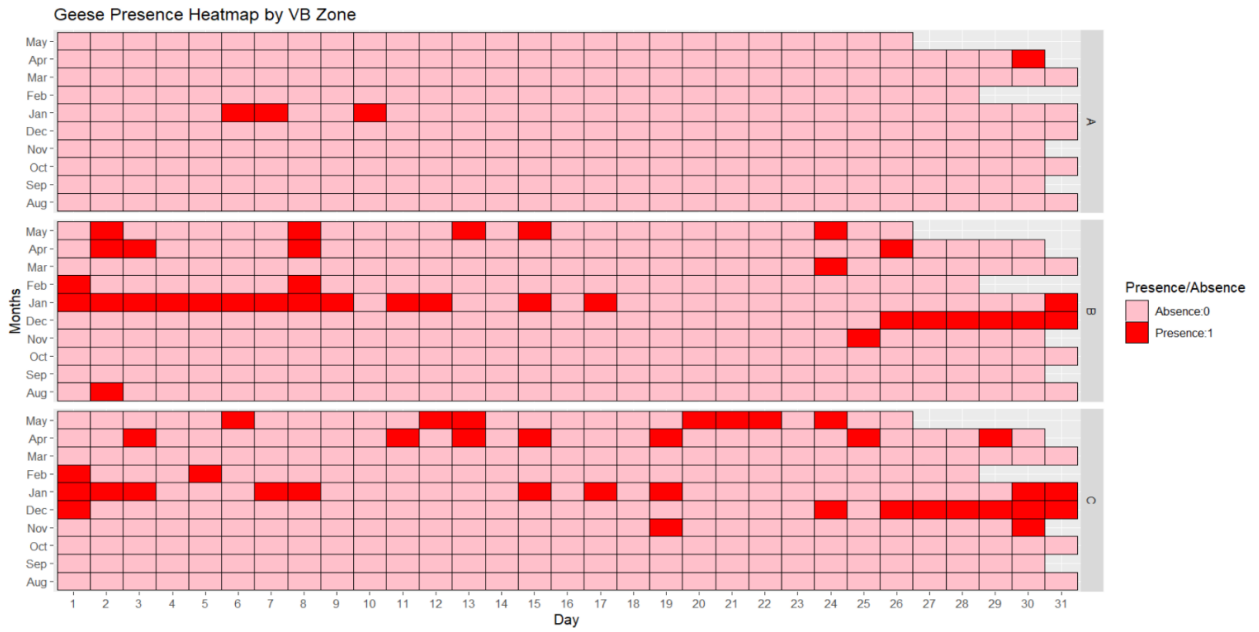


Figure 1. Geese heatmap across time in vegetation border zones.

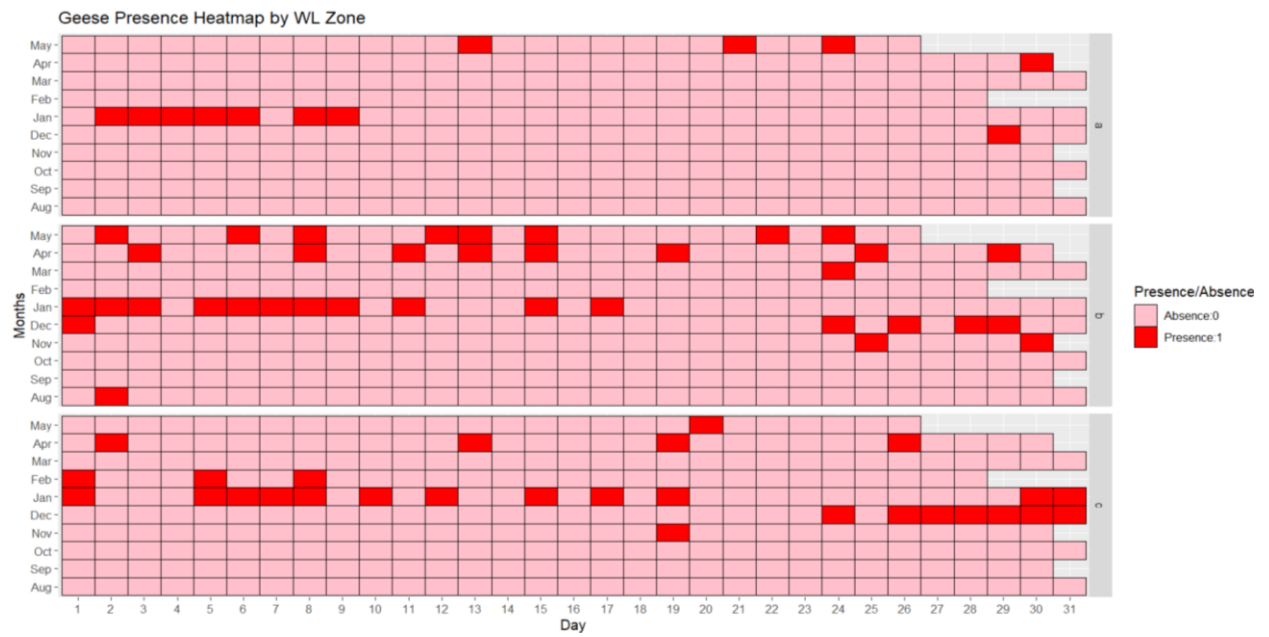


Figure 2. Geese heatmap across time in water level zones.



Image 1. Mammals' identification by Artificial Intelligence. The red squares highlight the location of deer (the target animal) within the entire image. Then, this image was cropped in three, because there were three animals in the same image. Therefore, after all the image processing 3 cropped images with the same date and time will be obtained. The Numbers mean the model's confidence level in the identification.