Freshwater Biology

WILEY

Freshwater Biology

ORIGINAL ARTICLE OPEN ACCESS

Effects of Goose Herbivory on Littoral Vegetation and Aquatic Macroinvertebrates During Breeding Season

Elsie Kjeller[1,2] | Céline Arzel[3] | Johan Elmberg[1] | Pär Söderquist[1] | Gunnar Gunnarsson[1]

[1]Department of Environmental Science, Kristianstad University, Kristianstad, Sweden | [2]Department of Biology and Environmental Science, Linnaeus University, Kalmar, Sweden | [3]Department of Biology, University of Turku, Turku, Finland

Correspondence: Elsie Kjeller (elsie.kjeller@hkr.se)

Received: 20 December 2024 | **Revised:** 26 June 2025 | **Accepted:** 26 September 2025

Funding: The study was supported by the Swedish Environmental Protection Agency (grants 2020-00099 and 2023-00006). The contribution by CA is supported by grant 333,400 from the Research Council of Finland.

Keywords: exclosure study | grazing | greylag goose | waterbirds | wetland ecosystem

ABSTRACT

1. During recent decades, increased populations of geese have raised concerns about their potential impact on the abundance and composition of shoreline vegetation through grazing, and how this may affect other organisms relying on the same vegetation for food or refuge.
2. We investigated the direct effects of goose grazing on shoreline vegetation and the potential indirect effects on aquatic macroinvertebrates, assessed through an exclosure experiment. The study was carried out over one growing season (March–August) in ten eutrophic wetlands with varying goose density, all located in agricultural landscapes in southern Sweden. We predicted that exclosures protected from grazing would have higher vegetation aboveground biomass, height, cover and species diversity (H′), as well as greater macroinvertebrate total abundance, taxon richness and taxon diversity compared to control plots.
3. Aboveground biomass was 27% higher in exclosures. However, goose density correlated positively with vegetation cover (%) and species diversity, but negatively with vegetation height. Aquatic macroinvertebrate total abundance was significantly lower in exclosures, whereas neither taxon richness nor diversity differed between controls and exclosures. Moreover, the total abundance of aquatic invertebrates was generally higher in wetlands with moderate goose density. No significant associations were found between goose density and taxon richness or diversity of macroinvertebrates.
4. In conclusion, predictions regarding direct grazing effects on vegetation were confirmed only for aboveground biomass. However, in some sites, dense stands of reed and cattails may have reduced grazing pressure by physically restricting accessibility. Additionally, substantial differences in vegetation species composition among study sites contributed to high data variability, which potentially could have masked treatment effects.
5. The results add to a growing number of studies suggesting that geese do not invariably cause or contribute to the degradation of aquatic ecosystems, at least in highly productive wetlands and when goose density is moderate. Our study highlights the need for more experiments investigating the grazing effects of large herbivorous waterbirds in aquatic ecosystems in different environmental settings. Identifying thresholds at which grazing effects begin to impact the ecosystem would provide a valuable tool for wildlife and wetland management.

Freshwater Biology, 2025; 70:e70114
https://doi.org/10.1111/fwb.70114

1 | Introduction

Plant-herbivore interactions are central for wetland functioning because vegetation has a key structuring role, for example, affecting nutrient flow and providing habitat for both aquatic and semi-aquatic organisms (Engelhardt and Ritchie 2001; Ma et al. 2010; Law et al. 2019). In recent decades, herbivorous waterfowl have been presumed to significantly reduce wetland vegetation, yet results vary among grazing studies, and little is known about the indirect effects of grazing on other aquatic organisms (e.g., Vymazal and Krőpfelová 2005, Valkama et al. 2008, Buij et al. 2017, Wood et al. 2017). Such potential top-down effects are of particular concern in freshwater wetlands undergoing negative environmental changes, such as eutrophication and biodiversity loss (Bakker et al. 2016).

Geese represent conservation concerns since several populations have reached unprecedented size, largely explained by increased food availability on arable land and favourable climatic conditions (Fox and Madsen 2017; Liljebäck et al. 2021). While grazing pressure generally increases with both bird density (Wood et al. 2017) and the duration of stay (Gayet et al. 2011), even relatively low densities can have significant impacts in eutrophic systems. This can be attributed to increased palatability and nutrient content of vegetation growing in nutrient-rich wetlands (Bakker and Nolet 2014). Studies show that even low densities of smaller omnivorous waterbirds, such as mallard *Anas platyrhynchos* and Eurasian coot *Fulica atra*, can increase turbidity in eutrophic systems by reducing the amount of submerged vegetation, which plays a crucial role in maintaining clear water (Lauridsen et al. 1993; Perrow et al. 1997; van Altena et al. 2016).

While top-down effects of waterfowl grazing on submerged vegetation are well documented (Søndergaard et al. 1996, Hansson et al. 2010), less is known about the effects on different types of emergent vegetation. This includes common reed *Phragmites australis*, cattails *Typha* spp., graminoids and other herbaceous plants that grow along wetland shorelines. Moreover, there seems to be no consensus whether substantial grazing by waterfowl on this type of vegetation is detrimental or not. While some studies, for example Bakker et al. (2018), found that grazing by greylag geese *Anser anser* has a negative impact on littoral vegetation stands, others argue that it can be beneficial, as their grazing may increase vegetation diversity and heterogeneity by reducing interspecific competition among plants when feeding on species that otherwise become dominant (Gough and Grace 1998; Reijers et al. 2019).

Composition of plant species in the wetland littoral may affect not only nutrient retention, hydrologic flow and erosion, but also abundance and diversity of aquatic macroinvertebrates (Vymazal and Krőpfelová 2005, Valkama et al. 2008). From a top-down perspective on grazing effects, it is essential to consider macroinvertebrates, especially given their positive influence on abundance and reproductive success of many waterbird species (Čehovská et al. 2022; Gunnarsson et al. 2024), several of which are experiencing widespread declines (Reid et al. 2019, Rosenberg et al. 2019). Macroinvertebrates are not only important food sources for higher trophic levels, but essential in their own right, driving key processes such as detritus decomposition and bioturbation (e.g., Covich et al. 1999; Mermillod-Blondin et al. 2008). However, research on indirect effects of waterfowl grazing on macroinvertebrates remains limited, particularly in experimental contexts. Previous experiments addressing potential indirect relationships have rather focused on submerged vegetation, where no significant differences in total macroinvertebrate biomass or abundance were found between grazed and ungrazed sites (Marklund et al. 2002; Allin and Husband 2003). Conversely, observational studies have found an abundance of aquatic macroinvertebrates to increase with increasing goose density (Jensen et al. 2019, Flemming et al. 2022, Gunnarsson et al. 2024). However, this relationship has been primarily attributed to increased nutrient enrichment from goose defecation rather than grazing effects per se.

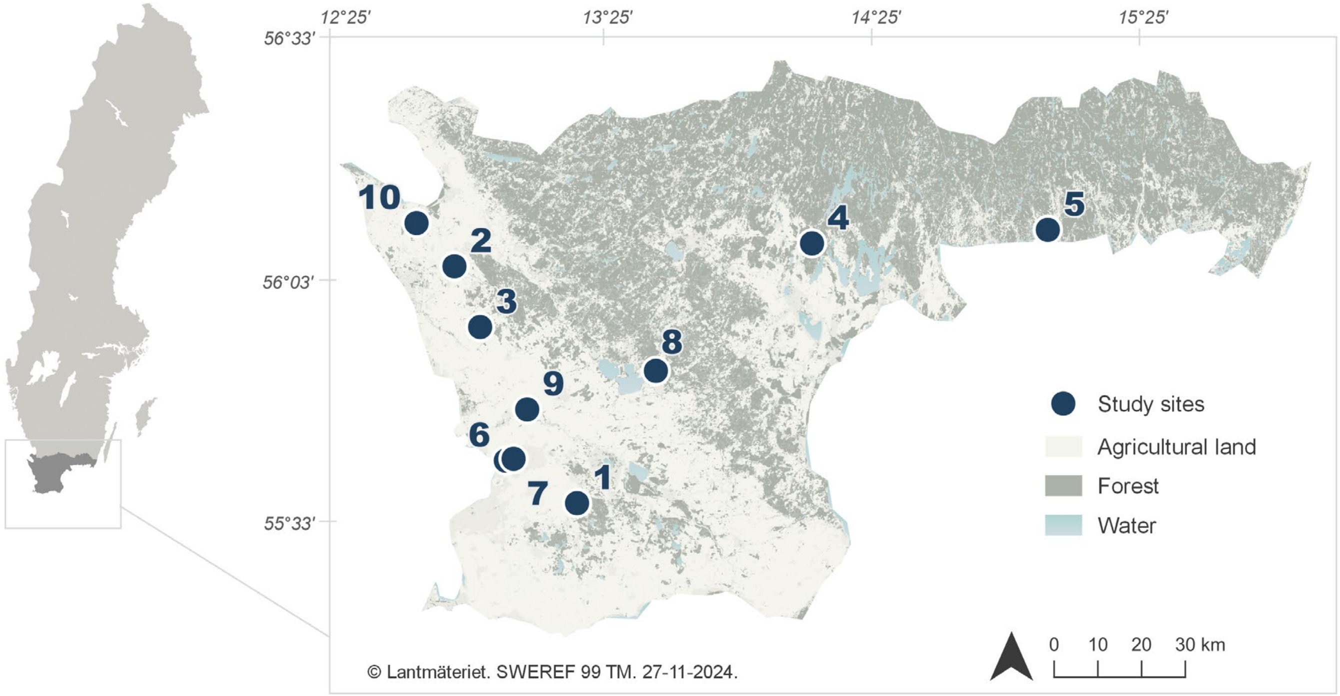
To test whether herbivory by large waterfowl such as geese can cause direct top-down effects on shoreline vegetation and indirect effects on aquatic macroinvertebrates, we conducted a grazing experiment in ten eutrophic wetlands with different goose densities in southern Sweden during their breeding season. Littoral vegetation and macroinvertebrate variables were compared between exclosures and open control plots at the end of one growing season. We hypothesised that geese negatively affect vegetation as well as macroinvertebrates, and specifically predicted (1) vegetation outside the exclosures to have lower aboveground biomass, height, cover, and species diversity (H′), leading to (2) lower abundance, taxon richness and taxon diversity (H′) of aquatic macroinvertebrates.

2 | Methods

2.1 | Study Sites

The study was carried out in wetlands located in southern Sweden (Figure 1), primarily in the province of Skåne (Scania), a region typically characterised by intensive agriculture and situated within the nemoral zone (Persson et al. 2010; Nilsson et al. 2013). We identified wetlands used by breeding geese by searching for reported sightings of *Anser* or *Branta* species from 2017 to 2021 using "Artportalen", a public Swedish species observation data base (https://www.artportalen.se/). To obtain additional information, local ornithologists and landowners were contacted. Ten wetlands were selected, ranging from 2.1 to 15.0 ha (mean ± SD: 4.7 ± 3.7). They were selected based on the following criteria: recent observations of breeding geese, location in agricultural landscapes, similar wetland sizes, absence of significant disturbance (e.g., recreational activities, adjacent settlements or major nearby roads) and accessibility for our experimental setup. The wetlands were surrounded by either pastures or cultivated fields with cereal crops. All selected wetlands were either restored or constructed several decades ago, allowed to develop naturally and can be considered representative of the study area. Six of the wetlands had shorelines dominated by tall, dense stands of common reed *P. australis* and cattails *Typha* spp., while the remaining four had shorelines characterised by lower graminoids and forbs (Table 1, Figure 2a).

To gather background information about the wetlands, we conducted four monthly surveys in 2022 (April 4–5, May 6–10, June 7–9 and July 12–13), collecting data on physiochemistry



© Lantmäteriet. SWEREF 99 TM. 27-11-2024.

FIGURE 1 | Map showing the study area in Sweden (left) and the locations of the ten wetland study sites in Skåne and Blekinge counties (right).

TABLE 1 | Wetland ID (see Figure 1), coordinates, dominating vegetation, size and goose density of adult breeding individuals and their young. The latter is given as the number of individuals per hectare, as well as by categories.

Site	Location coordinates	Dominating vegetation	Size (ha)	Goose density (individuals ha^{-1})	Goose density classification
1[a]	55°36′ N 13°22′ E	Reed	2.9	0.7	Low
2[a]	56°05′ N 12°53′ E	Reed/cattails	4.7	0.0	Low
3	55°58′ N 12°59′ E	Reed/cattails	6.1	3.9	Moderate
4[a]	56°09′ N 14°12′ E	Reed/cattails	3.5	4.6	Moderate
5	56°11′ N 15°04′ E	Graminoids/forbs	15.0	14.4	High
6[a]	55°41′ N 13°06′ E	Reed/cattails	5.6	11.9	High
7	55°42′ N 13°07′ E	Reed	2.1	0.0	Low
8	55°53′ N 13°36′ E	Graminoids/forbs	2.4	4.1	Moderate
9	55°48′ N 13°10′ E	Graminoids/forbs	2.4	21.3	High
10	56°10′ N 12°45′ E	Graminoids/forbs	2.4	15.4	High

[a] Wetlands sampled for macroinvertebrates.

and waterbird communities, using the same methods as in Gunnarsson et al. (2024). For physiochemistry data, a water sample was taken from the littoral zone of each wetland. Physiochemistry data included pH, chlorophyll ($\mu\text{g L}^{-1}$), turbidity (NTU), water colour (abs λ420 nm), total phosphorus ($\mu\text{g L}^{-1}$) and total nitrogen (mg L^{-1}). Overall, pH was neutral to alkaline (8.2 ± 0.8), and values were moderate to high for water colour (0.2 ± 0.2) as well as turbidity (28.9 ± 25.2 NTU). Concentrations of chlorophyll and nutrients indicated that wetlands were eutrophic to hypertrophic (chlorophyll: $47.3 \pm 36.9\,\mu\text{g L}^{-1}$; total phosphorus: $85.1 \pm 92.8\,\mu\text{g L}^{-1}$; total nitrogen: $1.6 \pm 1.0\,\text{mg L}^{-1}$). Detailed information about physiochemistry variables per wetland is given in Data S1.

Waterbird data were collected using the point count method (Koskimies and Väisänen 1991), with observations made from consistent vantage points at each wetland. Counts of breeding individuals and their young (> 3 weeks of age) were summed and separated from non-breeders (Koskimies and Väisänen 1991). This distinction was made because breeding individuals, particularly geese, are likely to use the same wetland more consistently during the breeding season than do non-breeders (e.g., Nilsson and Persson 1992; Olsson et al. 2017), potentially providing a more representative measure of grazing pressure at our study sites. All counts were then converted to density (individuals per wetland hectare) for each species; the maximum count among the four surveys was used to represent a species' density

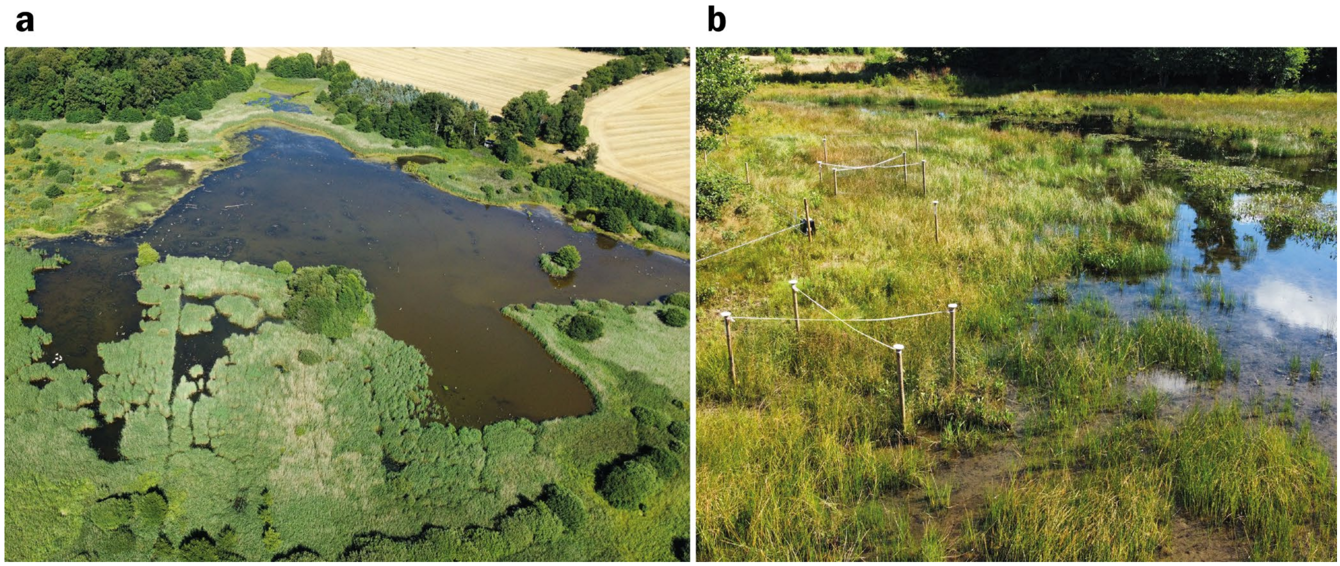


FIGURE 2 | Photos of (a) reed-dominated study site and (b) exclosure in the study site with the shoreline dominated by graminoids and forbs.

at a site. In total, 40 waterbird species were recorded, of which 27 were breeding. The average number of total species per wetland was 15.5 ± 4.4, while the average number of breeding species was 10 ± 3.1. The most common breeders were mallard *A. platyrhynchos*, Eurasian coot *F. atra* and greylag goose *A. anser*. Detailed information about waterbird density and their occurrence is given in Data S2. Regarding geese, the greylag goose is bred in eight wetlands, the Canada goose *Branta canadensis* in two and the barnacle goose *B. leucopsis* in one. All goose species were pooled to obtain a measure of total goose density (number of individuals ha^{-1}) at each site (Table 1), only including adult breeding individuals and their young. Goose densities were then further divided into three categories, denoted as "low" (0.2 ± 0.4 individuals ha^{-1}), "moderate" (4.2 ± 0.4 individuals ha^{-1}) or "high" (15.8 ± 4.0 individuals ha^{-1}), to be used in subsequent analyses. This categorisation was based on observed densities and intended to capture a realistic gradient of goose breeding density at wetlands in southern Sweden, from sparsely to more heavily used sites. Non-breeding geese were also recorded during surveys in nine of the wetlands. Their occurrence appeared to be mainly temporary, except for one high-density wetland (ID: 9; Table 1), where larger flocks were observed during all four surveys, including the moulting period (June–July).

2.2 | Grazing Experiment

To experimentally study effects of waterbird herbivory on shoreline vegetation and aquatic macroinvertebrates, we used the paired plot design (e.g., Sarneel et al. 2014), in which open ('grazed') control plots are paired with nearby fenced exclosures ('ungrazed'; Figure 2, Data S1). Thus, we compared vegetation and macroinvertebrate variables between plots that were either accessible or not to geese and other herbivorous waterbirds. Exclosures and control plots were installed in March (2022), prior to the arrival of breeding geese and the start of the growing season. Three pairs (plot size 2 × 3 m) were constructed in each of the ten wetlands, which resulted in 30 pairs in total. The plots were placed in water ca. 1 m from the shoreline, with their shortest side (2 m) oriented parallel to it. Pairs were placed in parts of the wetland having the most representative vegetation type (i.e., not based on a specific distance). Depending on the vegetation composition, pairs were not necessarily placed in the same vegetation type within a given site. Each exclosure consisted of four wooden poles, and it was enclosed by a polyethylene plastic net (mesh size 19 × 19 mm). Since we were mainly interested in the grazing effects of waterbirds and not of fish, a gap of approximately 15 cm was left at the bottom of the fence to allow fish to enter the exclosures (e.g., Hilt 2006; Tatu et al. 2007). Control plots were marked with a single wooden pole, placed in the centre of the plot about 5 m from its paired exclosure. Three of the wetlands were surrounded by pasture grazed by cattle. In those wetlands, an electric fence was erected around the experimental area to exclude cattle from grazing while still allowing geese to enter, which was confirmed by observed goose droppings and signs of goose grazing within the electrically fenced areas.

To avoid disturbance, sampling of vegetation and invertebrates took place at the end of the breeding season, in August 2022. At this time, vegetation biomass had also reached its peak (Karlsen et al. 2006). We only sampled within the 1 × 2 m inner area of each plot to avoid possible edge effects, e.g., shading. The sampled area was in turn divided into six subplots (0.5 × 0.5 m), two of which were systematically chosen for sampling of vegetation and two others for collecting invertebrates. Although the plots were placed in water during construction, they were dried out by August in six of the wetlands. As the dried plots remained accessible to goose grazing, they were included in the analyses of vegetation data. However, this meant that aquatic invertebrates could only be sampled in four of the ten wetlands.

2.2.1 | Vegetation Sampling

A 0.25 m^2 quadrat frame was used to delineate subplots in which vegetation height, cover and aboveground biomass were measured (16–22 August 2022). Height (cm) was only measured on emergent vegetation. It was obtained by averaging three measurements of each species (length of the tallest stems) in each subplot. Plant cover was measured for all present species within the sampling frame and estimated to the closest percentage value by two observers in the field. Lastly, we harvested the aboveground vegetation with hedge shears, including all vegetation except free-floating macrophytes, i.e., common duck weed (*Lemna minor*) and green algae (*Cladophora glomerata*). After harvesting, the vegetation was sorted into species and oven dried in an EHRET TK/L 4250 drying oven (EHRET GmbH, Mahlberg, Germany) at 60°C for ca. 48 h to obtain dry weight (g DW; e.g., Rivers and Short 2007).

2.2.2 | Aquatic Macroinvertebrate Sampling

We used activity traps (Murkin et al. 1983) to sample nektonic and benthic invertebrates within the paired plots. One trap was placed in each of the two subplots (i.e., two per plot) for 48 h. Activity traps consisted of a glass jar (1 L) with a funnel (opening radius: 102 mm, narrow end radius: 23 mm) attached to its opening (Gunnarsson et al. 2024). They were placed with the opening parallel to the shoreline, all facing the same direction within a wetland (Elmberg et al. 1993). When emptying activity traps, the contents were counted and sorted by taxonomic groups following a protocol modified from Nudds and Bowlby (1984) (for details, see Data S4). Small fish and amphibians that unintentionally became bycatch were also recorded in the protocol as they are important prey for waterbirds. We recorded two traps containing nine-spine stickleback (*Pungitus pungitus*) and one containing European eel (*Anguilla anguilla*), with one individual per trap of respective species. Ten traps contained smooth newt (*Lissotriton vulgaris*), and one adult frog (*Pelophylax kl. esculentus*). Previous studies suggest that fish and newts may affect the catches of invertebrates in activity traps (Elmberg et al. 1992). Nevertheless, we did not find any such effects in our catches, i.e., on taxon richness and the abundance of invertebrates (separate paired t-tests for fish and newts; taxon richness ($p \geq 0.319$), total abundance ($p \geq 0.552$); cf. Gunnarsson et al. 2024). Samples, including fish and newts, were therefore retained for the statistical analyses.

2.3 | Data Analyses

All data exploration and statistical analyses were done using the R 4.3.0 software (R Core Team 2023). Prior to statistical analysis, datasets were explored for outliers, distribution patterns, collinearity among variables and homogeneity of variance (Zuur et al. 2010). Data were then analysed using linear mixed models (LMMs) and generalised linear mixed models (GLMMs) with nested random effects. Model fit and assumptions such as normality and homoscedasticity of residuals were evaluated by graphic tools as well as diagnostics in the package DHARMa (Hartig 2022). For details on DHARMa diagnostics of each model, see Data S5. The package lme4 (Bates et al. 2015) was used to fit separate LMMs for vegetation cover, height, aboveground biomass and Shannon diversity index (H′) of plant species and macroinvertebrate taxa. We used the glmmTMB package (Brooks et al. 2017) to fit GLMMs of the total abundance of macroinvertebrates separately.

2.3.1 | Direct Grazing Effects on Vegetation

To test whether grazing affected aboveground biomass, height, cover and species diversity (H′) of vegetation, we built separate LMMs for each of these response variables. To meet normality, biomass was log transformed, vegetation cover was arcsine transformed, while height and diversity (H′) were left untransformed. Fixed factors were treatment (control vs. exclosure plots) and goose density class. The fixed structure for each model was evaluated by maximum likelihood estimation (Zuur et al. 2009). Random effects were site and pair (paired exclosure and control plot), with pair nested within site. They were fitted with a random intercept.

2.3.2 | Indirect Grazing Effects on Aquatic Macroinvertebrates

To test whether grazing indirectly affected total abundance, taxon richness and taxon diversity (H′) of aquatic macroinvertebrates, we built separate GLMMs for the two former response variables and an LMM for the latter. Neither of the response variables was transformed. The distribution family in the R software was specified as negative binomial for total abundance, and Conway–Maxwell–Poisson for taxon richness. In all three models, fixed factors were treatment (control vs. exclosure plots) and goose density (same as above). The fixed structure of each model was determined by maximum likelihood estimation (Zuur et al. 2009). Since we had fewer samples for macroinvertebrates and aimed not to overfit models, we also explored the optimal random structure for each of these models. This was done by comparing models with both random effects (site and pair nested within site) to models with only one (pair nested within site) using restricted maximum likelihood (Zuur et al. 2009) and evaluating the random effect estimates.

3 | Results

3.1 | Direct Grazing Effects on Vegetation

Aboveground biomass was 27% higher ($\beta = 0.24$, $SE = 0.10$) in exclosures compared to open control plots (LMM, $t = 2.40$, $p = 0.023$; Table 2). No significant differences in biomass were found between goose density classes (LMM, low vs. high $t = 1.73$, $p = 0.128$, moderate vs. high $t = -0.43$, $p = 0.683$). According to the ICC (intraclass correlation coefficient) of this model, 61% of the total variance was due to among-site differences (Data S6).

Vegetation height did not differ significantly between treatments (LMM, $t = 1.51$, $p = 0.142$). However, the height in both exclosure and control plots was significantly related to goose density (Table 2). Specifically, emergent vegetation in general (i.e., in both control and exclosure plots) appeared to be taller in wetlands with low compared to high goose density (LMM, $\beta = 111.73$, $SE = 41.44$, $t = 2.70$, $p = 0.031$; Figure 3). According to the ICC of this model, 82% of the total variance was due to among-site differences (Data S6).

Cover (%) was also unaffected by treatment (LMM, $t = -0.01$, $p = 0.989$), but it was significantly associated with goose density

TABLE 2 | Linear mixed model results of fixed effects on vegetation aboveground biomass (log transformed), height, cover (arcsine transformed) and species diversity H′. The table includes β (estimates), SE (standard error), t-value and p-value (significant threshold $p < 0.05$*).

	β	SE	t	p
Aboveground biomass (log)				
Intercept	4.97	0.22	22.23	**< 0.001***
Treatment (exclosure)[a]	0.24	0.10	2.40	**0.023***
Goose density (low)[b]	0.58	0.33	1.73	0.128
Goose density (moderate)[c]	−0.14	0.33	−0.43	0.683
Height				
Intercept	91.67	27.35	3.35	**0.012***
Treatment (exclosure)[a]	10.40	6.90	1.51	0.142
Goose density (low)[b]	111.73	41.44	2.70	**0.031***
Goose density (moderate)[c]	10.78	41.44	0.26	0.802
Cover (arc)				
Intercept	1.18	0.11	10.41	**< 0.001***
Treatment (exclosure)[a]	< 0.01	0.04	−0.01	0.989
Goose density (low)[b]	−0.42	0.17	−2.47	**0.043***
Goose density (moderate)[c]	−0.46	0.17	−2.70	**0.031***
Species diversity H′				
Intercept	0.62	0.11	5.75	**< 0.001***
Treatment (exclosure)[a]	−0.02	0.06	−0.33	0.741
Goose density (low)[b]	−0.44	0.16	−2.76	**0.028***
Goose density (moderate)[c]	−0.05	0.16	−0.31	0.768

[a] Exclosure treatment (ungrazed) compared to control (grazed).
[b] Low goose density compared to high goose density.
[c] Moderate goose density compared to high goose density.

(Table 2). In general, cover was substantially lower in wetlands with low and moderate goose densities, compared to high (LMM, low: $\beta = -0.42$, SE = 0.17, $t = -2.47$, $p = 0.043$; moderate: $\beta = -0.46$, SE = 0.17, $t = -2.70$, $p = 0.031$; Figure 3). According to the ICC of this model, 70% of the total variance was due to among-site differences (Data S6).

Across all wetlands, we recorded 33 vegetation species in the experimental plots, with a mean of 6.7 ± 3.6 per wetland. The most common species were common spike-rush (*Eleocharis palustris*), reed canary grass (*Phalaris arundinacea*) and common reed (*P. australis*), recorded at seven, six and five wetlands, respectively (Data S7). No significant difference in diversity (H′) of vegetation species was found between exclosure and control plots (LMM, $t = -0.33$, $p = 0.741$). However, species diversity was significantly associated with goose density, being lower in wetlands with low compared to high densities (LMM, $\beta = -0.44$, SE = 0.16, $t = -2.76$, $p = 0.028$; Table 2). Based on ICC, 59% of the total variance was due to among-site differences (Data S6).

3.2 | Indirect Grazing Effects on Aquatic Macroinvertebrates

Total abundance of macroinvertebrates was affected by treatment and associated with goose density (Table 3). It was significantly lower in exclosures compared to open control plots (GLMM, $\beta = -0.52$, SE = 0.10, $z = -5.40$, $p < 0.001$), and generally lower in wetlands with low compared to high goose density (GLMM, $\beta = -0.71$, SE = 0.19, $z = -3.78$, $p < 0.001$). Interestingly, the highest macroinvertebrate abundance was observed for moderate goose density, which was significantly higher than in wetlands with high goose density (GLMM, $\beta = 0.49$, SE = 0.20, $z = 2.44$, $p = 0.015$; Figure 4). According to the ICC of this model, 43% of the total variance was due to among-site differences (Data S8).

A total of 20 aquatic macroinvertebrate taxa were recorded, on average 3.0 ± 1.3 taxa per wetland. Most abundant taxa, present in all four wetlands, in descending order were: predaceous diving beetles ("Coleoptera-Dytiscidae"), lesser water boatmen ("Heteroptera-Corixidae"), copepods ("Copepoda"), gastropods ("Gastropoda-others") and mayflies ("Ephemeroptera"; Data S9). Neither richness nor diversity (H′) of macroinvertebrate taxa differed significantly between exclosure and control plots (taxon richness: GLMM, $z = -0.41$, $p = 0.680$; diversity: LMM, $t = -0.34$, $p = 0.742$; Table 3). In addition, we found no differences between low and high goose density for either of the variables (taxon richness: GLMM, $z = -1.60$, $p = 0.110$; diversity: LMM, $t = -1.24$, $p = 0.247$), nor between moderate and high goose density (taxon richness: GLMM, $z = -1.18$, $p = 0.236$; diversity: LMM, $t = -2.11$, $p = 0.065$). Based on ICC, < 1% and 44% of the total variance was due to among-site differences for these models, respectively (Data S8).

4 | Discussion

This study investigated top-down effects of waterfowl grazing in wetlands with different densities of breeding geese by comparing open control plots and exclosures. We predicted that height, cover, aboveground biomass and species diversity (H′) of littoral vegetation would be lower in control plots, resulting in lower abundance, taxon richness and taxon diversity of aquatic macroinvertebrates. We found mixed effects on vegetation and macroinvertebrates. Among the vegetation response variables, only aboveground biomass showed a significant treatment effect in line with the prediction, being higher in exclosures. In contrast, vegetation height, cover and species diversity were significantly associated with goose density, but not with exclosure treatment

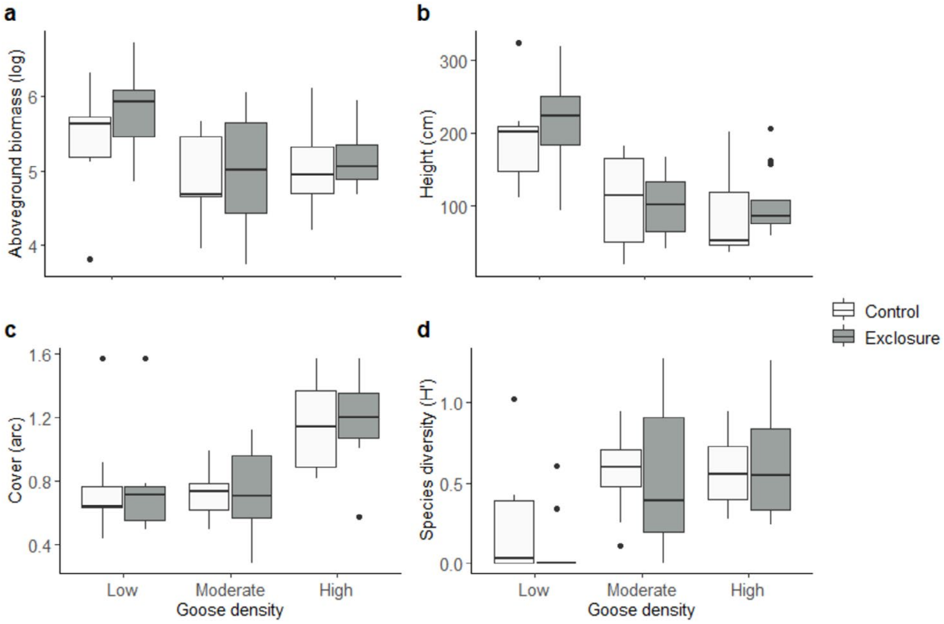


FIGURE 3 | Box plots of vegetation (a) aboveground biomass (g DW; log transformed), (b) height (cm), (c) cover (%; arc transformed) and (d) species diversity (H′) across goose density classes and between control and exclosure plots.

itself. In macroinvertebrates, only total abundance was affected by the treatment, being lower in exclosures, and it, too, was significantly associated with goose density.

4.1 | Direct Grazing Effects on Vegetation

We speculate that most of the vegetation variables were unaffected by the treatment because grazing pressure outside exclosures may not have been high enough across all study sites for a significant impact to arise. van Zuidam et al. (2022) found similar patterns when investigating submerged macrophytes, grazed mainly by mute swans (*Cygnus olor*). In their exclosure study, biomass outside exclosures was reduced by 50%, while cover remained as high as about 90% of that in the ungrazed area. On the other hand, Sarneel et al. (2014), who studied grazing effects of mixed waterfowl assemblages (including greylag geese) and herbivorous muskrat (*Ondatra zibethicus*) on littoral vegetation in wetlands, found aboveground biomass, cover and species richness all to be significantly reduced in the open control plots compared to exclosures after one growing season. Their plots were dominated by common reed, greater sweet grass (*Glyceria maxima*) and cattail species. In contrast, species composition in our plots varied more among study sites than between treatments, possibly masking grazing effects on specific species or groups (Geho et al. 2007; Veen et al. 2013). Furthermore, as Sarneel et al. (2014) included muskrat in their study, grazing pressure may have been higher overall compared to in our study, in which geese were the main obligate herbivores. Most of our study wetlands (seven out of ten) also hosted mute swans (Data S2), but we believe these herbivores had a negligible effect on the results since they mainly forage on submerged macrophytes in deeper water (Cramp et al. 1986).

We expected the treatment effect to vary with goose density, as grazing pressure in general tends to increase with increasing herbivore density (e.g., Wood et al. 2017). However, goose density did not interact significantly with the treatment effect in any of the vegetation response models. This is somewhat surprising given that grazing effects have been reported at similar goose densities elsewhere. From the Netherlands, Bakker et al. (2018) reported that a five-year exclusion of greylag geese resulted in both height and stem density of common reed being reduced four-fold in open control plots. Maximum goose density during May–August between those five years varied from 2.8–5.3 individuals ha^{-1}, which is comparable to our moderate goose density class. Furthermore, they found that the difference in reed stem density between exclosures and controls increased over time, although the proportion of grazed stems varied between years. Reed height, on the other hand, was significantly reduced regardless of time (Bakker et al. 2018). Altogether, their findings suggest that our shorter study duration might explain the lack of relationship between grazing pressure and goose density only to some extent, as certain vegetation variables may respond differently to grazing in relation to time. It is possible that the lack of relationship also could be associated with the goose density measure used in our study, as vegetation reduction has been shown to correlate more strongly with waterfowl density when calculated as bird biomass per wetland hectare (Wood et al. 2012, 2017). We chose to use the number of individuals instead because this allowed us to include young individuals, whose increasing body mass throughout the study period could have introduced uncertainty to density estimates. By not accounting for the lower body mass of young compared to adults, expected grazing pressure by density classes could potentially have been overestimated. At the same time, a potential overestimation could have been compensated for by non-breeding individuals observed at some of our study sites.

However, we did find general associations between vegetation (height, cover and species diversity) and goose density. In wetlands with high goose density (compared to low and moderate densities), vegetation height was generally lower in both control and exclosure plots, while cover and diversity were

TABLE 3 | Generalised linear mixed model results of fixed effects on macroinvertebrate total abundance and taxon richness, as well as results of fixed effects in the linear mixed model on taxon diversity (H′). The table includes β (estimates), SE (standard error), z-value, t-value and p-value (significant threshold $p < 0.05$*).

	β	SE	z	p
Total abundance				
Intercept	3.51	0.15	23.12	**<0.001***
Treatment (exclosure)[a]	−0.52	0.10	−5.40	**<0.001***
Goose density (low)[b]	−0.71	0.19	−3.78	**<0.001***
Goose density (moderate)[c]	0.49	0.20	2.44	**0.015***
Taxon richness				
Intercept	1.92	0.12	15.66	**<0.001***
Treatment (exclosure)[a]	−0.04	0.11	−0.41	0.680
Goose density (low)[b]	−0.22	0.14	−1.60	0.110
Goose density (moderate)[c]	−0.19	0.16	−1.18	0.236
	β	**SE**	**t**	**p**
Taxon diversity H′				
Intercept	1.56	0.17	9.16	**<0.001***
Treatment (exclosure)[a]	−0.03	0.10	−0.34	0.742
Goose density (low)[b]	−0.25	0.20	−1.24	0.247
Goose density (moderate)[c]	−0.48	0.23	−2.11	0.065

[a] Exclosure treatment (ungrazed) compared to control (grazed).
[b] Low goose density compared to high goose density.
[c] Moderate goose density compared to high goose density.

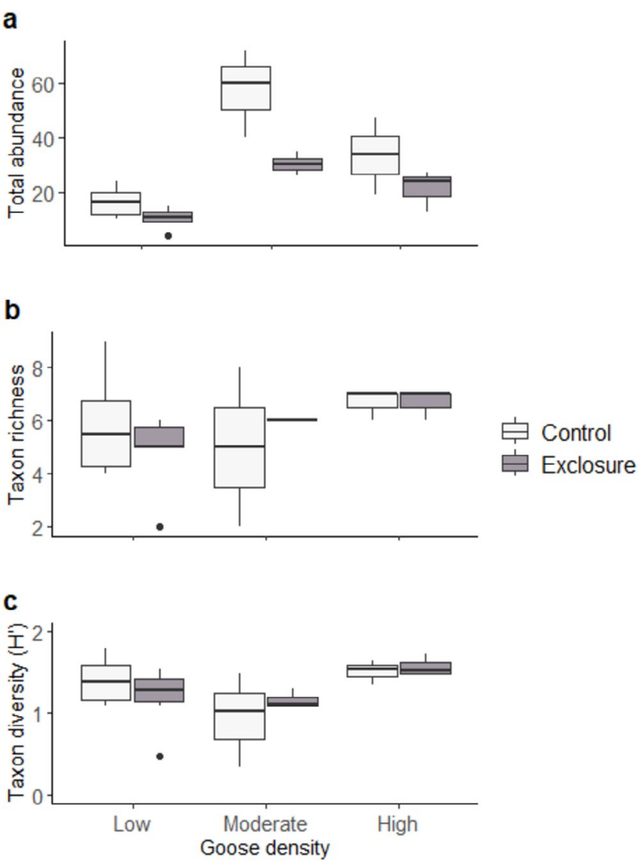


FIGURE 4 | Box plots of macroinvertebrate (a) total abundance, (b) taxon richness and (c) taxon diversity (H′) across goose density classes and between control and exclosure plots.

higher. Since there was no significant interaction in any of the vegetation response models, it is not possible to determine if these associations were in fact caused by geese. This outcome is perhaps more likely explained by the type of littoral vegetation surrounding the wetlands, i.e., suggesting that breeding geese are attracted to those with higher vegetation diversity and not dominated by tall species such as common reed and cattails. Although shorelines with tall vegetation may be suitable nesting sites for greylag geese (Kristiansen 1998), wetlands bordered by pastures with low vegetation (often grass swards) may be preferred as breeding sites, since they offer higher food availability and safer foraging conditions due to better visibility, enhancing predator detection (Olsson et al. 2017; Kleinhenz and Koenig 2018).

Other exclosure studies show that avian herbivores can increase plant diversity in eutrophic wetlands by targeting highly competitive species, thus providing relief for the less competitive (Gough and Grace 1998, Hidding et al. 2010). However, dense stands of competitive species like common reed and cattails may reduce overall grazing pressure by physically limiting grazer access (Svidenský et al. 2021; Temmink et al. 2022). Reijers et al. (2019) referred to this as "self-reinforcing feedback", where denser vegetation hinders herbivore access, which in turn leads to the accumulation of organic material in the vegetation stands, further inhibiting access. The authors tested this hypothesis by temporarily excluding greylag geese from parts of a highly productive marsh dominated by common reed. During the exclusion of geese, the reed expanded into previously open patches. This expansion did not reverse significantly after geese were reintroduced, as the birds instead favoured another species (sea clubrush *Bolboschoenus maritimus*). Consequently, Reijers et al. (2019) argued that reduced grazing pressure can lead to unfavourable homogeneous spatial vegetation structure in wetlands. Our study included several wetlands in which common reed and cattails grow in dense stands; yet, whether self-reinforcing processes explain the observed correlation between vegetation diversity and goose density, or the low treatment effects, are issues in need of further investigation.

4.2 | Indirect Grazing Effects on Aquatic Macroinvertebrates

Although taxon richness and diversity of aquatic macroinvertebrates were unaffected by our treatment, total macroinvertebrate abundance showed a significant unpredicted effect of the exclosures (lower abundance in exclosures). This is in line with similar findings from terrestrial habitats for mammal herbivores, i.e., abundance of macroinvertebrates being positively affected by livestock grazing (Seymour and Dean (1999), but see e.g., Ma et al. (2017) for contradicting results). However, in aquatic ecosystems, and to the best of our knowledge, no prior exclosure study has examined the combined effects of herbivorous waterbirds on both littoral vegetation and macroinvertebrates.

Among the few related studies we have found, only two were conducted in freshwater lakes, addressing grazing effects solely on submerged but not on emergent vegetation (Marklund et al. 2002; Matuszak et al. 2012). Comparisons with previous research are hence bound to be inferential and less straightforward. Matuszak et al. (2012) studied grazing effects by (mainly) Eurasian coot in Lake Constance (Central Europe) and found a strong reduction (40%) of submerged plant biomass but no significant difference in macroinvertebrate abundance inside versus outside exclosures. However, they carried out separate analyses for each taxon and not any for total abundance, and no geese were present in the study. Moreover, Marklund et al. (2002) conducted experiments with different treatments in a shallow eutrophic lake in southern Sweden, testing for effects of waterbirds as well as of fish on submerged macrophytes and macroinvertebrates. They observed no effect on vegetation or macroinvertebrates at moderate waterbird densities. However, they did find a significant negative correlation between the same variables in a literature review, suggesting that high densities of waterfowl can indeed cause a significant reduction of macroinvertebrates. The same authors cautioned that the comparison between their own experimental findings and evidence in their literature review was imperfect due to differences in waterfowl and macroinvertebrate taxa among studies (Marklund et al. 2002). In part, we acknowledge their suggestion of a grazing effect, based on our results showing higher macroinvertebrate abundances in moderate compared to high goose densities. However, we argue that patterns may not be linear, since our results also demonstrate that macroinvertebrate abundance is lower in wetlands with low compared to high goose densities. Thus, we propose that goose grazing may have a positive indirect effect on macroinvertebrates. Yet, further investigation is needed to determine the specific density threshold at which this effect is manifested. It also needs to be explored whether the relationship between geese and macroinvertebrates is due to actual grazing effects or increased nutrient input from goose faecal deposition, as the latter has also been suggested to enhance macroinvertebrate abundance (Jensen et al. 2019).

4.3 | Ecosystem View

Overall, we found some, but not fully conclusive, evidence for grazing effects on either trophic level at our study sites. The lack of observed grazing effects may be due to goose densities not being high enough to significantly reduce littoral vegetation or aquatic macroinvertebrates. On the other hand, it is noteworthy that the positive association we observed between goose density and several variables, as well as the unexpected negative treatment effect on macroinvertebrate abundance, align with descriptive patterns reported by Gunnarsson et al. (2024). Their study investigated the potential role of geese (and swans) as drivers of wetland degradation, such as biodiversity loss and increased eutrophication, across 37 Swedish wetlands located in different landscape types. Gunnarsson et al. (2024) found that the abundance of aquatic macroinvertebrates as well as other waterbirds generally showed a positive association with goose abundance (described as moderate density levels in their study). They concluded that moderate goose densities do not appear to drive ecosystem deterioration in southern Swedish wetlands. Instead, geese appear to benefit from changes such as increased eutrophication, as it may enhance the productivity of wetland breeding sites. The present study supports these findings by demonstrating that, even at high goose densities, grazing does not appear to drive negative changes in biodiversity, at least in eutrophic wetlands with relatively dense vegetation stands. Yet, grazing effects may be more significant in aquatic ecosystems that are more sensitive to environmental and biotic changes. For example, another large herbivore, the whooper swan (*Cygnus cygnus*), has recently colonised thousands of meso- to oligotrophic wetlands in Fennoscandia, an expansion with largely unknown effects on littoral vegetation (Elmberg et al. 2019).

5 | Concluding Remarks

When conducting exclosure studies, placement of experimental plots requires careful consideration. As observed in the present study, water level fluctuation may affect data collection and thereby the results obtained. To ensure that plots do not dry out, we suggest that study sites be monitored at least a year before setting up an experiment. Doing so could also provide more information about the annual development of littoral vegetation, which is another aspect to consider when choosing placement. This is especially relevant in temperate wetlands characterised by high weather variability between seasons.

The number of replicates (exclosures) was restricted due to limited resources (time and manpower), and we instead prioritised including a higher number of wetlands from different areas, since there is a lack of studies replicated at a larger spatial scale. Still, we acknowledge that a higher number of exclosure replicates is warranted and would increase the power of statistical analyses. Moreover, our study is a one-year snapshot. Accordingly, there is a general need for long-term studies to see how plant and macroinvertebrate communities react in relation to changes in goose abundance. This argument is supported by the fact that research on newly restored or constructed wetlands has observed strong reductions of littoral vegetation by geese (Jobe et al. 2022; Temmink et al. 2022).

To conclude, we could not fully confirm predictions about geese directly and indirectly decreasing shoreline vegetation and aquatic macroinvertebrates. Our study demonstrates some significant differences in vegetation and macroinvertebrates between paired control and exclosure plots, as well as among wetlands with different goose density, but results were inconclusive, not least how goose density related to treatment effects. Given that the present study is the first of its kind, future work needs to address the combined multi-trophic level effects of grazing by large avian herbivores on vegetation and macroinvertebrates in lentic freshwater systems. Even though several studies have shown that grazing effects increase with increasing waterfowl density (Tatu et al. 2007, Wood et al. 2017), there is still limited knowledge about the actual thresholds at which herbivory begins to significantly impact wetland ecosystems. Finding such thresholds would provide a valuable tool for wildlife and wetland management.

Author Contributions

Developing methods: E.K., G.G., J.E., P.S. Conceptualisation, conducting the research: E.K., G.G., J.E., P.S. Data analyses: E.K., C.A. Data interpretation: E.K., C.A., G.G., J.E., P.S. Writing: all authors.

Acknowledgements

The authors would like to express their gratitude to landowners for their consent and for providing background information about the study wetlands. The ornithological club KOF (*Kullabygdens Ornitologiska Förening*) is acknowledged for their insights and advice when selecting study sites. Furthermore, we are grateful for technical support by Åsa Gunnarsson, field assistance by Eric Trulsson, Zuzana Musilova, and Therése Igelström and laboratory assistance by Henric Djerf. We would also like to recognise Sari Holopainen for her guidance and support with statistical analyses. Lastly, the authors sincerely thank the reviewers, among them Benjamin Misteli, for their thoughtful and constructive comments, which helped clarify and improve the manuscript.

Conflicts of Interest

The authors declare no conflicts of interest.

Data Availability Statement

The datasets produced and/or analysed in this study are available from the corresponding author upon reasonable request.

References

Allin, C. C., and T. P. Husband. 2003. "Mute Swan (*Cygnus olor*) Impact on Submerged Aquatic Vegetation and Macroinvertebrates in a Rhode Island Coastal Pond." *Northeastern Naturalist* 10, no. 3: 305–318. https://doi.org/10.2307/3858700.

Bakker, E. S., N. Huig, C. G. F. Veen, G. J. Ter Heerdt, N. Huig, and J. M. Sarneel. 2018. "High Grazing Pressure of Geese Threatens Conservation and Restoration of Reed Belts." *Frontiers in Plant Science* 871: 1649. https://doi.org/10.3389/fpls.2018.01649.

Bakker, E. S., and B. A. Nolet. 2014. "Experimental Evidence for Enhanced Top-Down Control of Freshwater Macrophytes With Nutrient Enrichment." *Oecologia* 176, no. 3: 825–836. https://doi.org/10.1007/s00442-014-3047-y.

Bakker, E. S., K. A. Wood, J. F. Pagès, et al. 2016. "Herbivory on Freshwater and Marine Macrophytes: A Review and Perspective." *Aquatic Botany* 135: 18–36. https://doi.org/10.1016/j.aquabot.2016.04.008.

Bates, D., M. Maechler, B. Bolker, and S. Walker. 2015. "Fitting Linear Mixed-Effects Models Using lme4." *Journal of Statistical Software* 67, no. 1: 1–48. https://doi.org/10.18637/jss.v067.i01.

Brooks, M. E., K. Kristensen, K. J. van Benthem, et al. 2017. "glmmTMB Balances Speed and Flexibility Among Packages for Zero-Inflated Generalized Linear Mixed Modeling." *R Journal* 9, no. 2: 378–400. https://doi.org/10.32614/RJ-2017-066.

Buij, R., T. C. Melman, M. J. Loonen, and A. D. Fox. 2017. "Balancing Ecosystem Function, Services and Disservices Resulting From Expanding Goose Populations." *Ambio* 46, no. 2: 301–318. https://doi.org/10.1007/s13280-017-0902-1.

Čehovská, M., S. Kattainen, V. M. Väänänen, A. Putaala, and P. Nummi. 2022. "Compensating Freshwater Habitat Loss—Duck Productivity and Food Resources in Man-Made Wetlands." *European Journal of Wildlife Research* 68, no. 3: 35. https://doi.org/10.1007/s10344-022-01577-8.

Covich, A. P., M. A. Palmer, and T. A. Crowl. 1999. "The Role of Benthic Invertebrate Species in Freshwater Ecosystems." *Bioscience* 49, no. 2: 119–127. https://doi.org/10.2307/1313537.

Cramp, E., K. E. L. Simmons, I. J. Ferguson-Lees, et al. 1986. *Handbook of the Birds of Europe, the Middle East and North Africa: The Birds of the Western Palearctic*. Oxford University Press.

Elmberg, J., C. Arzel, G. Gunnarsson, et al. 2019. "Population Change in Breeding Boreal Waterbirds in a 25-Year Perspective: What Characterises Winners and Losers?" *Freshwater Biology* 65, no. 2: 167–177. https://doi.org/10.1111/fwb.13411.

Elmberg, J., P. Nummi, H. Pöysä, and K. Sjöberg. 1992. "Do Intruding Predators and Trap Position Affect the Reliability of Catches in Activity Traps?" *Hydrobiologia* 239: 187–193. https://doi.org/10.1007/BF00007676.

Elmberg, J., P. Nummi, H. Pöysä, and K. Sjöberg. 1993. "Factors Affecting Species Number and Density of Dabbling Duck Guilds in North Europe." *Ecography* 16, no. 3: 251–260. https://doi.org/10.1111/j.1600-0587.1993.tb00214.x.

Engelhardt, K. A. M., and M. E. Ritchie. 2001. "Effects of Macrophyte Species Richness on Wetland Ecosystem Functioning and Services." *Nature* 411, no. 2001: 687–689. https://doi.org/10.1038/35079573.

Flemming, S. A., P. A. Smith, L. V. Kennedy, A. M. Anderson, and E. Nol. 2022. "Habitat Alteration and Fecal Deposition by Geese Alter Tundra Invertebrate Communities: Implications for Diets of Sympatric Birds." *PLoS One* 17, no. 7: 1–19. https://doi.org/10.1371/journal.pone.0269938.

Fox, A. D., and J. Madsen. 2017. "Threatened Species to Super-Abundance: The Unexpected International Implications of Successful Goose Conservation." *Ambio* 46, no. 2: 179–187. https://doi.org/10.1007/s13280-016-0878-2.

Gayet, G., M. Guillemain, H. Fritz, et al. 2011. "Do Mute Swan (*Cygnus olor*) Grazing, Swan Residence and Fishpond Nutrient Availability Interactively Control Macrophyte Communities?" *Aquatic Botany* 95, no. 2: 110–116. https://doi.org/10.1016/j.aquabot.2011.04.003.

Geho, E. M., D. Campbell, and P. A. Keddy. 2007. "Quantifying Ecological Filters: The Relative Impact of Herbivory, Neighbours, and Sediment on an Oligohaline Marsh." *Oikos* 116, no. 6: 1006–1016. https://doi.org/10.1111/j.0030-1299.2007.15217.x.

Gough, L., and J. B. Grace. 1998. "Herbivor Effects on Plant Species Density at Varying Productivity Levels." *Ecology* 79, no. 5: 1586–1594. https://doi.org/10.1890/0012-9658(1998)079[1586:HEOPSD]2.0.CO;2.

Gunnarsson, G., E. Kjeller, S. Holopainen, et al. 2024. "The Hub of the Wheel or Hitchhikers? The Potential Influence of Large Avian Herbivores on Other Trophic Levels in Wetland Ecosystems." *Hydrobiologia* 851, no. 1: 107–127. https://doi.org/10.1007/s10750-023-05317-0.

Hansson, L. A., A. Nicolle, C. Brönmark, A. Hargeby, Å. Lindström, and G. Andersson. 2010. "Waterfowl, Macrophytes, and the Clear Water State of Shallow Lakes." *Hydrobiologia* 646, no. 1: 101–109. https://doi.org/10.1007/s10750-010-0169-z.

Hartig, F. 2022. "DHARMa: Residual Diagnostics for Hierarchical (Multi-Level/Mixed) Regression Models R Package Version 0.4.6 ed."

Hidding, B., B. A. Nolet, T. de Boer, P. P. de Vries, and M. Klaassen. 2010. "Above- and Below-Ground Vertebrate Herbivory May

Each Favour a Different Subordinate Species in an Aquatic Plant Community." *Oecologia* 162, no. 1: 199–208. https://doi.org/10.1007/s00442-009-1450-6.

Hilt, S. 2006. "Recovery of *Potamogeton pectinatus* L. Stands in a Shallow Eutrophic Lake Under Extreme Grazing Pressure." *Hydrobiologia* 570, no. 1: 95–99. https://doi.org/10.1007/s10750-006-0167-3.

Jensen, T. C., B. Walseng, D. O. Hessen, et al. 2019. "Changes in Trophic State and Aquatic Communities in High Arctic Ponds in Response to Increasing Goose Populations." *Freshwater Biology* 64, no. 7: 1241–1254. https://doi.org/10.1111/fwb.13299.

Jobe, J., C. Krafft, M. Milton, and K. Gedan. 2022. "Herbivory by Geese Inhibits Tidal Freshwater Wetland Restoration Success." *Diversity* 14, no. 4: 278. https://doi.org/10.3390/d14040278.

Karlsen, S. R., A. Elvebakk, K. A. Høgda, and B. Johansen. 2006. "Satellite-Based Mapping of the Growing Season and Bioclimatic Zones in Fennoscandia." *Global Ecology and Biogeography* 15, no. 4: 416–430. https://doi.org/10.1111/j.1466-822X.2006.00234.x.

Kleinhenz, A., and A. Koenig. 2018. "Home Ranges and Movements of Resident Graylag Geese (*Anser anser*) in Breeding and Winter Habitats in Bavaria, South Germany." *PLoS One* 13, no. 9: e0202443. https://doi.org/10.1371/journal.pone.0202443.

Koskimies, P., and R. A. Väisänen. 1991. *Monitoring Bird Populations*. University of Helsinki, Zoological Museum.

Kristiansen, J. N. 1998. "Nest Site Preference by Greylag Geese *Anser anser* in Reedbeds of Different Harvest Age." *Bird Study* 45, no. 3: 337–343. https://doi.org/10.1080/00063659809461105.

Lauridsen, T. L., E. Jeppesen, and F. Ø. Andersen. 1993. "Colonization of Submerged Macrophytes in Shallow Fish Manipulated Lake Væng: Impact of Sediment Composition and Waterfowl Grazing." *Aquatic Botany* 46, no. 1: 1–15. https://doi.org/10.1016/0304-3770(93)90061-Z.

Law, A., A. Baker, C. Sayer, et al. 2019. "The Effectiveness of Aquatic Plants as Surrogates for Wider Biodiversity in Standing Fresh Waters." *Freshwater Biology* 64, no. 9: 1664–1675. https://doi.org/10.1111/fwb.13369.

Liljebäck, N., G. Bergqvist, J. Elmberg, et al. 2021. "Learning From Long Time Series of Harvest and Population Data: Swedish Lessons for European Goose Management." *Wildlife Biology* 2021, no. 1: wlb00733. https://doi.org/10.2981/wlb.00733.

Ma, J., X. Huang, X. Qin, et al. 2017. "Large Manipulative Experiments Revealed Variations of Insect Abundance and Trophic Levels in Response to the Cumulative Effects of Sheep Grazing." *Scientific Reports* 7, no. 1: 11297. https://doi.org/10.1038/s41598-017-11891-w.

Ma, Z., Y. Cai, B. Li, and J. Chen. 2010. "Managing Wetland Habitats for Waterbirds: An International Perspective." *Wetlands* 30, no. 1: 15–27. https://doi.org/10.1007/s13157-009-0001-6.

Marklund, O., H. Sandsten, L. A. Hansson, and I. Blindow. 2002. "Effects of Waterfowl and Fish on Submerged Vegetation and Macroinvertebrates." *Freshwater Biology* 47, no. 11: 2049–2059. https://doi.org/10.1046/j.1365-2427.2002.00949.x.

Matuszak, A., M. Mörtl, P. Quillfeldt, and H. G. Bauer. 2012. "Exclosure Study on the Exploitation of Macrophytes by Summering and Moulting Waterbirds at Lower Lake Constance." *Hydrobiologia* 697, no. 1: 31–44. https://doi.org/10.1007/s10750-012-1168-z.

Mermillod-Blondin, F., D. Lemoine, J.-C. Boisson, E. Malet, and B. Montuelle. 2008. "Relative Influences of Submersed Macrophytes and Bioturbating Fauna on Biogeochemical Processes and Microbial Activities in Freshwater Sediments." *Freshwater Biology* 53: 1969–1982. https://doi.org/10.1111/j.1365-2427.2008.02020.x.

Murkin, H. R., P. G. Abbott, and J. A. Kadlec. 1983. "A Comparison of Activity Traps and Sweep Nets for Sampling Nektonic Invertebrates in Wetlands." *Freshwater Invertebrate Biology* 2, no. 2: 99–106. https://doi.org/10.2307/1467114.

Nilsson, L., and H. Persson. 1992. "Feeding Areas and Local Movement Patterns of Post-Breeding Greylag Geese *Anser anser* in South Sweden." *Ornis Svecica* 2, no. 2: 77–90.

Nilsson, S. G., M. Franzén, and L. Pettersson. 2013. "Land-Use Changes, Farm Management and the Decline of Butterflies Associated With Semi-Natural Grasslands in Southern Sweden." *Nature Conservation* 6: 31–48. https://doi.org/10.3897/natureconservation.6.5205.

Nudds, T. D., and J. N. Bowlby. 1984. "Predator-Prey Size Relationships in North American Dabbling Ducks." *Canadian Journal of Zoology* 62, no. 10: 2002–2008. https://doi.org/10.1139/z84-293.

Olsson, C., G. Gunnarsson, and J. Elmberg. 2017. "Field Preference of Greylag Geese *Anser anser* During the Breeding Season." *European Journal of Wildlife Research* 63, no. 1: 28. https://doi.org/10.1007/s10344-017-1086-5.

Perrow, M. R., J. H. Schutten, J. R. Howes, T. Holzer, F. J. Madgwick, and A. J. Jowitt. 1997. "Interactions Between Coot (*Fulica atra*) and Submerged Macrophytes: The Role of Birds in the Restoration Process." In *Shallow Lakes' 95: Trophic Cascades in Shallow Freshwater and Brackish Lakes*, 241–255. Springer. https://doi.org/10.1023/a:1017007911190.

Persson, A. S., O. Olsson, M. Rundlöf, and H. G. Smith. 2010. "Land Use Intensity and Landscape Complexity—Analysis of Landscape Characteristics in an Agricultural Region in Southern Sweden." *Agriculture, Ecosystems & Environment* 136, no. 1: 169–176. https://doi.org/10.1016/j.agee.2009.12.018.

R Core Team. 2023. *R: A Language and Environment for Statistical Computing*. 4.3.0 ed. R Foundation for Statistical Computing.

Reid, A. J., A. K. Carlson, I. F. Creed, et al. 2019. "Emerging Threats and Persistent Conservation Challenges for Freshwater Biodiversity." *Biological Reviews* 94, no. 3: 849–873. https://doi.org/10.1111/brv.12480.

Reijers, V. C., P. M. J. M. Cruijsen, S. C. S. Hoetjes, et al. 2019. "Loss of Spatial Structure After Temporary Herbivore Absence in a High-Productivity Reed Marsh." *Journal of Applied Ecology* 56, no. 7: 1817–1826. https://doi.org/10.1111/1365-2664.13394.

Rivers, D. O., and F. T. Short. 2007. "Effect of Grazing by Canada Geese *Branta canadensis* on an Intertidal Eelgrass *Zostera marina* Meadow." *Marine Ecology Progress Series* 333: 271–279. https://doi.org/10.3354/meps333271.

Rosenberg, K. V., A. M. Dokter, P. J. Blancher, et al. 2019. "Decline of the North American Avifauna." *Science* 366, no. 6461: 120–124. https://doi.org/10.1126/science.aaw1313.

Sarneel, J. M., N. Huig, G. F. Veen, W. Rip, and E. S. Bakker. 2014. "Herbivores Enforce Sharp Boundaries Between Terrestrial and Aquatic Ecosystems." *Ecosystems* 17, no. 8: 1426–1438. https://doi.org/10.1007/s10021-014-9805-1.

Seymour, C. L., and W. R. J. Dean. 1999. "Effects of Heavy Grazing on Invertebrate Assemblages in the Succulent Karoo, South Africa." *Journal of Arid Environments* 43, no. 3: 267–286. https://doi.org/10.1006/jare.1999.0552.

Søndergaard, M., L. Bruun, T. Lauridsen, E. Jeppesen, and T. V. Madsen. 1996. "The Impact of Grazing Waterfowl on Submerged Macrophytes: In Situ Experiments in a Shallow Eutrophic Lake." *Aquatic Botany* 53, no. 1: 73–84. https://doi.org/10.1016/0304-3770(95)01013-0.

Svidenský, R., A. Kučerová, and H. Čížková. 2021. "Causes of the Dieback of Littoral Stands in an Overpopulated Water-Bird Reserve: Role of Eutrophication, Fish and Geese." *European Journal of Environmental Sciences* 11, no. 2: 79–90. https://doi.org/10.14712/23361964.2021.9.

Tatu, K. S., J. T. Anderson, L. J. Hindman, and G. Seidel. 2007. "Mute Swans' Impact on Submerged Aquatic Vegetation in Chesapeake Bay."

Journal of Wildlife Management 71, no. 5: 1431–1439. https://doi.org/10.2193/2006-130.

Temmink, R. J. M., M. van den Akker, C. H. A. van Leeuwen, et al. 2022. “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.

Valkama, E., S. Lyytinen, and J. Koricheva. 2008. “The Impact of Reed Management on Wildlife: A Meta-Analytical Review of European Studies.” *Biological Conservation* 141, no. 2: 364–374. https://doi.org/10.1016/j.biocon.2007.11.006.

van Altena, C., E. S. Bakker, J. J. Kuiper, and W. M. Mooij. 2016. “The Impact of Bird Herbivory on Macrophytes and the Resilience of the Clear-Water State in Shallow Lakes: A Model Study.” *Hydrobiologia* 777, no. 1: 197–207. https://doi.org/10.1007/s10750-016-2779-6.

van Zuidam, B. G., E. S. Bakker, G. J. van Geest, and E. T. H. M. Peeters. 2022. “Submerged Vegetation Colonizes Behind Artificial Wave Shelter After a 10-Year Time-Lag and Persists Under High Grazing Pressure by Waterbirds.” *Aquatic Botany* 181: 103541. https://doi.org/10.1016/j.aquabot.2022.103541.

Veen, G. F., J. M. Sarneel, L. Ravensbergen, et al. 2013. “Aquatic Grazers Reduce the Establishment and Growth of Riparian Plants Along an Environmental Gradient.” *Freshwater Biology* 58, no. 9: 1794–1803. https://doi.org/10.1111/fwb.12168.

Vymazal, J., and L. Krőpfelová. 2005. “Growth of *Phragmites australis* and *Phalaris arundinacea* in Constructed Wetlands for Wastewater Treatment in The Czech Republic.” *Ecological Engineering* 25, no. 5: 606−621. https://doi.org/10.1016/j.ecoleng.2005.07.005.

Wood, K. A., M. T. O'Hare, C. McDonald, K. R. Searle, F. Daunt, and R. A. Stillman. 2017. “Herbivore Regulation of Plant Abundance in Aquatic Ecosystems.” *Biological Reviews* 92, no. 2: 1128–1141. https://doi.org/10.1111/brv.12272.

Wood, K. A., R. A. Stillman, R. T. Clarke, F. Daunt, and M. T. O'Hare. 2012. “The Impact of Waterfowl Herbivory on Plant Standing Crop: A Meta-Analysis.” *Hydrobiologia* 686, no. 1: 157–167. https://doi.org/10.1007/s10750-012-1007-2.

Zuur, A. F., E. N. Ieno, and C. S. Elphick. 2010. “A Protocol for Data Exploration to Avoid Common Statistical Problems.” *Methods in Ecology and Evolution* 1, no. 1: 3–14. https://doi.org/10.1111/j.2041-210X.2009.00001.x.

Zuur, A. F., E. N. Ieno, N. J. Walker, A. A. Saveliev, and G. M. Smith. 2009. *Mixed Efects Models and Extensions in Ecology With R*. Springer-Verlag New York Inc.

Supporting Information

Additional supporting information can be found online in the Supporting Information section. **Data S1:** fwb70114-sup-0001-Supinfo.docx.