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Trophic interactions in boreal wetlands: whooper swan *Cygnus cygnus* grazing and its effects on vegetation and macroinvertebrates

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Abstract The rapid population growth of whooper swan *Cygnus cygnus* in Fennoscandia raises concerns about their ecological impact on freshwater wetlands. As large herbivores, swans can potentially alter wetland vegetation through intensive grazing, which in turn suggestively affects other trophic levels, including aquatic macroinvertebrates. However, studies examining both direct and indirect effects across trophic levels remain limited. To address this gap, we conducted a field experiment across ten boreal wetlands in Finland during the breeding season (April–August) of 2023, using fenced exclosures to prevent swan grazing, paired with open control plots. We expected that swan exclusion would result in higher vegetation aboveground biomass, cover, height, and species richness, which in turn would support greater abundance and taxon richness of aquatic macroinvertebrates. Our results indicate that swan exclusion led to increases of all vegetation variables, particularly aboveground vegetation biomass. Among vegetation types, the strongest grazing effects were observed for water horsetail *Equisetum fluviatile* and graminoid species. However, there was weak support for indirect effects on macroinvertebrate abundance and taxon richness. These results suggest that swan herbivory may shape wetland ecosystems primarily by altering vegetation. Further research is needed to particularly assess the long-term consequences of swan herbivory on wetland ecosystem functioning and community composition.

Keywords Macrophytes · Cascade effects · Herbivory · Waterfowl · Freshwater ecology · Aquatic ecosystems

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Introduction

Waterfowl communities fluctuate over time, and while their relative abundances shift, the rapid recovery of some species may have consequences for others through complex interspecific interactions. In Europe and North America, several swan and goose species have experienced rapid population growth in recent decades (Fox and Madsen 2017; Rees and Clausen 2024). For example, mute swan *Cygnus olor*

in Britain recovered markedly following regulation of toxic lead fishing weights (Wood et al. 2019), and reintroduced trumpeter swan *C. buccinator* in North America expanded their breeding range 16-fold in 19 years after protective hunting regulations (Handrigan et al. 2016). The expanded populations have raised concerns about their potential impact on aquatic ecosystems (Bakker et al. 2016; Wood et al. 2017). As some of the largest aquatic herbivores in these regions, these birds may exert high grazing pressure on wetland vegetation, potentially affecting not only water quality (e.g., Sarneel et al. 2014; Reijers et al. 2019) but also fauna within the aquatic food web (Nummi et al. 2006). Previous studies have indeed shown that large waterfowl can substantially reduce wetland vegetation and alter community structure such as species composition (Sarneel et al. 2014; Reijers et al. 2019). However, there is limited knowledge about their indirect grazing effects, particularly on aquatic macroinvertebrates associated with wetland vegetation abundance (Heino 2000, 2008; Okun et al. 2005). Gaining a better understanding of the ecological role of these birds is therefore essential, not only for improved management of their populations, but also for the conservation of freshwater wetlands faced with challenges such as rapid biodiversity declines, increased browning, eutrophication and pollution (Pöysä et al. 2018; Holopainen et al. 2022).

The whooper swan *C. cygnus* population breeding in Fennoscandia is often considered a conservation success (Haapanen 1991; Nilsson 2014; Laubek et al. 2019). According to Laubek et al. (2019), this population more than doubled in Fennoscandia between 1995 and 2015, rising from an estimated 59,000 to 138,500 individuals. By 2020, the population had reached approximately 140,000 individuals and was still increasing (Rees and Clausen 2024). This expansion has been largely attributed to improved protection through hunting regulations, greater access to resources from agricultural fields, and milder winters (Laubek 1995; Laubek et al. 1999). While the whooper swan has increased, alarming downward trends have been observed for other waterbirds, including several smaller duck species that share similar breeding sites (Reid et al. 2019; Elmberg et al. 2020; Holopainen et al. 2024). Interestingly, Elmberg et al. (2020) found that boreal waterbirds relying on an herbivorous diet had increased significantly over 25 years in Fennoscandia, in contrast to decreasing invertivorous species such as Eurasian teal *Anas crecca* and common goldeneye *Bucephala clangula* in the same time period. They argued that the opposing trends might be connected, and specifically that the increase of whooper swan, being an obligate herbivore, potentially caused a decline in other waterbirds, either through interference or habitat alteration (Elmberg et al. 2020). However, when the relationship between local whooper swans and other waterbirds in Finland and Sweden has been studied, results have yielded positive associations (Pöysä et al. 2018; Holopainen et al. 2022). Nevertheless, there is a lack of studies quantifying potential direct and indirect effects of whooper swan herbivory, leaving a gap in the understanding about their role in regulating ecosystem dynamics in wetland communities.

Studies on swan herbivory have mainly been conducted on focal species other than the whooper swan. Gayet et al. (2014) summarized effects of mute swan in wetlands and called this species an ecosystem engineer due to its great potential to influence species composition of submerged aquatic vegetation. For instance, it has been found that mute swan, together with great flamingo *Phoenicopterus roseus*, affected the dominance relationship between dwarf eelgrass *Zostera noltii* and macroalgae *Chaetomorpha* sp. in a Mediterranean lagoon. By feeding on the dominant macroalgae, these birds mediated growth of dwarf eelgrass as competition for light decreased (Gayet et al. 2012). The idea that swan herbivory may favor some plant species and thereby influence vegetation communities and diversity is supported in other studies as well (Sandsten and Klaassen 2008; Gayet et al. 2011). However, grazing effects on total aboveground biomass differ between studies, some finding clear reductions of submerged aquatic vegetation in grazed areas (O'Hare et al. 2007; Tatu et al. 2007), while others found no significant decrease (Stafford et al. 2012). Differences among studies may be related to study duration and timing, as grazing effects have been observed to vary both between and within seasons (Hidding et al. 2010; Wood et al. 2012b; Kjeller et al. 2024). For instance, Wood et al. (2012b) found that grazing by mute swan in a freshwater river was strongest in the peak and recession phases of the growing season, when plants had limited capacity for compensatory growth. Observed grazing effects may also intensify with increasing swan density and decreasing water depth, as higher densities lead to

more foraging pressure and shallow waters provide easier access to vegetation (Allin and Husband 2003; Tatu et al. 2007; Dos Santos et al. 2012; Wood et al. 2017). Notably, the whooper swan's diet may be broader than that of the mute swan due to its stronger beak, which allows it to consume more rigid emergent vegetation (Kouzov et al. 2024). This highlights the need for grazing studies that examine not only the whooper swan but also a diverse range of wetland vegetation types, rather than focusing exclusively on submerged species.

To date, few studies have addressed the potential indirect effects of swan herbivory on aquatic macroinvertebrates in freshwater wetlands, here, broadly defined as effects mediated through changes in interactions or environmental conditions (Wootton 1994), including vegetation-mediated trophic cascades resulting from herbivory. However, Marklund and Sandsten (2002) conducted an exclosure study in a eutrophic lake in southern Sweden, investigating potential differences in aquatic vegetation and macroinvertebrates between fenced and unfenced plots during waterbirds' autumn migration. They found that swans significantly reduced aboveground biomass of the submerged fennel pondweed *Potamogeton pectinatus*, leading to a significant reduction of benthic macroinvertebrates (i.e., chironomids and pea clams *Pisidium* sp.). While pea clams appeared to be reduced as a result of aboveground swan foraging, chironomids were mainly affected by the swans' trampling activities when digging for below-ground tubers (Marklund and Sandsten 2002). After conducting a similar study in the same lake, with no significant grazing effects on aquatic macroinvertebrates, Marklund et al. (2002) argued that waterfowl only reduce macroinvertebrates substantially when the density of waterfowl is high or submerged vegetation is sparse. Although further research is needed to determine the specific conditions under which herbivore-induced top-down effects on aquatic macroinvertebrates occur, the findings from the above-mentioned studies imply that swans may indeed influence aquatic macroinvertebrates through their foraging activities.

To examine the direct and indirect effects of whooper swan herbivory across trophic levels, we conducted a grazing experiment with fenced plots (exclosures) protected from swans, paired with open control plots. Specifically, we tested whether grazing by this rapidly increasing large-bodied herbivore affects aquatic vegetation directly, and whether potential vegetation changes indirectly influence aquatic macroinvertebrates through habitat alteration. We predicted that (1) vegetation aboveground biomass, height, cover, and species richness would be higher in exclosures than control plots, resulting in (2) exclosures containing higher abundance and taxon richness of aquatic macroinvertebrates. In addition, we investigated how these variables related to swan density and physiochemical variables. The study was conducted in ten wetlands in Finland over one growing season.

Methods

Study sites

The study was conducted in 2023 in inland wetlands located in southern Finland (Fig. 1), within rural landscapes characterized by a mosaic of forests, agricultural fields, and smaller settlements. Wetlands used by breeding whooper swans were identified using observation records from the Finnish Biodiversity Information Facility database (https://laji.fi/), managed by the Finnish Museum of Natural History. Additional insights were obtained through consultations with local ornithologists and landowners. Based on this information, ten wetlands were selected for the study. They ranged in size from 2 to 32 hectares (mean ± SD: 17 ± 10 ha; Appendix 1) and were chosen based on the following criteria: (1) observations of breeding whooper swans the previous year, (2) location within rural landscapes, (3) minimal human disturbance, e.g., absence of notable recreational activities, nearby residential areas, or heavily trafficked roads, and (4) logistical accessibility for fieldwork and experimental studies. The selected wetlands were surrounded primarily by mixed forests and quaking bogs. They featured floating aquatic vegetation, predominantly *Nymphaea* species, and supported diverse macrophytes in the shoreline zones, commonly sedges *Carex* spp., common reed *Phragmites australis*, and water horsetail *Equisetum fluviatile* (Table 1).

Water samples were taken from the littoral zone of each wetland to be analyzed for physiochemical properties, following the protocols described in Gunnarsson et al. (2024). Sampling occurred at

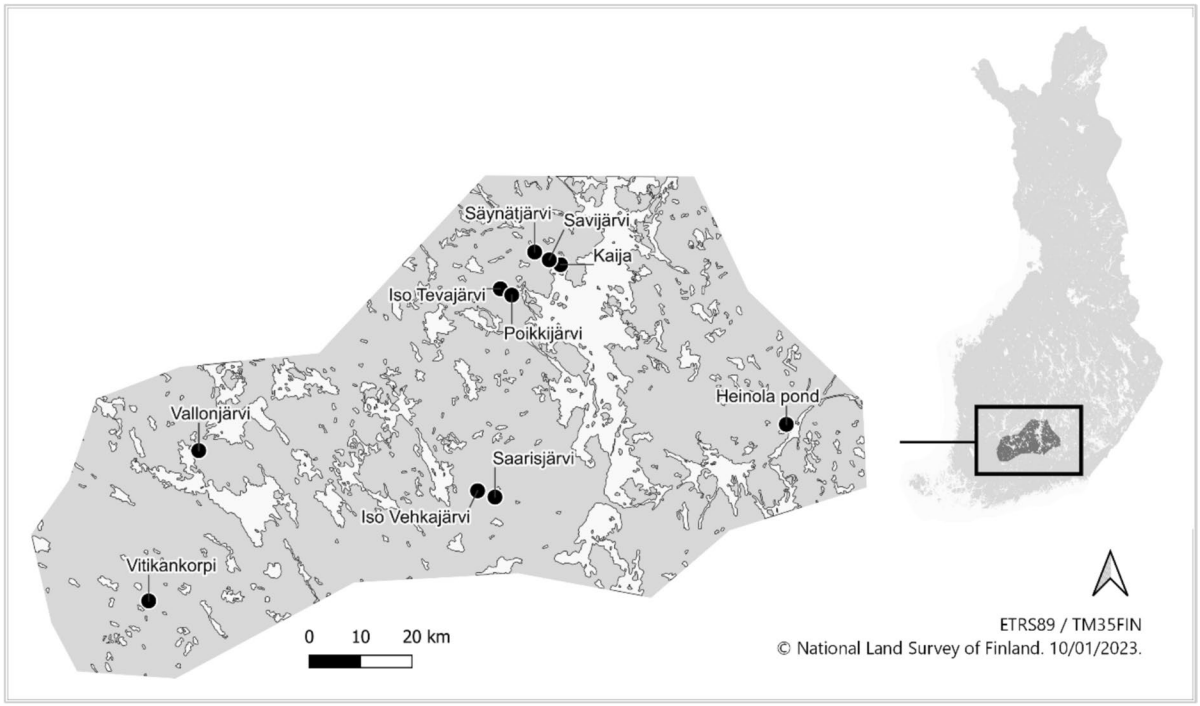


Fig. 1 Locations of the ten study wetlands in Finland. See also Table 1. Created in QGIS 3.22.16

Table 1 Most common vegetation taxa observed across the ten study sites

Vegetation group/species	*N0*. of sites observed
Water horsetail *Equisetum fluviatile*	7
Graminoids: Sedge *Carex* spp.	7
Common club-rush *Schoenoplectus lacustris*	2
Floating sweet grass *Glyceria fluitans*	1
Common reed *Phragmites australis*	6
Common bulrush *Typha latifolia*	2
Water lilies Nymphaeaceae spp.	8

three occasions (April 27–May 1, July 4–12, August 14–22). The analyses showed neutral to slightly acidic pH levels, while water color (abs λ420) and turbidity (NTU) ranged from neutral to high values. Chlorophyll (µg/l) and nutrient (µg/l) concentrations suggested that the wetlands exhibited mesotrophic conditions (see Holopainen and Lehikoinen 2021). Complete and detailed physiochemical data for each wetland are available in Appendix 1.

To describe waterbird community composition and to classify species into foraging guilds for potential use as covariates in statistical analyses, waterbird observations were conducted in three surveys (same dates as for water sampling) using the point count method as described by Koskimies and Väisänen (1991), with consistent vantage points at each wetland. Observations included both adult birds and their offspring older than three weeks. Younger offspring were excluded since they in general have a higher mortality rate during the first weeks and are thereby less likely to become fledged (Talent et al. 1983; Brown and Brown 2002; Paasivaara and Pöysä, 2007). The maximum counts among the surveys were converted into density (individuals per wetland hectare) for each species. A total of 21 waterbird species were observed (mean ± SD: 7.2 ± 2.9), and the most frequent ones were whooper swan, common gull *Larus canus*, mallard *Anas platyrhynchos* and common goldeneye *Bucephala clangula*. The foraging guilds used were herbivores, surface feeders, benthic feeders, invertivores, piscivores and generalists. Among herbivorous waterfowl (geese and swans), the whooper swan was the only species present, observed

at nine out of the ten wetlands. Successful breeding by whooper swans was documented on five wetlands, based on observations of broods. Further details on species densities, guild belonging and their distribution across the wetlands are presented in Appendix 2.

Experimental setup

To test direct grazing effects on vegetation as well as indirect effects on aquatic macroinvertebrates, we conducted an experiment which enabled comparison between plots that were either accessible or not to swan grazing (e.g., Allin and Husband 2003; Sarneel et al. 2014). This treatment experiment consisted of open control plots paired with fenced exclosures (2.5 × 2.5 m), placed in open water along the shoreline (Figs. 2, 3). The experimental plots were constructed between April 27 and May 1, 2023, before the whooper swans began to breed and the growing season had started in the study area. The exclosures were built by driving wooden poles into the sediment at each corner and enclosing them with high-density polyethylene plastic netting (mesh size 19 × 19 mm). Since our primary focus was to measure whooper swan grazing, about 15 cm was left open at the bottom of the exclosures, which enabled fish to enter (Hilt 2006; Tatu et al. 2007). Three exclosure-control pairs were constructed on each study site, i.e., 6 plots per site and 60 plots in total. The distance between a control plot, marked at its center with a single pole, and its paired exclosure was approximately 5 m (Fig. 2), whereas the distance between pairs varied. The latter was justified by our ambition to place the plots in areas with similar vegetation, as inferred from dead matter left from the previous year. Likewise, the distance between the plots to the shoreline varied, decided by the occurrence of vegetation from the previous season and by water depth. At the time of construction, the average distance to the shoreline measured from the outer boundary of the plot pairs was 9.9 m (SD = 3.7), whereas average water depth was 70.8 cm (SD = 22.1).

To sample vegetation and aquatic macroinvertebrates, we delineated nine 0.25 m^2 subplots inside the plots, not including the 0.5 m strip closest to the plot boundary in order to exclude potential edge effects, e.g., shading or grazing from birds reaching in from the outside (Sarneel et al. 2014). A sampling scheme was created and applied to all plots according to Fig. 4. Additionally, water depth (cm) was measured in respective subplots upon vegetation and aquatic macroinvertebrates sampling.

Vegetation sampling

Within each plot, vegetation sampling was conducted in four of the nine subplots between August 14–23 (Fig. 4), measuring vegetation height, percentage

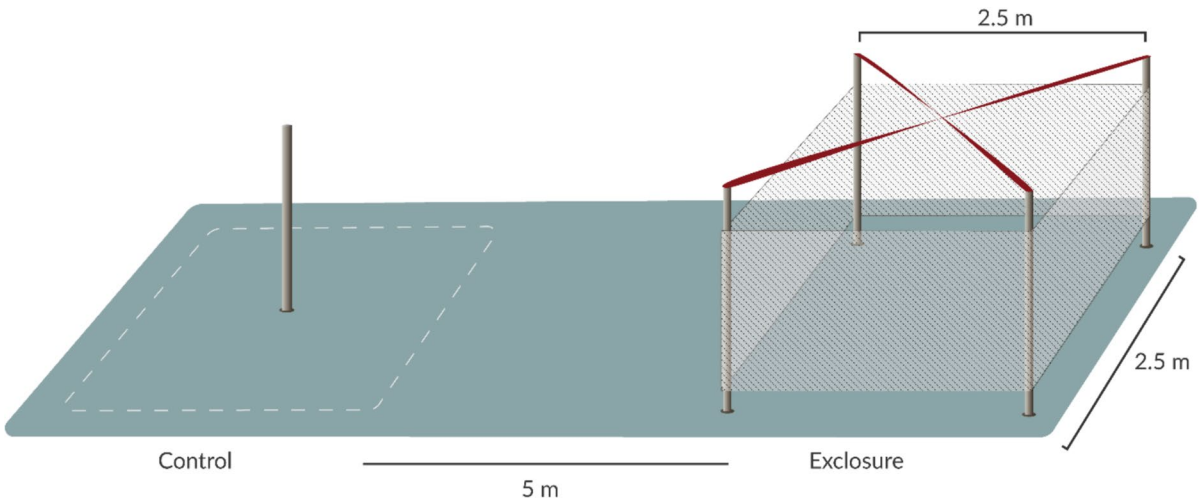


Fig. 2 Experimental setup with paired exclosure and control plot (2.5 × 2.5 m). Distance between plots within a pair was approximately 5 m. Created in Adobe Illustrator 2023

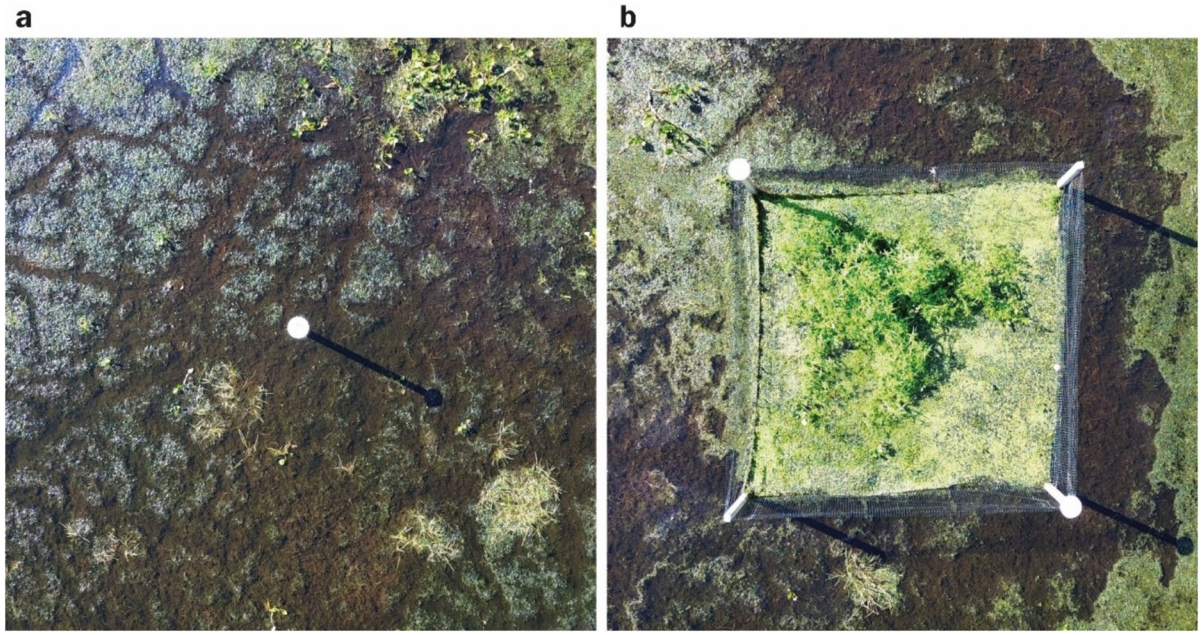


Fig. 3 A paired control (**a**) and exclosure (**b**) plot in one of the study sites with highest swan density (Vitikankorpi). The aerial photo was taken on August 15, 2023. Photo: Gunnar Gunnarsson

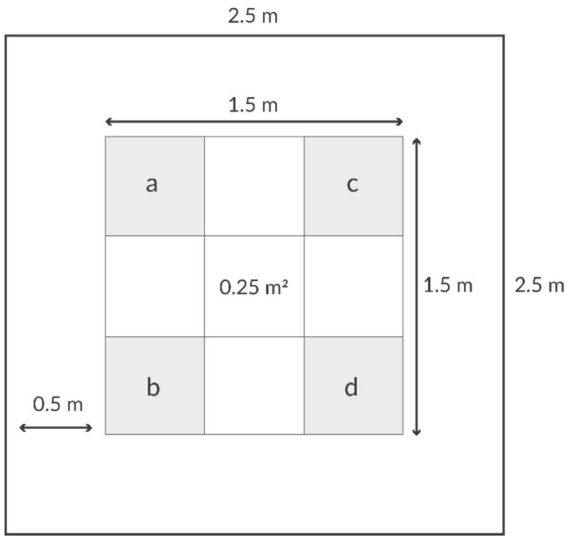


Fig. 4 Sampling scheme within the inner area (1.5 × 1.5 m) of experimental plots, with a 0.5 m buffer zone to avoid edge effects. Subplots (0.25 m^2) **a–d** were all sampled for vegetation, while aquatic macroinvertebrates were only collected in **a** and **d**. Created in Adobe Illustrator 2023

cover, and aboveground biomass, i.e., live matter above the soil or sediment, for each species. Vegetation height (cm) was obtained for emergent species only, based on the average of three measurements of the tallest stems for each species within a subplot. Percentage cover was estimated to the nearest whole number, as assessed by two observers. All vegetation samplings were conducted by the same two observers during all sampling events. Aboveground vegetation was harvested using hedge shears and secateurs for all species present, except free-floating duckweed *Lemna* spp. and green algae *Cladophora glomerata*. The harvested vegetation was sorted by species and oven-dried at 60 °C for approximately 48 h to determine its dry weight (g DW) (Rivers and Short 2007). Ovens of different manufacturers and models were used for drying due to time limitations.

Aquatic macroinvertebrate sampling

Nektonic and benthic aquatic macroinvertebrates were sampled in two of the nine subplots (Fig. 4), between July 5–14. They were collected by using activity traps (Murkin et al. 1983) consisting of a 1-L glass jar with an attached funnel in the opening (opening radius: 102 mm, narrow end radius: 23 mm) (Gunnarsson et al. 2024). One activity trap was

placed in each of the two subplots (i.e., two traps per plot, six traps per site), and they were positioned with their opening parallel to the shoreline, oriented in the same direction within a site (Elmberg et al. 1993). The traps were emptied after 24 h, and the catches were counted and sorted by taxonomic group according to a protocol based on Nudds and Bowlby (1984) (for details, see Appendix 3). The protocol included macroinvertebrates for which vegetation may play an important role by either providing food resources for herbivores or structural habitat and refuge for predators and their prey (Dieahl, 1988, Crowder et al. 1998). In four sites, some traps (n = 8) contained bycatches of fish, which according to Elmberg et al. (1992) can reduce the number of macroinvertebrates in traps through consumption. We conducted paired *t*-tests to control whether there were significant differences in macroinvertebrate total abundance and taxon richness between traps with and without fish. Traps containing fish had significantly lower macroinvertebrate total abundance ($t = -4.23$, df = 4, $p = 0.013$) and taxon richness ($t = -5.33$, df = 4, $p = 0.006$), than traps without fish, consistent with expectations based on fish predation (Elmberg et al. 1992). Therefore, such traps were excluded from subsequent analyses (see below).

Statistical analysis

All data exploration and statistical analyses were conducted using R software version 4.3.0 (R Core Team 2023). Prior to performing statistical analyses, each dataset was examined for potential outliers, assessed for normality, collinearity, and homogeneity of variance following the guidelines of Zuur et al. (2010). Data analysis involved the application of linear mixed models (LMMs) and generalized linear mixed models (GLMMs). Model selection and model averaging were performed within an information-theoretic framework using Akaike's information criterion corrected for sample size (AICc; Burnham and Anderson 2002). Because treatment (control vs. exclosure) was the primary experimental factor, it was included in all candidate models. To avoid overfitting given the small sample size, each candidate model was restricted to include only one additional covariate, without interaction terms. The specific covariates used for vegetation and aquatic macroinvertebrate analyses are described in the respective sections below. The reason for including covariates was to assess whether any variable contributed meaningful explanatory power beyond the treatment effect. Model averaging was performed across the full set of candidate models for each response variable using the MuMIn package (Bartoń, 2023). We also calculated Akaike model weights (w_i, summing to 1), which represent the probability that a model is the best given the candidate set. Models with smaller Akaike model weights (w_i) have less support relative to other candidate models (Portet 2020). Furthermore, we defined a 95% confidence set of models as the minimal subset of models whose Akaike weights summed to ≥ 0.95, indicating 95% confidence that the best approximating model is contained within this set (Portet 2020). Model-averaged coefficients were calculated using AICc weights. Predictors whose 95% confidence intervals (CIs) included zero were considered uninformative i.e., suggesting weak evidence for meaningful effects.

Vegetation

To assess the influence of treatment on vegetation, we built separate LMMs for the response variables aboveground biomass, height, and cover, using the lme4 package (Bates et al. 2015). For vegetation species richness, candidate models were fitted with GLMMs from the glmmTMB package (Brooks et al. 2017) as it consisted of count data. Before analyzing cover, the variable was arcsine transformed to improve normality. In all vegetation models, treatment was included as a fixed factor, with swan density, water depth, total phosphorus, water color and turbidity as covariates. These covariates were normalized to ensure comparability of model-averaged estimates. Other physiochemical variables as well as other waterbird guilds were excluded from the analyses due to collinearity; Pearson correlation $|r| > 0.6$. Random effects were site and exclosure-control pair nested within site, fitted with random intercept. However, prior to model averaging we compared the optimal random structure of each global model with restricted maximum likelihood (Zuur et al. 2009) and by evaluating their random effect estimates to avoid overfitting. We evaluated the explanatory power of the models and prioritized parsimonious model structure when determining what random effects to include. This model selection resulted in only site

being included as random effect in models of all vegetation response variables.

Additionally, we assessed grazing effects on the most common vegetation types, i.e., with more than 10 paired observations, including the following grouped by taxa or physical traits: (1) water horsetail (hereafter "horsetail"), (2) graminoids (*Carex* spp., *Glyceria fluitans*, *Schoenoplectus lacustris*), (3) common reed and common bulrush *Typha latifolia* (hereafter "reed and bulrush"), and (4) water lilies Nymphaeaceae spp. For each group, we assessed the response variables aboveground biomass, cover and height between exclosure and control plots with paired *t*-tests. Height of reed and bulrush did not meet the assumption of normality and were therefore analyzed with Wilcoxon signed rank tests.

Aquatic macroinvertebrates

To assess the influence of treatment on macroinvertebrates, we built separate GLMMs for the response variables total abundance and taxon richness using glmmTMB package (Brooks et al. 2017). For total abundance, we specified family in the GLMM as negative binomial due to overdispersion (Zuur et al. 2009). For taxon richness, data were underdispersed, and family was therefore specified as Conway-Maxwell-Poisson in that case (Forthmann et al. 2020). For both response variables, predictors were treatment, and covariates were swan density, vegetation aboveground biomass, vegetation species richness, vegetation height, total phosphorus, water color and turbidity (other variables were excluded from the analyses due to collinearity; Pearson correlation $|r| > 0.6$). The optimal random structures were determined in the same stepwise procedure outlined previously in the *Vegetation* section. For total abundance, the random effect included was site, while the models for taxon richness included exclosure-control pair nested within site. One site (Poikkiärvi) was excluded from analysis since low water level impaired macroinvertebrate sampling and catches in most subplots.

To analyze the response of treatment on the abundance of different macroinvertebrate taxa, additional paired *t*-tests were conducted for taxa with more than 10 paired observations, including: "Copepoda", "Phyllopoda/Cladocera", "Arachnida-Acari", "Arachnida-Araneida", "Diptera-Chironomidae" (cf. Appendix 3). "Annelida-Oligochaeta", "Ephemeroptera", "Odonata-Anisoptera" and "Trichoptera" did not meet the assumption of normality and were analyzed with Wilcoxon signed rank tests.

Results

Vegetation

For aboveground biomass, one model out of six was sufficient to capture the 95% confidence set (Appendix 4). This model included treatment and water depth. The results indicate that treatment had a strong positive influence on aboveground biomass while the biomass decreased with water depth (Table 2). In general, the aboveground biomass was 84% higher in exclosures (mean = 52.2, SE = 5.1) compared to open control plots (mean = 28.4, SE = 5.1). Other candidate models had low explanatory power.

It took four models out of six to capture the 95% confidence set for vegetation height (Appendix 4). The covariates included in these models were total phosphorus, turbidity and swan density, all paired with treatment. Each covariate had a negative association with vegetation height, in particular total phosphorus and turbidity (Table 2). However, the model-averaged estimates of swan density had a wide confidence interval overlapping zero, indicating uncertainty about its association to vegetation height. Treatment had a positive effect, with increasing height in exclosures (Table 2).

For vegetation cover, four models out of six were required to capture the 95% confidence set (Appendix 4). The covariates included in these models were total phosphorus, turbidity and water depth paired with treatment. Treatment and turbidity had the strongest (positive) influence on vegetation cover (Table 2). Vegetation cover inside protected exclosures was in general 86% higher (mean = 22.5, SE = 3.1) compared to control plots (mean = 12.1, SE = 2.3). The association between cover and total phosphorus was also positive, while the association with water depth was negative. However, these variables had low relative importance (Table 2).

For vegetation species richness, it took five models out of six to capture the 95% confidence set. The covariates included in these models, paired with treatment, were turbidity, water color, water depth and

Table 2 Model-averaged estimates (β) and 95% confidence intervals (CI) for all predictors included in the candidate model set explaining variation in vegetation aboveground biomass, height and cover from linear mixed models

Variable	Estimate (β)	95% CI	
		Lower	Upper
Aboveground biomass			
Intercept	57.84	**36.98**	**78.71**
Treatment[a]	20.49	**12.21**	**28.76**
Water depth	−70.11	**−102.76**	**−37.47**
Swan density	−33.45	−83.99	17.09
Total phosphorus	−29.73	−89.14	29.68
Water color	21.80	−30.97	74.57
Turbidity	6.37	−55.99	68.72
Height			
Intercept	81.67	**50.44**	**112.90**
Treatment[a]	19.70	**2.83**	**36.56**
Total phosphorus	−88.96	**−152.65**	**−25.26**
Turbidity	−81.44	**−149.32**	**−13.57**
Swan density	−53.66	−120.27	12.95
Water depth	36.15	−36.43	108.74
Water color	7.40	−66.89	81.69
Cover			
Intercept	0.27	**0.12**	**0.42**
Treatment[a]	0.12	**0.04**	**0.20**
Turbidity	0.45	**0.14**	**0.77**
Total phosphorus	0.10	−0.32	0.52
Water depth	−0.04	−0.37	0.29
Swan density	−0.01	−0.39	0.36
Water color	0.00	−0.38	0.37

Predictors for each response variable are ranked by their confidence interval in relation to zero. Predictors with confidence intervals not overlapping zero are shown in bold

[a]Exclosure compared to control

swan density (Appendix 4). The associations with turbidity and swan density were positive, but negative with water color and water depth (Table 4). The model-averaged estimate of treatment was the only one with a narrow confidence interval not overlapping zero and indicating a positive treatment effect. In contrast, all other covariates had wide confidence intervals, indicating weak and inconsistent support for their effects across the candidate model set.

Specific vegetation types

When analyzing specific vegetation types, all response variables for horsetail differed significantly between exclosures and controls, i.e., aboveground biomass, cover, and height were greater in exclosures (Table 3). For graminoid species, aboveground biomass as well as cover were significantly higher in exclosures compared to control plots while height showed no significant difference. In contrast, no significant differences were found for aboveground biomass or height of reed and bulrush, though their cover was significantly greater in exclosures (Table 3). Lastly, water lilies showed no significant differences in aboveground biomass or cover (Table 3).

Aquatic macroinvertebrates

It took seven out of eight models to capture the 95% confidence set for aquatic macroinvertebrate abundance (Appendix 4). The five highest ranked models (all within $\Delta AICc < 2$) included treatment alone, or paired with either swan density, total phosphorus, water color and vegetation richness. Macroinvertebrate abundance had positive associations with all these variables, but there was weak support for any of them to have any strong explanatory power (Table 4).

Similarly, it took seven out of eight models to capture the 95% confidence set for macroinvertebrate taxon richness (Appendix 4). The five highest ranked models (all within $\Delta AICc < 2$) included treatment alone, or paired with either swan density, aboveground biomass, turbidity, and vegetation height. None of the variables showed strong explanatory power (Table 4). The macroinvertebrate taxon richness had weak, but negative, associations with treatment, dry weight, turbidity, and vegetation richness, while its association with swan density was positive yet weak.

Regarding the abundance of the most common macroinvertebrates, neither of the included taxa "Copepoda", "Phyllopoda/Cladocera", "Arachnida-Acari", "Arachnida-Araneida", "Diptera-Chironomidae", "Annelida-Oligochaeta", "Ephemeroptera", "Odonata-Anisoptera" or "Trichoptera" showed significant differences between exclosures and control plots (Table 5).

Table 3 Results of *t*-statistics and Wilcoxon signed rank test for grouped vegetation of water horsetail, graminoids, common reed and common bulrush, as well as water lilies. Included are *t*-value, V, degrees of freedom (df), and *p* value (significant threshold $p < 0.05$)

Response variable	*t*	df	*p*
Horsetail biomass	2.92	20	**0.009***
Horsetail cover	2.95	20	**0.008***
Horsetail height	2.71	20	**0.014***
Graminoids biomass	3.51	21	**0.002***
Graminoids cover	2.25	21	**0.035***
Graminoids height	1.74	21	0.097
Water lilies biomass	− 0.24	20	0.811
Water lilies cover	− 1.54	20	0.140
Reed and bulrush biomass	2.09	10	0.063
Reed and bulrush cover	2.46	10	**0.034***
	V	df	*p*
Reed and bulrush height	36	10	0.415

Variables with $p < 0.05$ are shown in bold and marked with an asterisk (*)

Discussion

The aim of this study was to examine direct grazing effects of whooper swans on vegetation and its potential indirect effects on aquatic macroinvertebrates across ten boreal wetlands during the breeding season, simultaneously accounting for swan density and physicochemical variables. To the best of our knowledge, this is the first experimental attempt to investigate such cascading effects with the whooper swan as the focal species. We expected that vegetation and macroinvertebrate variables would be greater in fenced exclosures than in open control plots. This was supported for all vegetation variables (aboveground biomass, emergent vegetation height, cover and species richness), but not macroinvertebrate abundance or taxon richness. Additionally, our results indicate that swans particularly reduced variables (aboveground biomass, height and cover) of horsetail and graminoid species.

Vegetation

Our study suggests that whooper swans can significantly reduce aboveground biomass in boreal wetlands. This contrasts with Gayet et al. (2011) who studied grazing effects of mute swan across 24 fishponds in Dombes, France, and found that the birds reduced the cover of vegetation, but not aboveground biomass. The authors suggested that their contrasting results were due to varying degrees of detectability between the two variables, changes in cover being more easily detectable than biomass. Across our study sites, the aboveground biomass was 84% higher in exclosures compared to control plots, which is similar to what has been found in other studies on swan grazing (Allin and Husband 2003; O'Hare et al. 2007; Dos Santos et al. 2012). Our results also indicate that vegetation height, cover and richness increased within protected exclosures.

Tatu et al. (2007) observed mute swan flocks reduce vegetation to a greater extent than breeding pairs, but no large flocks were observed in any of our wetlands, suggesting that mainly whooper swan pairs with cygnets were responsible for the observed effects. The whooper swan is highly territorial during breeding, and in most wetlands (< 100 ha) only one pair is normally present (Cramp et al. 1986). This was also the case in our study sites, and our results thus show that relatively low whooper swan densities can have clear effects on vegetation during breeding. This effect may possibly be explained by breeding individuals repeatedly using the same site over an extended period, as grazing pressure may increase with the number of days swans remain in an area (Gayet et al. 2011).

The greatest reduction of vegetation was observed, although not statistically tested, in one of the smaller

Table 4 Model-averaged estimates (β) and 95% confidence intervals (CI) for all predictors included in the candidate model set explaining variation in vegetation species richness, as well as aquatic macroinvertebrate abundance and taxon richness from generalized linear mixed models

Variable	Estimate (β)	95% CI	
		Lower	Upper
Vegetation species richness			
Intercept	0.67	**0.27**	**1.08**
Treatment[a]	0.31	**0.13**	**0.48**
Turbidity	0.61	−0.18	1.41
Water color	−0.40	−1.18	0.37
Water depth	−0.24	−0.99	0.51
Swan density	0.25	−0.55	1.05
Total phosphorus	−0.14	−1.08	0.80
Invertebrate total abundance			
Intercept	2.49	**2.22**	**2.75**
Treatment[a]	0.04	−0.15	0.24
Swan density	0.40	−0.07	0.87
Total phosphorus	0.41	−0.12	0.93
Water color	0.31	−0.19	0.81
Vegetation richness	0.29	−0.34	0.92
Vegetation aboveground biomass	0.23	−0.33	0.78
Turbidity	−0.20	−0.81	0.42
Vegetation height	0.00	−0.44	0.44
Invertebrate taxon richness			
Intercept	1.51	**1.41**	**1.61**
Treatment[a]	−0.01	−0.12	0.10
Swan density	0.11	−0.04	0.26
Vegetation aboveground biomass	−0.14	−0.35	0.08
Turbidity	−0.10	−0.28	0.07
Vegetation height	−0.08	−0.24	0.09
Vegetation richness	−0.08	−0.34	0.18
Water color	0.05	−0.11	0.20
Total phosphorus	0.04	−0.14	0.21

Predictors for each response variable are ranked by their confidence interval in relation to zero. Predictors with confidence intervals not overlapping zero are shown in bold

[a]Exclosure compared to control

and shallower wetlands with one breeding pair and six cygnets, i.e., a higher swan density compared to most of the other wetlands. Other studies have found grazing pressure to increase with increasing waterfowl density (van Altena et al. 2016; Wood et al. 2017). The relationship is usually stronger when the density variable is calculated as biomass of individual birds per hectare, as large-bodied birds may consume more vegetation (Wood et al. 2012a, 2017). We chose to not account for biomass of individual birds since the weight of cygnets varies throughout the season and can differ between breeding sites (Knudsen et al. 2002). Not only wetland size, but also depth, may influence grazing effects, as grazing is enabled in shallower wetlands (Jeppesen et al. 1997).

When analyzing grazing effects on specific types of vegetation, whooper swans particularly affected horsetail, which showed significantly lower aboveground biomass, cover as well as height in the open control plots compared to exclosures. These results are particularly interesting since whooper swan grazing on horsetail has been hypothesized to eradicate this keystone species from boreal wetlands, thereby reducing the suitability of breeding habitats for Eurasian wigeon *Mareca penelope,* which prefers horsetail-dominated areas (Pöysä et al. 2018). The hypothesis stems from Pöysä et al. (2017) where long-term declines of Eurasian wigeon were found in Finnish and Swedish lakes where also horsetail had decreased. However, when Pöysä et al. (2018) later tested the hypothesis by comparing waterbird numbers and vegetation measures collected approximately ten years apart in 60 lakes, they did not find any relationship between the decrease of horsetail and whooper swan colonization (Pöysä et al. 2018). Lack of support for the hypothesis was also confirmed by the fact that there was a positive association between the abundance of whooper swans and Eurasian wigeon, i.e., there was a higher abundance of Eurasian wigeon in lakes colonized by the swans compared to lakes that had not been colonized. Over the past decades, the whooper swan population has grown dramatically (Rees and Clausen 2024), while horsetail has declined in many wetland areas. Although Pöysä et al. (2018) found no direct link between these trends, our results point towards the opposite, and we thus suggest that swan grazing could be a contributing factor in this long-term vegetation change.

Graminoids were also negatively affected by whooper swans, as both their cover and aboveground biomass were significantly higher in exclosures. Similarly, the cover of reed and bulrush was lower in grazed areas, and we suggest that this effect may be due to selective feeding on leaves rather than the coarse stems, as aboveground biomass was not affected. Moreover, water lilies did not appear to be

Table 5 Results of *t*-statistics and Wilcoxon signed rank test for aquatic macroinvertebrate taxa of "Copepoda", "Phyllopoda/Cladocera", "Annelida-Oligochaeta", "Arachnida-Acari", "Arachnida-Araneida", "Diptera-Chironomidae", "Ephemeroptera", "Odonata-Anisoptera", and "Trichoptera"

Response variable	*t*	df	*p*
Copepoda	0.73	25	0.472
Phyllopoda/Cladocera	1.18	24	0.249
Arachnida-Acari	0.93	18	0.363
Arachnida-Araneida	0.83	10	0.424
Diptera-Chironomidae	−0.52	16	0.612
	V	df	*p*
Annelida-Oligochaeta	39	13	0.377
Ephemeroptera	38	13	0.681
Odonata-Anisoptera	20	9	0.821
Trichoptera	15	9	0.386

Included are *t*-value, V, degrees of freedom (df), and *p* value (significant threshold $p < 0.05$*)

significantly impacted by whooper swan grazing, and we argue this may be caused by limited palatability or preference. However, there are documentation of whooper swan foraging on several species of water lilies (Brazil 2003, Appendix 1). Most previous studies on swan foraging have focused on submerged aquatic vegetation, making direct comparisons difficult, particularly since analyses of such vegetation could not be done in our study due to lack of data. Nevertheless, our findings suggest that whooper swans may target a broader range of wetland plant species compared to mute swans, aligning with previous research (Kouzov et al. 2024). According to Cramp et al. (1986), whooper swans may forage on leaves, stems and shoots of a wide variety of aquatic vegetation. In freshwater systems they commonly forage on pondweed *Potamogeton*, stonewort *Chara*, horsetail and sweetgrass *Glyceria* species (Cramp et al. 1986). To summarize, the grazing effects of the increased whooper swan populations in boreal lakes seem to influence vegetation unevenly. This could potentially alter the relative abundances of plant species, as certain taxa may respond more strongly to grazing pressure than others.

When analyzing the influence of physiochemical variables, some showed support of having additional explanatory power on vegetation response. Specifically, total phosphorus and turbidity showed negative associations with vegetation height, and turbidity had positive associations with vegetation cover. However, because the experimental plots did not cover a substantial part of the shoreline vegetation these associations may need to be interpreted with caution. We did not analyze interactions between grazing and physicochemical variables, but previous studies suggest that increased nutrient enrichment may enhance top-down grazing effects on aquatic vegetation by waterbirds (Bakker and Nolet 2014), fish (Smulders et al. 2022) and invertebrates (Zhang et al. 2018; Liu et al. 2021) across different aquatic ecosystems. The main reason is suggested to be elevated nutrient content in the plants, making them more favorable for herbivores (Bakker and Nolet 2014). Incorporating interactions with other physicochemical variables such as water color would thus provide further information about influential factors in aquatic plant–herbivore dynamics.

Aquatic macroinvertebrates

Although the exclosure treatment had positive effects on vegetation, we found little support of it influencing aquatic macroinvertebrate abundance or taxon richness. The results align with Allin and Husband (2003) who conducted an exclosure study in a brackish coastal pond with mute swan in North America, where the species is considered invasive. Although the biomass of submerged aquatic vegetation was greatly reduced (up to 95% in shallow sites), the authors did not find an overall decline in aquatic macroinvertebrate abundance. Only three species, belonging to Amphipoda, Trichoptera and Gastropoda showed reduced abundance in some of the open control plots (Allin and Husband 2003). In contrast to our study, swans used the coastal pond all year round, with peak numbers exceeding 300 individuals in August. However, because the pond was much larger, swan density was similar to the highest density observed in our wetlands.

Marklund and Sandsten (2002) suggested that aquatic macroinvertebrates may be reduced under high grazing pressure by swans. However, their study was conducted in a clearly distinct setting, i.e., in a single large lake and on (autumn) migrating swans of several species occurring in mixed flocks. Moreover, it was conducted over a single year in contrast to the four-year exclosure study by Allin and Husband

(2003). It might be that potential reductions in macroinvertebrates due to swan grazing are temporary within a year and could potentially recover in the long term. However, given the limited number of comparable studies, further research is needed to better understand the short- as well as long-term effects of swan grazing on aquatic macroinvertebrates. In our study, conducted over a single growing-season, we found little evidence of significant negative impacts on aquatic macroinvertebrates. However, since macroinvertebrates were grouped it is still possible that specific species may be more strongly affected than others (Marklund and Sandsten 2002).

Finally, among the physiochemical factors, neither total phosphorus, water color or turbidity had strong support for any influence on the macroinvertebrate variables, which is surprising since at least nutrient concentration and water color are factors that have been found to influence macroinvertebrate communities (Mormul et al. 2012; Arzel et al. 2020; Blanchet et al. 2022; Gunnarsson et al. 2024). For instance, aquatic macroinvertebrate abundance has been found to relate negatively with water color (Arzel et al. 2020; Gunnarsson et al. 2024) and positively with total phosphorus (Gunnarsson et al. 2024). The absence of these relationships in our study may possibly be due to differences in the range or magnitude of physicochemical conditions across sites, or the influence of other unmeasured environmental factors. However, future studies should investigate more closely how these factors interact with grazing to influence food web dynamics.

Conclusions

Our study provides a snapshot of grazing effects by whooper swan during one growing season. Taken together, the results suggest that this herbivore can alter plant communities, but their effects on macroinvertebrates may be limited. However, the implications of these changes for wetland ecosystem functioning remain uncertain, particularly regarding the long-term effects of swan herbivory. This highlights the need for further research to understand the ecological consequences of swan grazing over time.

Given the rapid increase of whooper swan populations in NW Mainland Europe, continued monitoring of their impact on wetland ecosystems is crucial. We suggest that future studies should adopt a multi-year approach to capture potential carryover effects of grazing and investigate how variations in grazing intensity influence vegetation recovery over time. Additionally, research should incorporate experimental studies in different habitat types, ranging from nutrient-poor to more productive wetlands, to better understand context-dependent effects. We also recommend integrating remote sensing techniques to assess vegetation dynamics on a larger spatial scale, allowing for more comprehensive analyses of swan-induced habitat changes.

Finally, our findings underscore the need for adaptive wetland management strategies that ensure both the conservation of whooper swans and the protection of wetland biodiversity, particularly in areas experiencing high grazing pressure. Wetland ecosystems are facing increasing pressures from climate change and anthropogenic activities, and understanding the role of large herbivorous waterfowl in shaping these habitats is essential for developing effective conservation and management strategies while maintaining a balance between species protection with ecosystem sustainability.

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Data availability Datasets from this study can be obtained from the corresponding author upon reasonable request.

Declarations

Conflict of interest The authors declare no competing interests.

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