PRIMARY RESEARCH PAPER

The hub of the wheel or hitchhikers? The potential influence of large avian herbivores on other trophic levels in wetland ecosystems

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Abstract Goose and swan populations have increased concurrently with environmental degradation of wetlands, such as eutrophication, vegetation losses, and decrease in biodiversity. An important question is whether geese and swans contribute to such changes or if they instead benefit from them. We collected data from 37 wetlands in southern Sweden April−July 2021 to study relationships between geese, swans and other waterbird guilds, macrophytes, invertebrates, as well as physical and water chemistry variables. Neither goose nor swan abundance was negatively correlated with other trophic levels (abundance, richness, or cover). On the contrary, goose or swan abundances were positively related to abundances of surface and benthic feeding waterbirds, cover of specific macrophytes, and to invertebrate richness and abundance. Moreover, invertebrates (number of taxa or abundance) were positively associated with abundance of several waterbird guilds and total phosphorous with surface feeders, whereas water colour was positively (surface feeders) or negatively (benthic feeders) related. We conclude that waterbirds are more abundant in productive wetlands and that geese and swans do not show clear deleterious effects on other trophic levels included in this study. However, patterns may be masked at the species level, which should be addressed in further studies, complemented with experimental studies of grazing impact.

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Introduction

Wetlands are key ecosystems, not only in terms of biodiversity and productivity, but also by providing many ecosystem services, including water regulation, freshwater supply, nutrient cycling, flood control, as well as promoting human health and well-being (Bai et al., 2013; Mitsch et al., 2015; Reeves et al., 2021; for Ramsar Convention definition of

wetlands, see Carp, 1972). They are, however, highly threatened, mainly due to extensive anthropogenic degradation in the past and still ongoing in many areas of the world (Davidson, 2014; Tang et al., 2022). Since 1900 the global loss of wetlands is estimated at > 50% (Finlayson & Spiers, 1999; Davidson, 2014; but see Fluet-Chouinard et al., 2023 for a lower estimate), where most has occurred in temperate areas of the Northern hemisphere. For example, the loss in some European countries has been estimated to be more than 70% (Fluet-Chouinard et al., 2023). The main reason for this loss, at least in Europe and North America, is land conversion for agriculture (Finlayson & Spiers, 1999). Pressure on remaining wetlands is high, with additional threats from brownification (Monteith et al., 2007; Mitsch et al., 2015; Kritzberg et al., 2020), eutrophication, and other alterations of water chemistry (European Environment Agency, EEA, 2018). Changes in wetland communities related to such processes concern vegetation (Sand-Jensen et al., 2008), invertebrates (Corcoran et al., 2009), fish (Voutilainen & Huuskonen, 2010), and birds (Lewis et al., 2015). Acknowledging the roles of wetlands for ecosystem function and services, there have been major efforts in recent decades to restore and construct wetlands (European Commission, 2007; see also review by Spieles, 2022).

Waterbirds are essential components of wetland ecosystems. They comprise a diverse group including waterfowl (Anatidae, i.e. ducks, geese, and swans), grebes (Podicipedidae), rails (Rallidae), shorebirds (several families), as well as gulls (Laridae). Signalling wetland quality, for example, in terms of ecological stability, and being providers of many important ecosystem services, such as pest control and facilitation of seed and invertebrate dispersal (Green & Elmberg, 2014), waterbirds are key inhabitants in wetland communities. It is therefore worrying that nearly half of the waterbird populations in the world have declined in recent decades, a demise for which habitat change is a major cause (Kirby et al., 2008; Wetlands International, 2010). In Europe there are examples of such declines amongst shorebirds (for example, Eurasian curlew *Numenius arquata* Linnaeus, 1758, and black-tailed godwit *Limosa limosa* Linnaeus, 1758; Fraixedas et al., 2017; BirdLife International, 2021) and several duck species (for example, common pochard *Aythya ferina* Linnaeus, 1758, and common

eider *Somateria mollissima* Linnaeus, 1758; Nagy et al., 2015; BirdLife International, 2021).

However, there are also waterbird species showing significant population growth. In a long-term wetland level study of 25 species, Pöysä et al. (2019) demonstrated that although overall species richness tended to decrease, species turnover was high, which in part was explained by the fact that the occurrence of some species increased. This was evident for large avian herbivores, such as swans and geese. This group of waterbirds includes species that have shown dramatic population increases, not the least in western Europe, including most goose populations (Fox & Madsen, 2017) as well as mute swan (*Cygnus olor* Gmelin, 1789) and whooper swan (*Cygnus cygnus* Linnaeus, 1758) (Laubek et al., 2019; Rees et al., 2019). For example, greylag goose (*Anser anser* Linnaeus, 1758) and whooper swan were both sparse breeders in Fennoscandia 50 years ago (Haapanen & Nilsson 1979; Nilsson, 2014), in contrast to the most recent estimates of 41,000 pairs of greylag goose and 5,400 pairs of whooper swan in Sweden alone (Ottosson et al., 2012). In a wider perspective, the wintering population of greylag goose in the NW/SW European flyway was estimated at 960,000 birds in 2014 (Fox & Leafloor, 2018), and the corresponding number of whooper swans in NW mainland Europe was 138,500 individuals in 2015 (Laubek et al., 2019). Reasons for these striking increases are several; in geese and probably also in whooper swan (Nilsson, 2014), they were initially likely due to implementation of hunting restrictions (Ebbinge, 1991), but maybe more importantly to the fact that these birds have gradually switched from foraging in natural habitats to in agricultural landscapes, particularly during the non-breeding season (Fox & Abraham, 2017). In the northern parts of NW Europe, geese and swans are migratory and traditionally show a high degree of fidelity to wintering and breeding sites (e.g. Saurola et al., 2013). However, these birds are favoured by climate change, and milder winters in Europe now permit prolonged access to foraging at northern sites (Ramo et al., 2015). They also show shortened migration distances, as current wintering sites are closer to the breeding sites than before (Padyšáková et al., 2010; see also Månsson et al., 2022).

Booming populations of geese and swans cause conflicts related to crop damage (Madsen et al., 2017), but also raise concerns about consequences

to the ecosystems where they occur. These birds are obligate herbivores and their food consumption is high due to the high content of undigestible cellulose in the ingested plants. To meet energy demands, the daily food intake of geese and swans may be up to about one-third of their body mass (Cramp et al., 1986; Gauthier et al., 2006; see also Dessborn et al., 2016). Based on the premises that their body masses are substantial (normally 8−10 kg in adult whooper swans and 3−4 kg in adult greylag geese (Cramp et al., 1986)), and that they often occur at high densities, the impact on vegetation by grazing may be considerable. The most classic example is the profound and detrimental effects caused by massive numbers of lesser snow goose (*Anser caerulescens caerulescens* Linnaeus, 1758) on breeding grounds in the Canadian Arctic (e.g. Jefferies et al., 2006). Other examples include pink-footed goose (*Anser brachyrhynchus* Baillon, 1834) and barnacle goose (*Branta leucopsis* Bechstein, 1803), demonstrated by Bjerke et al. (2021) to clearly reduce the amount of terrestrial vegetation during spring migration in Norway (see also, e.g. Madsen et al., 2011; Bjerke et al., 2014; Olsen et al., 2017). Corresponding studies in aquatic ecosystems provide more diverging patterns, with intermittent effects of swans grazing on macrophytes (see review by Guillaume et al., 2014 and references therein; Pöysä et al., 2018), whereas geese have been shown to reduce stands of common reed (*Phragmites australis* Cavanilles, 1799) (Bakker et al., 2018) and other aquatic vegetation (Jobe et al., 2022). Waterfowl herbivory has indeed been highlighted as a potentially important factor in macrophyte dynamics (Marklund et al., 2002 and references therein; Wood et al., 2012 with special emphasis on large-bodied waterfowl). In fact, the effect of herbivory in general (i.e. not only avian herbivores) is probably of larger significance in aquatic than in terrestrial ecosystems (Bakker et al., 2016). This presumption is motivated by a lower ratio of carbon to nitrogen in aquatic macrophytes compared to terrestrial plants, forcing herbivores of aquatic plants to eat more to fulfil their nutrient demands (Bakker et al., 2016).

To understand the drivers determining the structure of aquatic ecosystems it is important to consider top-down effects caused by herbivory (Wood et al., 2017). This does not only concern the direct impact on macrophytes per se through grazing, but also the indirect influences on chemical conditions (for eutrophication promoted by geese, see Dessborn et al., 2016; Hessen et al., 2017), as well as through cascading effects on other trophic levels in the food chain (Wood et al., 2017). For terrestrial habitats, there are several studies implying a negative impact of geese on other levels than macrophytes, including invertebrates, shorebirds, and small rodents (Milakovic & Jefferies, 2003; Samelius & Alisauskas, 2009; Kellett, 2021). Corresponding studies of large herbivorous waterfowl in aquatic environments are rare, although some address interspecific competition between swans or geese and smaller-bodied waterfowl within the same foraging guild. The general pattern in these studies, covering breeding as well as non-breeding seasons, seems to be that swans and geese do not clearly associate with other waterfowl negatively, but rather the other way around (Pöysä & Sorjonen, 2000; Guillaume et al., 2014; Pöysä et al., 2018; Holopainen et al., 2022). However, a broader ecosystem approach, including bottom-up as well as top-down perspectives and taxa at several trophic levels, is lacking in previous studies of the impact of large avian herbivores in aquatic environments.

Addressing the potential influence of large avian herbivores in aquatic ecosystems, the aim of the present study is to analyse relationships between their abundances and other patterns at different trophic levels in wetlands. Such patterns include abundances of other foraging guilds of waterbirds, macrophyte cover, as well as number of taxa and abundance of invertebrates. To account for differences between studied wetlands, explanatory variables also include total nitrogen, total phosphorous, water colour, turbidity, shoreline length, structural heterogeneity, and landscape type. The study was carried out in wetlands in southern Sweden, where greylag goose as well as whooper swan have expanded strongly in recent decades. Implications of the study are highly relevant for successful management of wetlands per se, but also for their inhabitants, not the least since several of them (waterfowl) are important game species (Madsen et al., 2015).

Methods

Study area and wetlands

Data were collected in 2021 in 37 wetlands in southernmost Sweden, spread over the province Skåne and

parts of the province Blekinge (Fig. 1). Studied wetlands had the following characteristics: (1) they are in the nemoral vegetation zone or in the transition area to the boreonemoral zone; (2) they are situated in landscapes in either open agricultural land or in forest; each wetland was hence classified based on the main surrounding landscape type (farmland, deciduous forest, or coniferous forest); (3) they represent a gradient from oligotrophic to eutrophic; (4) they are small to medium sized, ranging from 0.5 to 30.6 ha (mean: 4.8; SE: 1.0); two wetlands are too large to be covered from one vantage point for waterbird censuses (see below), for which segments instead were used, to be more comparable to areas of other wetlands (Supplementary Material 1); (5) waterbirds can be surveyed, and aquatic vegetation (hereafter denoted *macrophytes*) estimated, from one vantage point; (6) they are not subject to major disturbances such as fishing camps, human settlement, or heavy traffic; and (7) they did not harbour introduced farmed

mallards, which otherwise is a common practice in this part of Sweden (e.g. Söderquist et al., 2012). Wetland locations and other details are given in Fig. 1 and Supplementary Material 1.

Data collection

Survey scheme

All wetlands were visited once a month from April to July (four occasions in total) to cover the full breeding season of geese, swans, and other waterbirds, from pair settlement through the brood rearing period. Survey 1 was carried out April 6−8, survey 2 May 9−11, survey 3 May 31−June 7, and survey 4 July 5−7. Data on geese, swans, other waterbirds, and water chemistry were collected during all four surveys. Data on invertebrates and macrophytes were collected once (survey 3 and 4, respectively).
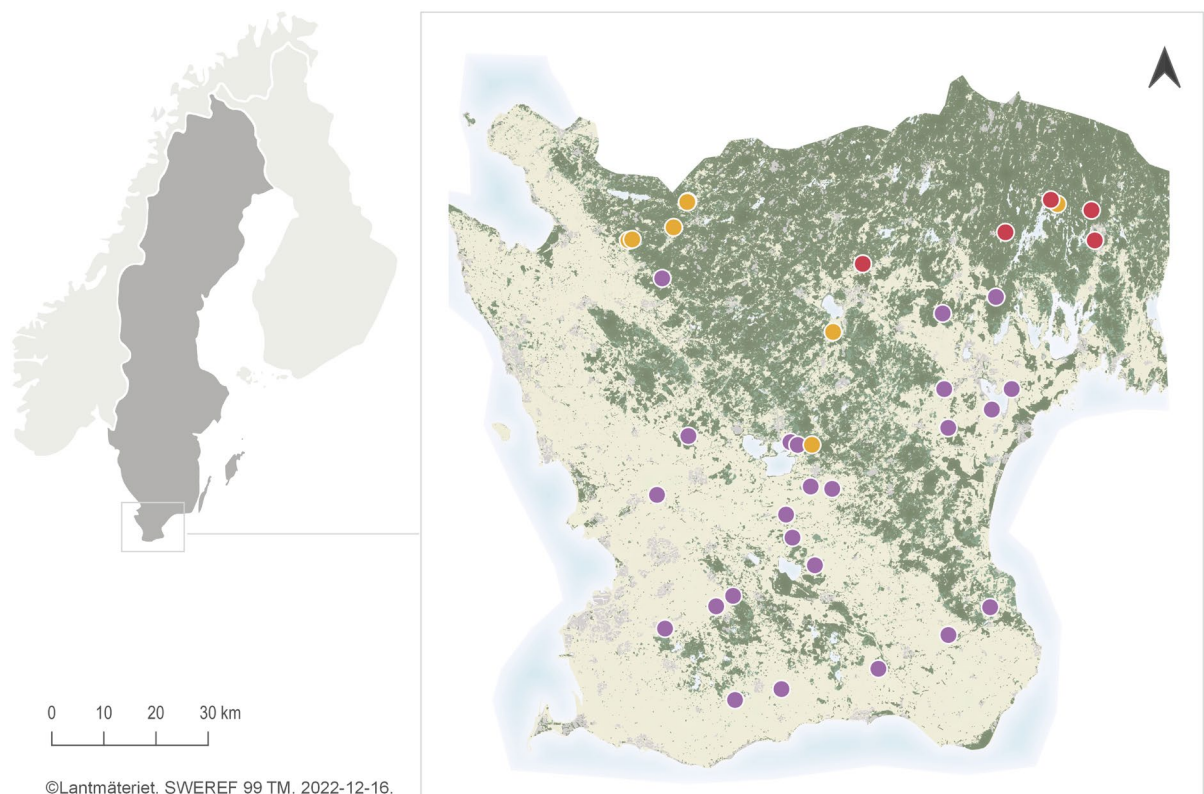

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Fig. 1 Location of the 37 study wetlands in southernmost Sweden. Main landscape types surrounding the wetlands are shown by the colour of the dots and were classified as farmland (purple), deciduous forest (orange), or coniferous forest (red)

Water chemistry

At each wetland, water samples were collected near the littoral zone right below water surface in a 1-l bottle for further analyses. On site measurements included conductivity (µS cm^{-1}), oxygen (% and mg l^{-1}), pH, and temperature (°C) measured with a Hach Lange portable Meter HQ40, turbidity (NTU) using a HACH portable turbidity meter USEPA, and chlorophyll measured with a Turner Design Aquafluor fluorometer. For water colour, total phosphorous, and total nitrogen samples, water was pumped through a 0.45-µm filter and poured into separate bottles. Water colour samples were stored in a refrigerator (+4 °C) and nutrient samples were frozen (− 18 °C) until laboratory analyses. Water colour was measured in a 5 cm cuvette at λ420 nm in accordance with the Swedish standard (SS-EN ISO 7887). Total phosphorous was measured according to the Swedish standard method (SS-EN ISO 6878:2005), and total nitrogen was estimated by persulphate digestion and spectrophotometric analysis at 275 nm according to method 4500-N described by Baird et al. (2017). See Supplementary Material 2 for mean values and ranges (min−max) of water chemistry variables in the study wetlands.

Geese, swans, and other waterbirds

Using a spotting scope and the point count method of Koskimies and Väisänen (1991), data on abundance of pairs, broods, and young of geese, swans, and other waterbirds were collected from one vantage point for ca 30 min at each wetland, at any time during daylight (range: 4.30 am–8.30 pm). Pairs, broods, and young were analysed separately, because they may respond differently to biotic and abiotic factors, as demonstrated in earlier studies of some species (Nummi & Pöysä, 1993; see also Elmberg et al., 2003, 2005). Geese and swans included species belonging to the genera *Anser*, *Branta*, and *Cygnus*, whereas other waterbirds included ducks (Tadorninae, Anatinae, and Aythyinae), divers (Gaviidae), grebes (Podicipedidae), cormorants (Phalacrocoracidae), herons (Ardeidae), rails (Rallidae), cranes (Gruidae), shorebirds (Charadriidae, Haematopodidae, and Scolopacidae), and gulls and terns (Laridae). The number of breeding pairs was assessed according to the *Waterfowl Route Form 4A* by Koskimies and Väisänen (1991).

This protocol includes counting of paired individuals (i.e. one female and one male seen together) and visible nests (with caution not to double count adults as other pairs). Moreover, it also accounts for the fact that in many species there may be cryptic incubating individuals (i.e. concealed nests), for which pair abundance was based on taxon-specific criteria. For example, for duck species except those belonging to the genera *Aythya* and *Bucephala*, males occurring in groups of ≤ 4 individuals were noted as the corresponding abundance of breeding pairs, whereas grebes and divers were noted as pairs if occurring as single or two birds together. In the subsequent statistical analysis (see below), we only used data on waterbirds qualifying as 'breeders' based on these criteria. We acknowledge that also non-breeders may affect wetland ecosystems. However, such birds are often not bound to specific wetlands for longer periods, which was the main reason to exclude them. Likewise, birds that were obvious transient visitors were also omitted (applicable for surveys 1 and 2), i.e. individuals in larger flocks and species known not to breed in the study area.

The maximum abundance of pairs for each species from any of the four surveys was used in the analyses. This was also applied to broods and young, except when age classification showed that a brood or chick had not been observed before. We used the schemes in Pirkola & Högmander (1974) to age ducklings and that in Hunter (1995) to age goslings. For other waterbirds, we used a self-developed scheme equivalent to those in the aforementioned papers (i.e. based on body size relative to full-grown birds and development of feathers), based on seven age categories from 'newly hatched' to 'nearly fledged'.

Mortality of waterbird young is generally highest during the first weeks after hatching (e.g. Talent et al., 1983; Paasivaara & Pöysä, 2007; Watts et al., 2018). To obtain a measure of abundance of young reflecting a high likelihood of becoming fledged, only those assessed to be more than ca 3 weeks old (i.e. age class ≥ 2a for ducks (Pirkola & Högmander, 1974) and category ≥ 4 for geese, swans, and other waterbirds (e.g. Hunter, 1995)) were used in subsequent analyses (see below).

Geese and swans, the focal species of this study, are obligate herbivores. Other waterbirds were categorised into alternative guilds based on their foraging behaviour, viz. surface feeder, benthic feeder,

invertivore, piscivore, and generalist (see Supplementary Material 3 for species list and foraging guild categorizations).

Macrophytes

Shoreline cover (percentage) was estimated in terms of macrophyte taxa, width, and height. Macrophyte taxa were trees (coniferous as well as deciduous), bushes (mainly *Salix* spp.), common reed, sedge (*Carex* spp.), water horsetail (*Equisetum fluviatile* Linnaeus, 1753), cattail (*Typha* spp.), and other herbaceous plant species pooled. Classifying plant taxa in this way is motivated by previous research on identifying important macrophytes for large herbivorous waterfowl (e.g. grazing effects of greylag geese on common reed; Bakker et al., 2018), and other waterbirds (dabbling ducks; sedge, water horsetail, cattail; Nummi et al., 1994). Width, i.e. perpendicular from shoreline to open water, was categorised into 0−1 m, 1−5 m, 5−10 m, and > 10 m and height into 0−0.25 m, 0.26−0.50 m, 0.51−1 m, and > 1 m. In addition to the shoreline macrophyte measurements, percent cover of floating macrophytes (algae and floating vascular plants) and structural heterogeneity were estimated. The latter was a measure of complexity of the wetland, estimated by counting the number of transitions between open water and > 1 m² macrophyte patches or islands from the shore to the wetland centre at ten evenly distributed points around the wetland. The mean of the ten values was used in the data analyses (see below). In all, we therefore followed the protocol for shoreline and floating macrophyte estimations described in Elmberg et al. (1993), with the modification that we used scanning with a spotting scope from one vantage point instead of walking around wetlands. The latter was judged to be unnecessary for accurate macrophyte size estimations since (1) the width and height intervals used were broad, (2) wetlands were generally quite small (i.e. with relatively short distances between observation spots and shoreline), and (3) adjacent obstacles with known sizes (e.g. boats, docks, waterbirds) were often present for relative comparison. If there was still any doubt, macrophytes were approached to ascertain the correct width and height intervals.

Invertebrates

Nektonic and benthic invertebrates were collected using activity traps, i.e. a 1-l transparent jar complemented with a funnel (opening: 102 mm; narrow end: 23 mm) attached to the opening (cf. Elmberg et al., 1993). Six traps in each wetland were placed at least 3 m apart at 0.5 m depth along a section of the shoreline representative of the wetland. Traps were oriented parallel to the shoreline and the opening of all traps faced the same direction within a wetland. After 48 h, traps were emptied and the invertebrate content assessed on site, that is, counted and identified to taxonomic group according to Supplementary Material 4, which is based on Table 2 in Nudds and Bowlby (1984). Bycatches included amphibian larvae (Anura spp.), newts (smooth newt (*Lissotriton vulgaris* Linnaeus, 1758) and northern crested newt (*Triturus cristatus* Linnaeus, 1758), as well as small fish (less than 50% of the fishes could be identified to species, and they included northern pike (*Esox lucius* Linnaeus, 1758), European perch (*Perca fluviatilis* Linnaeus, 1758), nine-spined stickleback (*Pungitius pungitius* Linnaeus, 1758), crucian carp (*Carassius carassius* Linnaeus, 1758), and Eurasian carp (*Cyprinus carpio* Linnaeus, 1758)). Although these are vertebrate taxa, they were included in the invertebrate nomenclature of this study since they are prey for some of the analysed waterbird foraging guilds.

Elmberg et al. (1992) demonstrated that vertebrate predators (fish and newts) in activity traps may reduce the number of taxonomic groups in catches. Contrasting catches with or without such predators did not, however, affect invertebrate data in our study, neither the number of taxonomic groups, nor total abundance (separate analyses for fish and newts; paired *t* tests, $P \geq 0.196$). Data from traps containing such predators were therefore included.

Invertebrates were divided into different size categories according to Nudds and Bowlby (1984): 1−2.5 mm, 2.6−7.5 mm, 7.6−12.5 mm, 12.6−20 mm, 21−40 mm, 41−60 mm, and > 60 mm. To get a general (weighted) measure of invertebrate abundance accounting for their size distribution, the number of trapped individuals in a certain size category was multiplied by the size interval's mid-size (i.e. 1.75, 5.05, 10.05, 16.30, 30.50, 49.50 mm; for the biggest size class, 60.00 mm was used instead of a central value), and the values of the size intervals

then summed. Finally, in line with previous studies (e.g. Elmberg et al., 2005), weighted abundance was standardised to 100 trap days, i.e. in our case using 50 as multiplier.

Statistical analyses

Dependent variables

To study associations with goose and swan abundances accompanied by other explanatory variables described below, modelling analyses were run in which different waterbird foraging guilds (abundance), macrophytes (cover), and invertebrates (abundance and number of taxa, respectively) were dependent variables in separate analyses. Some of the waterbird foraging guilds had too few observations of pairs, broods, or young to be analysed statistically (cf. Supplementary Material 5). Those that were included as dependent variables were surface feeders (pairs, broods, and young, respectively), benthic feeders (pairs and broods, respectively), and invertivores (pairs only). Concerning the latter and compared to other analyses, one wetland was excluded from the original sample because black-headed gull (*Chroicocephalus ridibundus* Linnaeus, 1766) bred there in very high numbers (250 pairs), thus constituting a distinct outlier compared to data from other wetlands. For macrophytes as dependent variables, percentage cover of sedge, cattail combined with water horsetail (see below), and other herbaceous plants were analysed separately. Cover of bushes and trees and common reed were not used as dependent variables due to scarce data or not fulfilling assumptions of residual normality. Concerning the latter, data for weighted abundance of invertebrates and the different macrophyte taxa were log-transformed.

Explanatory variables

The explanatory variables of main interest were goose and swan abundances, for which paired individuals and young were combined. Attempting to explain additional variation in data, other explanatory variables were also considered. For macrophytes and in line with Elmberg et al. (1993), a principal component analysis (PCA) was run for the different categories of taxa, width, and height (see above). Some macrophyte taxa yielded little data and were therefore

combined, which was justified by similar loadings on the first axis from the PCA. Data on trees and bushes were hence combined, and the same was done for water horsetail and cattail, after which a PCA was run once more. The loading on the first axis (PC1; explaining 24% of the variance) was eventually used as a general shoreline macrophyte variable in the modelling analyses, whereas floating macrophytes and structural heterogeneity were included as separate variables. Other explanatory variables considered were number of invertebrate taxa, weighted invertebrate abundance, wetland area, shoreline length, main landscape type (a three-level factor; farmland, deciduous forest, coniferous forest), and the various water chemistry measurements according to above. However, several of these variables were left out from the analyses since they turned out to be correlated (Pearson correlation $|r| > 0.6$; variance inflation factor > 3; e.g. Zuur et al., 2010); see Supplementary Material 6. Explanatory variables finally included were goose abundance, swan abundance, macrophytes (PC1), main landscape type (factor), and normalised measures of the following continuous variables: cover of floating macrophytes, structural heterogeneity, number of invertebrate taxa, weighted invertebrate abundance, total nitrogen, total phosphorus, water colour, turbidity, and shoreline length.

Modelling

Generalised linear modelling with negative binomial error structures was used for pairs and broods of surface and benthic feeders, for which package glmmTMP with negative binomial family (quadratic parametrization) was used (Brooks et al., 2017). Data for surface feeder young and invertivore pairs were frequently zero-valued and overdispersed, for which zero-inflated negative binomial models were used instead (i.e. same package as above, but with zero-inflation; Brooks et al., 2017). All other analyses, i.e. with macrophyte taxa and invertebrates as dependent variables, were done with linear modelling. Exhaustive screening of candidate sets was done with package glmulti (Calcagno & de Mazancourt, 2010) run with R 4.1.2 (R Core Team, 2021), using all the combinations of the main terms, but limited to no more than three in each model, and a null model with the intercept only. Consequently, 312 candidate models were considered for each dependent variable of the

waterbird foraging guilds and 244 candidate models for other dependent variables (macrophytes and invertebrates). From these candidate models, new model sets were formed including all models reaching 95% of evidence weight (model outputs for the 10 top models for each set are presented in Supplementary Material 7). Given model selection uncertainty, the Akaike weights (w_i) were summed for each variable across all the models in the 95% sets where the variable occurred to obtain variable-specific values (Burnham & Anderson, 2002). The higher the weight of a specific variable, the higher the importance relative to the other variables considered. Model-averaged estimates (β-values) of the variables weighted by w_i were calculated and 95% confidence intervals were used to evaluate importance.

Results

Waterbirds

In total, 28 breeding waterbird species were observed. Mean species richness per wetland was 6.8 (SE: 0.7). In terms of wetland occupancy (i.e. present as breeder or not), the most common species were mallard (*Anas platyrhynchos* Linnaeus, 1758), common goldeneye (*Bucephala clangula* Linnaeus, 1758), and Eurasian coot (*Fulica atra* Linnaeus, 1758), observed at most of the wetlands (i.e. 36, 25, and 24 wetlands, respectively; Supplementary Material 3). Instead looking at the mean number of breeding pairs, black-headed gull and tufted duck (*Aythya fuligula* Linnaeus, 1758) also stand out as common waterbirds (7.2 (SE: 6.8), and 2.0 (SE: 0.6), respectively; Supplementary Material 3). The mean abundance of breeding pairs per wetland (data from a colony of black-headed gull excluded; see "Methods section") was 17.2 (SE: 2.2) for all waterbird species combined. The corresponding mean abundance of broods and young was 3.6 (SE: 0.8) and 8.3 (SE: 2.2), respectively. For number of pairs, broods, and young of different foraging groups by wetland, see Supplementary Material 5.

Large herbivores

The focal species of this study, i.e. swans and geese, bred on almost half of the wetlands; mean 0.5 (SE: 0.1) pairs of swans and 2.0 (SE: 0.6) pairs of geese.

Table 1 Model-averaged estimates (β, with 95% confidence intervals; CI) for variables in the model set reaching 95% evidence weight (62 out of 312 models), explaining the variation in pair abundance of surface feeders

Variable	Estimate (β)	95% CI
Intercept	1.18	0.38; 1.98
Goose abundance*	0.01	0.00; 0.03
Main landscape type[a]*	0.93	0.17; 1.68
Number of invertebrate taxa*	1.39	0.26; 2.51
Total phosphorous*	1.69	0.50; 2.88
Weighted abundance of invertebrates*	1.45	0.32; 2.57
Cover of floating macrophytes	0.43	− 0.39; 1.29
Macrophytes (PC1)	0.12	− 0.01; 0.26
Main landscape type[b]	− 0.17	− 1.06; 0.71
Shoreline length	0.12	− 1.31; 1.54
Structural heterogeneity	0.45	− 0.97; 1.88
Swan abundance	0.13	− 0.02; 0.28
Total nitrogen	0.73	− 0.45; 1.92
Turbidity	− 0.44	− 1.75; 0.88
Water colour	− 1.28	− 2.86; 0.30

Important variables, based on the 95% CI values, are placed first and marked by an asterisk (*). See "Methods section" for details

[a]Coniferous forest compared to farmland

[b]Coniferous forest compared to deciduous

Mute swan and whooper swan were present on an equal number of wetlands, whereas greylag goose was clearly the most common goose species (Supplementary Material 3). The mean abundances of broods and young were 0.2 (SE: 0.1) and 0.3 (SE: 0.2) for swans and 1.5 (SE: 0.5) and 4.4 (SE: 1.8) for geese (cf. Supplementary Material 3).

Surface feeders

For pairs, broods, and young as dependent variables, it took 62, 119, and 13 models, respectively, to reach 95% of evidence weight. Modelling revealed that, based on the averaged variable estimates, abundances of surface feeder pairs and young were positively associated with weighted abundance of invertebrates and total phosphorous (Tables 1 and 2, Fig. 2). Surface feeder pairs were also positively related to goose abundance, number of invertebrate taxa, and was also higher in farmland wetlands compared to those in coniferous forest (Table 1, Fig. 2). Other explanatory

variables analysed for surface-feeding waterbirds were not important, as judged by the 95% confidence intervals of the estimates (Tables 1, 2, 3), except for water colour which was positively associated with abundance of young (Table 3, Fig. 2).

Benthic feeders

It took 147 and 197 models to reach 95% evidence weight for pairs and broods, respectively. For pairs, model-averaged variable estimates imply positive relationships with goose abundance and number of invertebrate taxa (Table 4, Fig. 2). Moreover, there were more pairs in farmland wetlands than in coniferous forest. There was also a strong negative relationship with water colour, i.e. the darker the latter, the lower the abundance of benthivore waterbird pairs (Table 4, Fig. 2). Other explanatory variables of benthic feeding waterbirds were not important (Tables 4 and 5).

Invertivores

For this guild data permitted modelling analyses for pair abundance only. Only one model was needed to reach 95% evidence weight, in which the three included variables were all important; shoreline length was positively related to pair abundance and the latter was also less in coniferous forest wetlands

compared to wetlands in deciduous forest and farmland (Table 6, Fig. 2).

Macrophytes

The most common shoreline macrophytes were "other herbaceous plants" (28%; SE: 5.4), followed by trees and bushes (24%; SE: 4.6), sedge (18%; SE: 3.8), common reed (14%; SE: 4.1), and cattail combined with water horsetail (13%; SE: 3.8). Most of the shoreline macrophytes were 1−5 m wide (57%; SE: 5.8), followed by the other width classes: 0−1 m: 22% (SE: 4.7), > 10 m: 11% (SE: 3.7), and 5−10 m: 9% (SE: 3.3). Corresponding values for shoreline macrophyte height were, also in descending order, > 1 m (60%; SE: 5.7), 0.26−0.5 m (20%; SE: 5.2), 0.51−1 m (15%; SE: 4.0), and 0−0.25 m (3%; SE: 1.2). Mean cover of floating macrophytes was 16% (SE: 3.8), and the mean structural heterogeneity was 1.4 (SE: 0.1).

Analyses of the macrophyte groups sedge, cattail combined with water horsetail, and "other herbaceous plants" as dependent variables required 86, 128, and 52 models, respectively, to reach 95% evidence weight. Sedge was positively related to water colour, and negatively related to cover of floating macrophytes (Table 7, Fig. 2). Cattail combined with water horsetail was positively related to total phosphorous and also had a higher cover in farmland wetlands than in coniferous forest wetlands (Table 8, Fig. 2). Finally, results of "other herbaceous plants" revealed

Table 2 Model-averaged estimates (β, with 95% confidence intervals; CI) for variables in the model set reaching 95% evidence weight (119 out of 312 models), explaining the variation in brood abundance of surface feeders

Based on the 95% CI values, no variables are considered important. See "Methods section" for details

[a] Coniferous forest compared to farmland

[b] Coniferous forest compared to deciduous

| Variable	Estimate (β)	95% CI
Intercept	− 0.90	− 2.80; 1.06
Cover of floating macrophytes	1.10	− 0.76; 2.95
Goose abundance	0.01	− 0.02; 0.04
Macrophytes (PC1)	0.05	− 0.29; 0.39
Main landscape type[a]	1.38	− 0.47; 3.22
Main landscape type[b]	− 20.37	− 29918.59; 29877.86
Number of invertebrate taxa	1.36	− 1.85; 4.56
Shoreline length	− 2.14	− 6.11; 1.84
Structural heterogeneity	0.68	− 2.14; 3.49
Swan abundance	0.19	− 0.20; 0.58
Total nitrogen	0.96	− 2.33; 4.25
Total phosphorous	2.02	− 1.14; 5.18
Turbidity	0.26	− 2.16; 2.68
Water colour	0.07	− 3.85; 3.99
Weighted abundance of invertebrates	0.73	− 2.17; 3.63
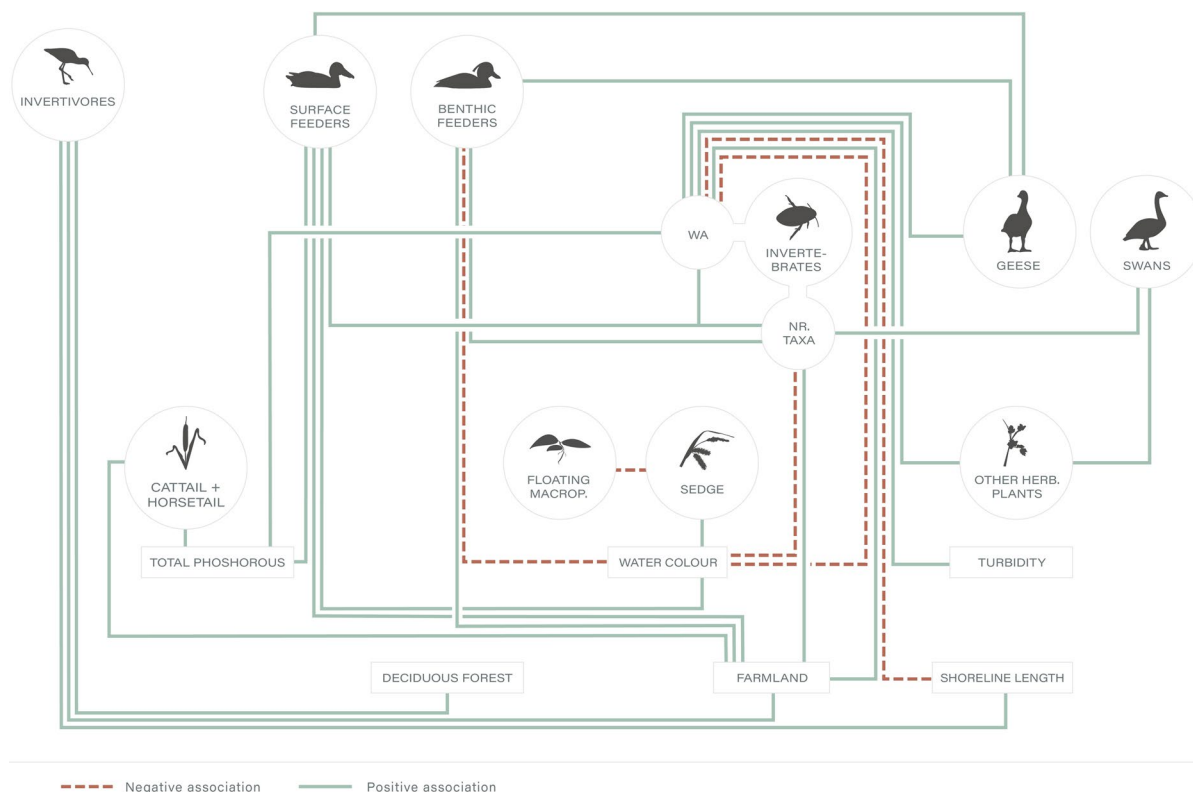
Fig. 2 Positive and negative associations between variables in the studied wetlands, including different foraging guilds of waterbirds (abundances of surface feeders, benthic feeders, invertivores, geese, and swans), invertebrates (number of taxa (*NR. TAXA*), and weighted abundance (*WA*)), different shoreline macrophyte taxa (cover of sedge, cattail in combination with water horsetail, and other herbaceous plants, respectively), floating macrophytes (cover), water chemistry variables (turbidity, water colour, and total phosphorous), shoreline length, and main landscape type (farmland and deciduous forest). All graphically presented associations are considered important as judged by model-averaged estimates in model sets reaching 95% evidence weight. For detailed results, see "Results section" and specifically Tables 1, 2, 3, 4, 5, 6, 7, 8, 9, 10, and 11. For details about variables and analyses, see "Methods" section"

positive associations with swan abundance as well as with weighted abundance of invertebrates (Table 9, Fig. 2). Other explanatory variables for the different macrophyte groups were not important.

Invertebrates

Amongst 27 taxa of invertebrates in the activity trap samples, mean catch per wetland was 11.6 (SE: 0.4) taxa. The most common taxon in terms of weighted abundance was Hirudinea (4447; SE: 2071), followed by Amphibia (2245; SE: 829) and Pisces (2195; SE: 748) (Supplementary Material 8). Other common taxa were Acari (1979; SE: 1675), Corixidae (1747; SE: 690), Ostracoda (1530; SE: 1259), Dytiscidae (1188; SE: 265), and Phyllopoda/Cladocera (1175;

SE: 965) (Supplementary Material 8). Almost half (13) of the total number of taxa was found in most (>50%) wetlands, of which the aforementioned (except Ostracoda) together with Chironomidae, Trichoptera, Ephemeroptera, Oligochaeta, Copepoda, and Isopoda were included.

Number of taxa

121 models were needed to reach 95% evidence weight in analyses with number of invertebrate taxa as dependent variable, which was positively related to swan abundance and negatively related to water colour (Table 10, Fig. 2). Moreover, there were more taxa in farmland wetlands than in coniferous

Table 3 Model-averaged estimates (β, with 95% confidence intervals; CI) for variables in the model set reaching 95% evidence weight (13 out of 312 models), explaining the variation in abundance of young of surface feeders

Variable	Estimate (β)	95% CI
Intercept	− 0.81	− 3.38; 1.77
Intercept from zero-inflation	− 0.34	− 1.91; 1.23
Total phosphorous*	2.20	0.09; 4.31
Water colour*	4.26	0.07; 8.44
Weighted abundance of invertebrates*	4.93	0.49; 9.36
Cover of floating macrophytes	1.38	− 1.03; 3.80
Goose abundance	− 0.01	− 0.06; 0.04
Main landscape type[a]	0.86	− 0.93; 2.66
Main landscape type[b]	− 20.62	− 28253.52; 28212.28
Number of invertebrate taxa	3.00	− 0.73; 6.73
Structural heterogeneity	− 1.81	− 5.08; 1.46
Swan abundance	0.19	− 0.18; 0.56
Turbidity	− 2.18	− 4.86; 0.49

Important variables, based on the 95% CI values, are placed first and marked by an asterisk (*). See "Methods section" for details

[a]Coniferous forest compared to farmland

[b]Coniferous forest compared to deciduous

forest wetlands. Other explanatory variables were not important (Table 10).

Weighted abundance

For weighted invertebrate abundance as dependent variable, 41 models were needed to reach 95% evidence weight. Several explanatory variables were associated, including positive relationships with goose abundance, number of invertebrate taxa, total phosphorous, and turbidity. In contrast, there were negative relationships with shoreline length and water colour. Finally, there was a higher weighted abundance of invertebrates in farmland wetlands compared to coniferous forest wetlands (Table 11, Fig. 2). Other explanatory variables were not important (Table 11).

Discussion

Many goose and swan populations have increased strongly in numbers in recent decades, raising concerns about their potential negative impacts through herbivory in aquatic ecosystems. To address this, we studied how abundance and richness of other inhabitants of wetlands across multiple trophic levels are associated with abundances of geese and swans.

Acknowledging that our approach is correlative and therefore cannot demonstrate causality, we found limited evidence for deleterious effects. Firstly, pair and brood numbers of other waterbirds were not negatively associated with numbers of geese and swans for any of the feeding guilds analysed (surface feeders, benthic feeders, and invertivores). To the contrary, important relationships rather indicated positive association between geese/swans and other taxa. Secondly, the cover of herbaceous plants other than common reed, sedge, cattail, and water horsetail was positively related to swan abundance, and finally, the number of invertebrate taxa was positively associated with swan abundance, whilst overall abundance of invertebrates was positively associated with goose abundance.

Associations between large herbivores and other waterbirds

Our findings of positive associations between geese and other waterbirds are largely in line with those of Holopainen et al. (2022), who studied relationships between two large avian herbivores, the whooper swan and Canada goose (*Branta canadensis* Linnaeus, 1758), and other waterbirds in Finland. These authors found that abundances of surface feeders,

Table 4 Model-averaged estimates (β, with 95% confidence intervals; CI) for variables in the model set reaching 95% evidence weight (147 out of 312 models), explaining the variation in pair abundance of benthic feeders

Variable	Estimate (β)	95% CI
Intercept	0.55	− 1.20; 2.29
Goose abundance*	0.02	0.00; 0.04
Main landscape type[a]*	1.43	0.25; 2.61
Number of invertebrate taxa*	2.23	0.48; 3.97
Water colour*	− 3.35	− 6.51; − 0.19
Cover of floating macrophytes	0.27	− 1.02; 1.56
Macrophytes (PC1)	0.17	− 0.04; 0.37
Main landscape type[b]	0.28	− 1.07; 1.63
Shoreline length	− 0.01	− 2.21; 2.19
Structural heterogeneity	0.47	− 2.00; 2.93
Swan abundance	0.15	− 0.11; 0.42
Total nitrogen	1.33	− 0.76; 3.41
Total phosphorous	1.75	− 0.25; 3.75
Turbidity	− 1.38	− 4.11; 1.35
Weighted abundance of invertebrates	1.41	− 0.43; 3.25

Important variables, based on the 95% CI values, are placed first and marked by an asterisk (*). See "Methods section" for details

[a]Coniferous forest compared to farmland

[b]Coniferous forest compared to deciduous

diving ducks, and piscivorous waterbirds were generally higher at sites where whooper swan was present, compared to sites where it was absent, whilst abundances of surface feeders and piscivores, but not of benthic diving ducks, were positively associated with Canada goose presence (Holopainen et al., 2022). In addition, the Finnish data indicate that the numbers of surface feeders and diving ducks were positively associated with whooper swan colonisation, i.e. although smaller waterbirds have been largely declining, the decrease has not been as strong at sites colonised by whooper swans between the 1980s and 2020s.

Combining results of this study and those of Holopainen et al. (2022), from the nemoral and the boreal vegetation zones, respectively, suggest that large herbivorous waterbirds do not have direct negative impact on populations of other waterbirds. It should be noted, though, that both studies are based on data in which breeding numbers of different species are pooled into foraging guilds. Within a foraging guild, species may differ in susceptibility to impacts from swans and geese. For example, surface-feeding dabbling duck species differ in how similar they are to whooper swan in terms of ecomorphological characteristics and feeding depth. Even so, a negative impact of whooper swan colonisation was not found on breeding numbers of three dabbling duck species, viz. Eurasian wigeon (*Mareca penelope* Linnaeus, 1758), Eurasian teal (*Anas crecca* Linnaeus, 1758), and mallard (Pöysä & Sorjonen, 2000). In another

Table 5 Model-averaged estimates (β, with 95% confidence intervals; CI) for variables in the model set reaching 95% evidence weight (197 out of 312 models), explaining the variation in brood abundance of benthic feeders

Variable	Estimate (β)	95% CI
Intercept	− 3.46	− 13051.15; 13044.23
Cover of floating macrophytes	0.65	− 1.81; 3.12
Goose abundance	0.00	− 0.04; 0.05
Macrophytes (PC1)	0.01	− 0.46; 0.48
Main landscape type[a]	20.88	− 32525.78; 32567.54
Main landscape type[b]	18.93	− 32527.73; 32565.59
Number of invertebrate taxa	1.60	− 1.87; 5.06
Shoreline length	− 5.92	− 12.14; 0.31
Structural heterogeneity	0.28	− 3.90; 4.47
Swan abundance	0.36	− 0.17; 0.89
Total nitrogen	1.63	− 2.46; 5.72
Total phosphorous	2.41	− 2.00; 6.82
Turbidity	− 2.85	− 8.88; 3.18
Water colour	1.16	− 4.54; 6.86
Weighted abundance of invertebrates	0.85	− 2.97; 4.68

Based on the 95% CI values, no variables are considered important. See "Methods section" for details

[a]Coniferous forest compared to farmland

[b]Coniferous forest compared to deciduous

Table 6 Estimates (β, with 95% confidence intervals; CI) for variables in the model set reaching 95% evidence weight (1 out of 312 models), explaining the variation in pair abundance of invertivores

Variable	Estimate (β)	95% CI
Intercept	− 3.46	− 6.15; − 0.77
Intercept from zero-inflation	− 1.16	− 2.78; 0.46
Main landscape type[a]*	3.18	0.96; 5.41
Main landscape type[b]*	2.97	0.78; 5.15
Shoreline length*	4.03	1.35; 6.71

Based on the 95% CI values, all variables are considered important and marked by an asterisk (*). See "Methods section" for details

[a]Coniferous forest compared to farmland

[b]Coniferous forest compared to deciduous

Table 7 Model-averaged estimates (β, with 95% confidence intervals; CI) for variables in the model set reaching 95% evidence weight (86 out of 244 models), explaining the variation in shoreline cover of sedge (*Carex* spp.)

Variable	Estimate (β)	95% CI
Intercept	− 1.60	− 2.26; − 0.94
Cover of floating macrophytes*	− 0.85	− 1.61; − 0.08
Water colour*	1.74	0.50; 2.98
Goose abundance	0.00	− 0.02; 0.01
Main landscape type[a]	− 0.13	− 0.95; 0.70
Main landscape type[b]	0.56	− 0.23; 1.34
Number of invertebrate taxa	− 0.59	− 1.74; 0.57
Shoreline length	− 0.15	− 1.23; 0.92
Structural heterogeneity	− 0.01	− 1.13; 1.12
Swan abundance	− 0.07	− 0.20; 0.06
Total nitrogen	− 0.01	− 1.06; 1.05
Total phosphorous	− 0.54	− 1.57; 0.48
Turbidity	− 0.13	− 1.26; 1.00
Weighted abundance of invertebrates	− 0.81	− 1.87; 0.26

Important variables, based on the 95% CI values, are placed first and marked by an asterisk (*). See "Methods section" for details

[a]Coniferous forest compared to farmland

[b]Coniferous forest compared to deciduous

Table 8 Model-averaged estimates (β, with 95% confidence intervals; CI) for variables in the model set reaching 95% evidence weight (128 out of 244 models), explaining the variation in shoreline cover of cattail (*Typha* spp.) in combination with water horsetail (*Equisetum fluviatile*)

Variable	Estimate (β)	95% CI
Intercept	− 1.83	− 2.50; − 1.16
Main landscape type[a]*	0.85	0.11; 1.58
Total phosphorous*	1.25	0.22; 2.29
Cover of floating macrophytes	− 0.21	− 1.00; 0.58
Goose abundance	0.00	− 0.02; 0.01
Main landscape type[b]	0.34	− 0.37; 1.06
Number of invertebrate taxa	− 0.69	− 2.05; 0.67
Shoreline length	− 0.61	− 1.67; 0.45
Structural heterogeneity	− 0.10	− 1.22; 1.02
Swan abundance	0.00	− 0.14; 0.13
Total nitrogen	0.23	− 0.82; 1.29
Turbidity	0.18	− 1.17; 1.54
Water colour	− 0.93	− 2.18; 0.31
Weighted abundance of invertebrates	− 0.06	− 1.16; 1.03

Important variables, based on the 95% CI values, are placed first and marked by an asterisk (*). See "Methods section" for details

[a]Coniferous forest compared to farmland

[b]Coniferous forest compared to deciduous

species-level study, lake occupation by Eurasian wigeon was positively associated with presence of whooper swan (Pöysä et al., 2018). Similar findings are reported for mute swan, whose presence has been found to be positively correlated to numbers of other smaller-bodied waterbirds, such as Eurasian coot, common pochard, and red-crested pochard *Netta rufina* Pallas, 1773 (Broyer, 2009; Gayet et al., 2011). However, addressing impacts of swans and geese on other waterbirds more generally, focusing on similarity in terms of foraging ecology only, may not be comprehensive enough. For example, species may differ also in terms of nesting ecology; those that nest in the part of a wetland where large herbivores nest may benefit relatively more from their presence (see discussion in Holopainen et al., 2022 for possible warning and indirect nest defence function of whooper swan).

Other reasons for positive relationships between swans or geese and other foraging guilds may include heterospecific attraction and foraging niche facilitation. The former has previously been demonstrated in bird communities (Mönkkönen & Forsman, 2002), including waterfowl (Elmberg et al., 1997), for

Table 9 Model-averaged estimates (β, with 95% confidence intervals; CI) for variables in the model set reaching 95% evidence weight (52 out of 244 models), explaining the variation in shoreline cover of "other herbaceous plants"

Variable	Estimate (β)	95% CI
Intercept	− 2.03	− 2.63; − 1.44
Swan abundance*	0.22	0.08; 0.37
Weighted abundance of invertebrates*	1.56	0.39; 2.72
Cover of floating macrophytes	0.09	− 0.79; 0.96
Goose abundance	0.01	− 0.00; 0.03
Main landscape type[a]	0.41	− 0.40; 1.22
Main landscape type[b]	− 0.50	− 1.32; 0.31
Number of invertebrate taxa	1.12	− 0.11; 2.35
Shoreline length	0.42	− 0.71; 1.55
Structural heterogeneity	0.46	− 0.78; 1.69
Total nitrogen	0.81	− 0.32; 1.94
Total phosphorous	− 0.57	− 1.72; 0.58
Turbidity	− 0.55	− 1.81; 0.71
Water colour	− 0.71	− 2.02; 0.60

Important variables, based on the 95% CI values, are placed first and marked by an asterisk (*). See "Methods section" for details

[a]Coniferous forest compared to farmland

[b]Coniferous forest compared to deciduous

Table 10 Model-averaged estimates (β, with 95% confidence intervals; CI) for variables in the model set reaching 95% evidence weight (121 out of 244 models), explaining the variation in number of invertebrate taxa

Variable	Estimate (β)	95% CI
Intercept	5.30	3.48; 7.13
Main landscape type[a]*	2.09	0.46; 3.72
Swan abundance*	0.36	0.03; 0.68
Water colour*	− 3.34	− 6.31; − 0.37
Cover of floating macrophytes	0.23	− 1.75; 2.20
Goose abundance	0.01	− 0.03; 0.05
Macrophytes (PC1)	0.18	− 0.14; 0.50
Main landscape type[b]	0.39	− 1.34; 2.13
Shoreline length	− 0.97	− 3.71; 1.77
Structural heterogeneity	1.64	− 1.18; 4.45
Total nitrogen	− 0.27	− 3.50; 2.96
Total phosphorous	− 1.53	− 4.29; 1.22
Turbidity	− 2.63	− 5.30; 0.03
Weighted abundance of invertebrates	2.44	− 0.26; 5.13

Important variables, based on the 95% CI values, are placed first and marked by an asterisk (*). See "Methods section" for details

[a]Coniferous forest compared to farmland

[b]Coniferous forest compared to deciduous

which the proximate explanation is that birds present signal safe and productive sites in less predictive environments (Mönkkönen et al., 1990). Foraging niche facilitation on the other hand is a commensal

Table 11 Model-averaged estimates (β, with 95% confidence intervals; CI) for variables in the model set reaching 95% evidence weight (41 out of 244 models), explaining the variation in weighted abundance of invertebrates

Variable	Estimate (β)	95% CI
Intercept	8.12	7.03; 9.21
Goose abundance*	0.02	0.00; 0.03
Main landscape type[a]*	1.07	0.21; 1.92
Number of invertebrate taxa*	2.59	1.22; 3.95
Shoreline length*	− 1.31	− 2.58; − 0.04
Total phosphorous*	1.43	0.22; 2.64
Turbidity*	1.49	0.19; 2.79
Water colour*	− 1.76	− 3.34; − 0.18
Cover of floating macrophytes	0.83	− 0.09; 1.76
Macrophytes (PC1)	0.11	− 0.05; 0.27
Main landscape type[b]	0.43	− 0.48; 1.34
Structural heterogeneity	− 0.91	− 2.30; 0.49
Swan abundance	− 0.02	− 0.22; 0.18
Total nitrogen	− 0.26	− 1.69; 1.17

Important variables, based on the 95% CI values, are placed first and marked by an asterisk (*). See "Methods section" section for details

[a]Coniferous forest compared to farmland

[b]Coniferous forest compared to deciduous

interaction that has been suggested to be provided by swans (Kjällander, 2005; Gyimesi et al., 2012). Their digging and trampling in the bottom substrate may facilitate foraging by other birds by exposing benthos or vegetative parts, such as roots or tubers. Moreover, there are observations that swan faeces may be used as a food resource by ducks (Shimada, 2012).

Associations between large herbivores, macrophytes, and invertebrates

In addition to the positive associations between large avian herbivores and other waterbirds described above, we found either a few positive associations or no association at all, with swans and geese across other trophic levels studied. For macrophytes, this is in line with the review by Guillaume et al. (2014) on ecological effects of mute swan, concluding that this species does not systematically affect aquatic plants negatively. However, other swan and goose studies show the opposite. For example, Allin and Husband (2003) demonstrated reduced biomass of submersed macrophytes caused by mute swan grazing

in a Rhode Island coastal pond, and Reijers et al. (2019) used exclosures in a brackish marsh in the Netherlands to show that greylag geese affected the spatial structure of common reed negatively. Likewise, Bakker et al. (2018) found, in a series of field experiments performed in two Dutch lakes, that grazing pressure by greylag geese in summer negatively affected reed stem density and height. However, unlike the breeding density of geese and swans in the wetlands studied by us, the summer-time density of greylag geese in the lakes studied by Bakker et al. (2018) was very high (maximum monthly counts were typically several hundreds or even thousands of birds). Although the lakes in the latter study are much larger (85 and 160 ha, respectively) than those in our study, i.e. defining the actual density (number/ha), we still argue that the densities of geese and swans in our study were simply too low to affect macrophytes. In fact, out of our 37 study wetlands, less than 10 had relatively high numbers of pairs, broods, or young of geese and swans (see Supplementary Material 5).

To our knowledge, there are few prior studies relating goose and swan abundances to aquatic invertebrates, i.e. similar to what has been reported for mammal herbivory, such as from the muskrat (*Ondatra zibethicus* Linnaeus, 1766) (Nummi et al., 2006). One exception is Allin and Husband (2003), who showed that grazing by mute swan may lead to cascade effects reducing the abundance of some invertebrate taxa. On the other hand, Jensen et al. (2019) reported positive relationships between goose abundance and invertebrate taxon richness and species composition, possibly due to a fertilisation effect from goose droppings. There are some additional studies from terrestrial habitats, in which goose grazing has been suggested to lead to lower richness, diversity, and abundance of some invertebrate taxa, possibly due to habitat degradation (Milakovic & Jefferies, 2003; Sherfy & Kirkpatrick, 2003). However, as for aquatic environments, other studies show the opposite, i.e. a higher abundance and biomass of some terrestrial invertebrate taxa in areas affected by goose grazing compared to those that were not (Flemming et al., 2022). In line with Jensen et al. (2019), the authors of the latter study suggest that geese may enhance conditions for invertebrates by faecal deposition, although there may be also other underlying explanations linked to micro-habitat characteristics. With the present data, we cannot say if this is true also at our sites, for which

we demonstrate positive relationships between goose or swan abundance and invertebrate abundance or richness. If not so, such patterns may reflect habitat preference in which productive wetlands are more frequently used by swans and geese than less productive ones.

Water chemistry associations

Eutrophication, causing overgrowth of open water and increased abundance of cyprinid fish competing with some waterbirds for food, has been identified as one of the reasons for population declines of waterbirds in boreal lakes and elsewhere (Pöysä et al., 2013; Fox et al., 2016; Lehikoinen et al., 2016; see also Elmberg et al., 2020; Pöysä & Linkola, 2021). Against this background it is noteworthy that abundances of several foraging guilds of waterbirds in the present study were positively associated with variables that typically are coupled with eutrophication. Phosphorous has indeed been used as a measure of eutrophication, and waterbodies surrounded by agricultural land have been recognised as highly susceptible to eutrophication (e.g. Ekholm & Mitikka, 2006; Withers & Haygarth, 2007). Interestingly, invertebrate variables, too, were positively related to farmland landscapes, which in part may explain the aforementioned associations. Nevertheless, our finding is in line with those from Finland, which demonstrate that whilst populations of surface-feeding waterbirds and diving ducks have decreased more in eutrophic lakes than in oligotrophic, their abundances are still higher in eutrophic lakes (Holopainen et al., 2022). We do not know if or how the trophic status of the wetlands studied by us has changed over time, nor do we have long-term data to assess any changes in their waterbird abundances. Yet, the positive associations between several waterbird foraging guilds and phosphorous and farmland landscapes suggest that the eutrophic wetlands studied by us are still attractive breeding habitats to these birds.

Negative associations between water colour and benthic feeders and invertebrates are interesting, and explanations may be several, although not mutually exclusive. Benthic feeders rely on visual cues when searching for invertebrate prey, the detectability of which is reduced as water colour increases. Moreover, previous research shows that zoobenthos are controlled indirectly by water colour, via benthic primary production negatively affected by light attenuation, and linked to water colour (Karlsson et al., 2009). The latter study even argues that light is more important than nutrients for production in some wetlands. At any rate, water colour is a variable of current relevance since the concentration of dissolved organic carbon has increased (a process known as "brownification") in recent decades (Monteith et al., 2007). Hence, one novel implication of our results is that at least benthic feeding waterfowl may be disfavored by this trend. In fact, in a long-term study of boreal lakes in Finland it was found that the abundance of aquatic invertebrates decreased concurrently with increasing water brownification (Arzel et al., 2020). If this is a causal pattern, one explanation suggested by the latter authors is that increasing brownification has negative impacts on the vegetative habitat and food resources of invertebrates.

Conclusions

The present study, which demonstrates mainly positive associations between large avian herbivores (i.e. geese and swans) and other trophic levels, largely concurs with Holopainen et al. (2022) and provides a welcome corroborating nemoral counterpart. Studies like ours covering a large spatial scale, several trophic levels, and abiotic factors are rare, likely due to complex, time-consuming, and expensive data collection. Yet, studies of this type are necessary to understand ecosystem dynamics and to make reliable and accurate decisions in the management of ecosystems and their components.

A conservation implication for wetland ecosystems emanating from the patterns in our study is that one should not be overly concerned about the expansion of large avian herbivores. However, we must bear in mind that the guild-level approach in the present study and in Holopainen et al. (2022) might mask negative associations at the species level. Moreover, and maybe more importantly, we acknowledge the facts that the design of this study, being correlative and short term (one year), and that the densities of swan and goose pairs were relatively low in most wetlands do not allow us to rule out the possibility that large avian herbivores when occurring at high densities still may be involved in driving negative changes—acting as a *hub of the wheel*—in

wetlands in the long term. Alternatively, when densities are moderate, as in most of our study wetlands, we suggest that geese and swans function as *hitchhikers*, i.e. being promoted by productive ecosystems without causing negative effects to them. To further address this issue, we encourage future research to focus on long-term patterns and in systems with high densities of large herbivorous waterfowl.

To obtain a deeper understanding of the causal processes behind the patterns observed in this study, we also call for lake-level studies of behavioural interactions between large avian herbivores and smaller-sized species in other foraging guilds. Specifically, we need to explore interference competition at the species level, interspecific aggression, and the role of large avian herbivores as possible enhancers of nesting success in smaller waterbirds. Finally, important management implications may emerge from quantitative studies in which the effects of large avian herbivores on aquatic vegetation and invertebrate abundance are studied experimentally, for example, using exclosure designs. Such studies could be of special importance in aquatic ecosystems facing brownification or high levels of turbidity, where the amount of submerged vegetation is crucial for food web stability and water quality and where the knowledge about waterfowl herbivory is sparse.

Data availability The datasets generated and/or analysed during the current study are available from the corresponding author on reasonable request.

Declaration

Competing interest The authors have no competing interests to declare that are relevant to the content of this study.

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