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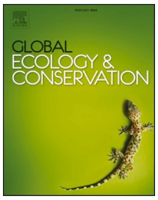

A rapid increase of large-sized waterfowl does not explain the population declines of small-sized waterbird at their breeding sites

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ABSTRACT

Certain species experience rapid population increases in human-modified and -affected environments. Conservation actions and increased wintertime food availability have led to a population increase of several large herbivorous waterbird species. In Northern Europe, this trend is opposite to the overall decrease of several smaller waterbird species. We examined whether the recovery of a flagship species, the whooper swan (*Cygnus cygnus*), and the spreading of the non-native Canada goose (*Branta canadensis*), cause asymmetric competition with other sympatric waterbirds at their breeding sites. We used data from the national Finnish waterbird surveys collected in the late 1980s and early 2020 s at 942 sites, to assess the site-level effects of large herbivore occurrence on other waterbird species, while considering their trophic overlap. We hypothesised that there could be competitive effects of large herbivorous on smaller species, especially those with similar foraging niches. We however found that other waterbird populations have decreased less at sites occupied by whooper swans since the 1980 s. Canada goose site occupation was not associated with the abundance of other waterbirds. Thereby, our findings are not consistent with the suggestion that population increases of large herbivore species lead to asymmetric competition on the breeding wetlands. The whooper swan may potentially act as an indicator of habitat quality and further on as a flagship umbrella species with multidisciplinary conservation benefits, of which may accrue benefits also to other waterbirds exhibiting declining population trends. Our findings underline the importance of considering species interactions when designing and implementing management actions in conservation strategies.

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1. Introduction

Humans interfere directly with animal communities and their functions by harvesting and subsidising species, and indirectly by affecting habitat quality and quantity (Santulli et al., 2014; Boyce, 2018). Anthropogenic pressures include global drivers, such as climate change, which pushes populations towards the poles (Pavón-Jordán et al., 2019), but also local drivers such as habitat loss and degradation, or hunting and persecution (BirdLife International, 2015). While modern conservation biology has produced great success stories of restored species and ecosystem functions (Deinet et al., 2013; Chapron et al., 2014; Boyce, 2018), rapid recovery of one species may cause unintended conservation consequences via complex interspecific interactions. This has occasionally triggered situations, in which a locally increasing, protected species heightens the vulnerability of threatened co-occurring species, often due to anthropogenic-driven changes in the environment. For example, populations of apex predators, such as the white-tailed eagle (*Haliaeetus albicilla;* Hipfner et al., 2012; Reusch et al., 2018) and the grey wolf (*Canis lupus*, Kojola et al., 2009; Chapron et al., 2014), have increased widely after the species were protected from persecution and pollution. However, both are now observed to be threatening some of their prey populations, as their communities and habitats have experienced prominent anthropogenic-driven changes (e.g. introductions of alien predators or apparent competition; Kojola et al., 2009; Hipfner et al., 2012; Jaatinen et al., 2022).

Europe and North America have long lacked several large waterbird species, such as swans and geese, due to intensive hunting. However, after increasing conservation efforts, several of these larger species are recovering (Boiko, 2010; Deinet et al., 2013; Baldassarre, 2014) and represent flagship species for wetland conservation (Stroud et al., 2017). For example, in Northwest Europe, wintering whooper swan (*Cygnus cygnus*) population increased from c. 59 000 in 1995–138 500 in 2015 (Laubek et al., 2019) and Canada goose (*Branta canadensis*) population from 60 000 in 1990 s to 90 000 in 2009 (Fox et al., 2010). These positive trends contrast to many smaller waterbird species in Northern Europe, where population trends of many waterbirds are alarmingly negative (Elmberg et al., 2020). The rapid increases in the breeding numbers of swans and geese, including the non-native Canada goose, raise concerns about the potential for asymmetric competition over food and/or space leading to negative impacts on the breeding success of smaller waterbirds (e.g. Pöysä and Sorjonen, 2000; Hilli-Lukkarinen et al., 2011; Pöysä et al., 2018).

Within communities, competition for resources is often asymmetric and unequal, leading to superior competitors, which can in some cases be non-native species (Mack et al., 2000; Santulli et al., 2014), excluding other species from their niches (Begon et al., 2006). Therefore, population changes of superior competitors may affect other sympatric species (Chen et al., 2020). Asymmetric competition is expected to be emphasised when competing species exhibit size differences (Begon et al., 2006). As large herbivores, swans and geese consume substantial amounts of vegetation (Cramp et al., 1986). Overgrazing and habitat degradation are potential risks, especially when populations are freed from natural limiting factors. Agricultural landscapes offer superior foraging opportunities as compared to the natural habitats of large herbivorous waterbirds, and so subsidise the carrying capacities of the winter habitats of these species (Moser and Kalden, 1992; van Eerden et al., 2005; Fox et al., 2017), creating potential conflicts with other smaller species (i.e. resource depletion) as well as farmers (Strong et al., 2021). In Canada, snow geese (*Chen caerulescens*) populations have increased strongly, resulting in overgrazing and a subsequent long-term decline in Savannah sparrow (*Passerculus sandwichensis*) populations, due to a dramatic reduction in the shrub habitat preferred by the sparrows for breeding (Peterson et al., 2013, 2014). Furthermore, many swan and goose species have been observed to behave aggressively towards other waterbird species possibly leading to asymmetric interference competition (Wood et al., 2020).

The perception that large waterfowl are harmful to smaller waterfowl has management and conservation implications, since these perceptions might affect hunters' attitudes and social norms (Jager et al., 2016). In Finland, the whooper swan, a conservation flagship species, currently exhibits a strong ongoing population increase after near extinction in the 1950s (Väisänen et al., 1998, 2011). At the same time many smaller waterbird species – especially those preferring eutrophic waters – have decreased and are currently classified as threatened (Lehikoinen et al., 2016, 2019; Pöysä and Linkola, 2021). In public discourse, the recovery of the whooper swan has been suggested as one of the reasons for the general waterbird declines. Within the scientific community, evidence is mounting for anthropogenic impacts such as increasing alien predator pressure and changes in the physico-chemical status of lakes being the main culprits behind the declining waterbird numbers (see Pöysä et al., 2019; Holopainen and Lehikoinen, 2022).

Knowing the true nature of species interactions underpins our understanding of community functioning, which in turn is of crucial importance for implementing suitable conservation and management actions. Here, we assess the long-term, lake-level effects of whooper swan and Canada goose occurrence on other waterbird species, while accounting for their trophic overlap. We hypothesise that the occurrence of large herbivores has a negative effect on surface-feeding waterbirds due to food and space competition, while no such effect is seen in other foraging guilds (with differing diet and habitat preferences). The expected patterns supporting this hypothesis would be lower numbers of surface-feeding waterbirds at sites that host whooper swans or Canada geese, and, in particular, a steeper decline of surface-feeding waterbirds at sites that have been colonised by large herbivores after the 1980 s as compared to sites that have not been colonised by them. This pattern is expected to be accompanied by a more positive trend in surface-feeding waterbirds at sites where the large herbivores have disappeared.

2. Material and methods

2.1. Study species

The whooper swan and Canada goose are large herbivorous species typically breeding in the boreal zone (Kampe-Persson, 2010; Keller et al., 2020; Birdlife International, 2022). After implementation of conservation actions (e.g., a hunting prohibition), the population of the whooper swan has increased during the past few decades throughout its range (Luigujõe et al., 2002; Butkauskas et al., 2012; Elmberg et al., 2020). Hunting regulations for the whooper swan took place gradually in Northern Europe: in Sweden hunting was banned in 1927 (Nilsson et al., 1998), in Finland in 1934 (Hautala and Suominen, 1991) and in Estonia in 1957 (Luigujõe et al., 2002). Complete ban on shooting birds at Lake Constance in Germany/Switzerland in 1985 subsequently increased the wintering population of whooper swan because of the reduced disturbance (Schneider-Jacoby et al., 1991).

In Finland, pair numbers increased from 15 in the 1940s to 9 000–12 000 in the 2010s, and the species' range now covers the entire country (Väisänen et al., 1998; Lehikoinen et al., 2019a,2019b). The Canada goose was introduced to Northern Europe at the beginning of the 20th century and to Finland in the 1960 s. Their population growth in Finland was low until recent decades, when the population increased rapidly from 300 to 500 pairs in the late 1980s to 4 900–6 300 pairs in the 2010 s, with population growth strongest in southern and central parts of the country (Väisänen et al., 1998; Lehikoinen et al., 2019).

To evaluate whether there are foraging niche-related differences in the effects caused by whooper swans and Canada geese within the waterbird community, we classified waterbirds into three foraging guilds according to their foraging niches: surface feeders, invertivore diving ducks and piscivores (Cramp et al., 1986; Table A1; see Table A2 for trends). Out of these groups, surface feeders utilise the most similar habitat and food compared to swans and geese, while piscivores only share the same habitat. Invertivore diving ducks (hereafter diving ducks) share the same habitat and partly utilise the same food source as swans and geese. The horned grebe (*Podiceps auritus*) was classified as a diving duck, as the species' diet constitutes mainly of invertebrates during the breeding season (Fjeldså, 1973).

2.2. Survey data

The voluntary-based Finnish national waterbird pair surveys that began in 1986 is a standardised method used for monitoring waterbirds in Finland (Anon, 1991; see Appendix A). After a high effort in the beginning of the survey scheme, several sites were later left outside the survey. However, in 2020 and 2021, a large effort was put into repeating surveys at these sites, and the same volunteers conducted the surveys when possible. Thus, the data included in our study were collected during two periods: 1986–1989 (period 1) and 2020–2021 (period 2). In the analyses, we used the site-, year- and species-specific numbers of observed waterbird pairs as the response variable.

While surveying waterbirds, voluntary birdwatchers also classify wetland habitat types based on vegetation, shoreline structure and water depth (Table A3). The main habitat classification has been made between freshwater lakes vs. coastal seashores and according to nutrient richness, from oligotrophic to eutrophic waters. As the number of coastal survey sites (i.e. shores near the mainland, mainly bays) was limited, we omitted the oligotrophic seashores and combined the two eutrophic classes. We also omitted the class "other" (i.e. rivers and peatlands). In two cases, a site was classified as "overgrown" in the 2020 s. We included these sites into the analysis and used their original habitat classifications. Sites that had been destroyed by drying or filling were excluded from the analyses. Altogether, we included five habitat classes in our analyses: lakes had one oligotrophic, two mesotrophic, and one eutrophic

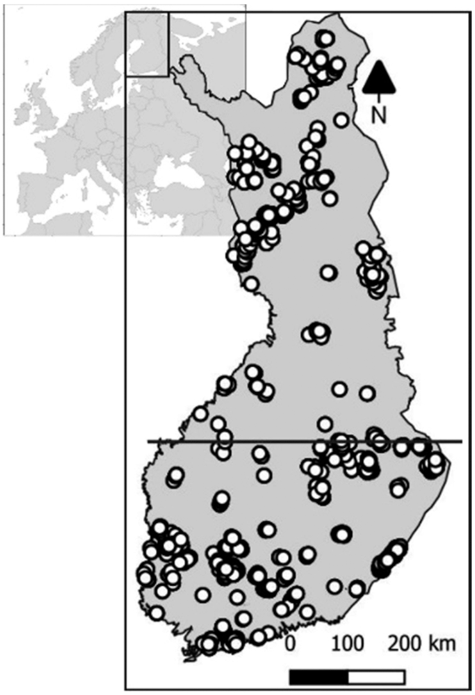

Fig. 1. Location of Finland in Europe and the map of the 942 Finnish waterbird survey sites (habitat classes 1–4, and 6–7; Table A3) covered in both the 1980s and 2020s. Only sites below the vertical line were included in the Canada goose analyses due to the species' southern range.

class, and seashores had one eutrophic class (see Holopainen and Lehikoinen, 2022). We only used sites that had been studied at least once during both periods, resulting in 942 sites that were distributed widely around Finland (Fig. 1). On average, every site was surveyed 2.6 times in the 1980 s and 1.7 times in the 2020 s. The known surface areas of the sites differ greatly (all areas are not reported), ranging from small ponds (< 1 ha) to larger lakes or parts of large lakes (max. 1 600 ha).

2.3. Statistics

In total, 3 785 surveys were conducted on the 942 sites over the years, and a total of 67 and 435 whooper swan occurrence observations were made for periods 1 and 2, respectively. In the Canada goose analysis, we only included sites south of 63°20‘N, which was the most northern observation point of the species, as it is limited to the southern part of the country. A total of 603 sites and 2 494 surveys included 3 and 59 Canada goose occurrences for periods 1 and 2, respectively.

We used two variables to study the effects of whooper swans and Canada geese. First, we divided the occurrence of both whooper swan and Canada goose at the sites into four occurrence categories: 1) absent in both the 1980s and 2020s (hereafter “aa”), 2) absent in the 1980s, present in the 2020s (hereafter “ap”), 3) present in both the 1980s and 2020s (hereafter “pp”), 4) present in the 1980s and absent in the 2020s (hereafter “pa”). The whooper swan had the following numbers of sites per categories: aa 583, ap 315, pp 27, and pa 17; while Canada goose site numbers were: aa 556 and ap 44 (the other categories had too few observations and were therefore excluded). Any whooper swan or Canada goose observation from one period (during at least one year) indicated that the species was present at the given lake during that period. We acknowledge that the number of average survey years differs between the periods, which may affect the observation probability. We also note that using this method does not allow us to determine whether the large herbivores occurred at the sites between the study periods. However, this categorisation sets levels for the assumed waterbird preferences (see Fig. 2): lakes that have never had large herbivores apparently also maintain low levels of other waterbirds. Secondly, we created a quantitative occurrence category-based dummy variable (swan/goose change) indicating change: this change is what we are especially interested in. Categories aa and pp show no change in large herbivore occurrence and therefore receive a value of 0 for this

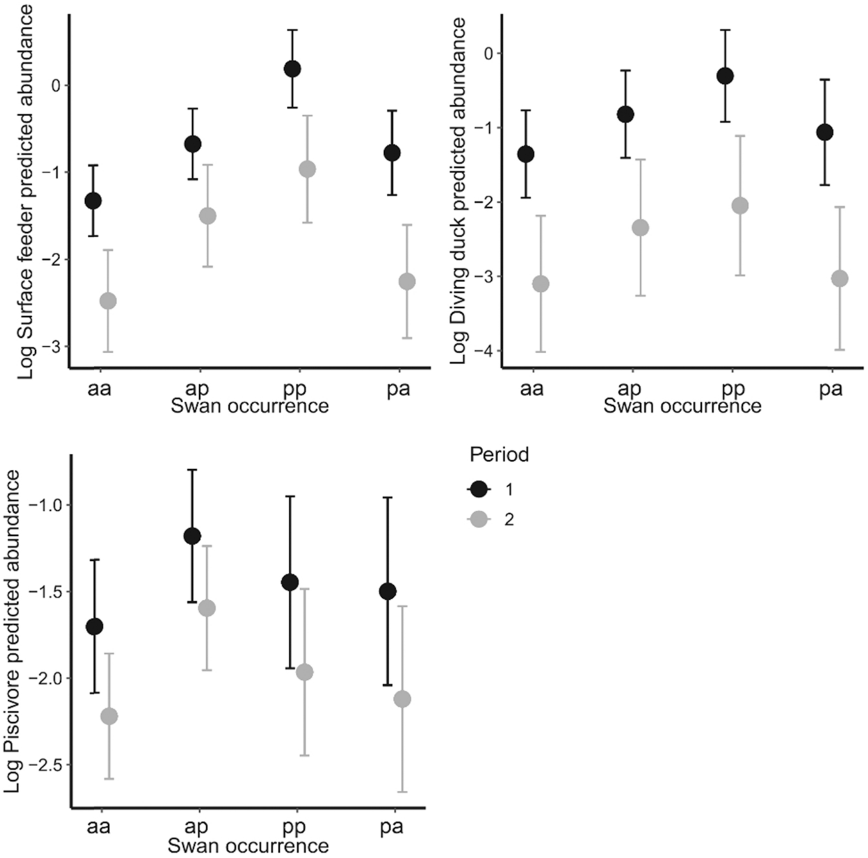

Fig. 2. Predicted changes in waterbird guild abundances (log-transformed) from period 1 (1980s) to period 2 (2020 s) at whooper swan occurrence sites (aa = absent in both periods, ap = absent in the 1980s and present in the 2020 s, pp = present in both periods, pa = present in the 1980 s, absent in the 2020 s). The conditional predictions are for the negative binomial part of the model, excluding the zero-inflation part of the model (for all the species model#1 used with period*species interaction as a random factor). Further, they are evaluated for the geographical midpoint of the data and averaged over all habitats. Circles represent the mean and whiskers ± the standard error.

variable for both periods, while categories ap and pa represent treatment categories with opposing directions. Thus, categories ap and pa were given a value of 0.5 for those periods when large herbivores were present and –0.5 when they were absent (i.e. we assume that the effect of large herbivores disappearing is inverse to the effect of colonisation), indicating change between periods with ± 1 unit difference.

The waterbird data were zero-inflated and when exploring the non-zero part, there was still overdispersion. We therefore used zero-inflated negative binomial models (function glmmTMB in R, Brooks et al., 2017; R Development Core Team, 2021). Data exploration revealed some outliers in the diving duck data and therefore we omitted observations from two sites with more than 140 pairs. We explained waterbird pair numbers with the following variables: latitude and longitude (Finnish uniform coordinate system YKJ; centralised), habitat (categorical), occurrence of whooper swan or Canada goose (categorical; aa, ap, pp, pa), and the pattern of change in species occupancies. Period (categorical; 1980 s, 2020 s) was used to model the background temporal trend in abundance, often in interaction with other variables. For example, a positive interaction between latitude and period would indicate an abundance shift towards the north. As waterbird distribution may not be even along the latitudinal gradient, we allowed the main effect of latitude to take the shape of a second-order polynomial function. Factor variables 'wetland ID' and 'species', in interaction with 'period' were included as random effects, hence allowing for variable intercepts and temporal trends between the sites and species. However, since species*period interaction produced a singular fit for the diving ducks (whooper swan and Canada goose models) and piscivores (Canada goose models), in these cases we omitted the interaction term from random effects.

We formed eight model configurations (Table A4) for each three waterbird foraging guilds (see above) and compared their Akaike's information criterion AICc values to find the best-fitting models ($\Delta AICc_{best} < 2$, Burnham and Anderson, 2004). Period*species interaction and latitude and longitude were included in all the models, but the other variables differed to compete over the best fit. All the analyses were performed with R 4.1.2 (R Development Core Team, 2021).

3. Results

For all the foraging guilds, the most complicated model (model 1), which included swan occurrence and swan occurrence change in addition to the interaction between habitat and period, was among the best models to explain waterbird abundance in relation to whooper swans (Table A5). In diving ducks and piscivores, the AICc values of the two competing swan models did not differ; and in this case we chose to present the more complex models because our interest was in examining the effect of the swan occurrence change variable. Canada goose association was not as clear and, considering surface feeders and diving ducks, several models fell into the 95% confidence set (the most complicated model presented), thus reflecting some model selection uncertainty (Table A6).

All foraging guilds showed an average decline from the first to the second study period. Population abundances of surface feeders were higher in eutrophic habitats, but these habitat classes had also experienced stronger population declines compared with

Table 1

Parameters of the best-fitting model explaining the abundance of surface feeding waterbirds in 942 sites in Finland in relation to whooper swan occurrence (conditional and zero-inflation model parameters). Variable $Period_i$ is period 2 (2020 s) compared with period 1 (1980 s represented by intercept). Hab = Habitat class (S-Meso-Lake = semi mesotrophic lake, Meso-Lake = mesotrophic lake, Eu-Lake = eutrophic lake and Eu-Shore = eutrophic seashore. Oligotrophic lake class represented by intercept). Swan is a four-level factor describing whooper swan occurrence (ap = absent–present, pp = present–present, pa = present–absent; aa = absent–absent represented by the intercept). Swan change is the change in swan occupancy (continuous). Lat is centred latitude (including a second-order polynomial) and Lon is centred longitude. Parameters that are statistically significantly different from zero ($P < 0.05$) are bolded, and trend-setting values ($P < 0.1$) are shown in italics. Dispersion parameter for nbinom2 family = 0.906. Random effect variances: fPeriod=sp intercept= 0.80, Period2 = 0.25; fPeriod=SiteID intercept = 1.00, Period2 = 0.96.

	Estimate	SE	z-value	P
Intercept	**-2.632**	**0.373**	**-7.058**	**< 0.001**
Period2	**-0.744**	**0.227**	**-3.271**	**0.001**
Hab (S-Meso-Lake)	**0.618**	**0.126**	**4.908**	**< 0.001**
Hab (Meso-Lake)	**0.923**	**0.124**	**7.457**	**< 0.001**
Hab (Eu-Lake)	**1.493**	**0.122**	**12.195**	**< 0.001**
Hab (Eu-Shore)	**2.114**	**0.293**	**7.205**	**< 0.001**
Swan (ap)	**0.815**	**0.083**	**9.823**	**< 0.001**
Swan (pp)	**1.516**	**0.212**	**7.158**	**< 0.001**
Swan (pa)	0.387	0.276	1.401	0.161
Swan change	**0.326**	**0.104**	**3.135**	**0.002**
poly(Lat)1	**-24.323**	**7.318**	**-3.324**	**0.001**
poly(Lat)2	**-32.995**	**7.164**	**-4.606**	**< 0.001**
Lon	**-0.133**	**0.043**	**-3.119**	**0.002**
Period2:Hab (S-Meso-Lake)	0.014	0.172	0.080	0.936
Period2:Hab (Meso-Lake)	**-0.425**	**0.152**	**-2.787**	**0.005**
Period2:Hab (Eu-Lake)	**-0.398**	**0.152**	**-2.619**	**0.009**
Period2:Hab (Eu-Shore)	-0.509	0.356	-1.430	0.153
Period2:poly(Lat)1	-12.822	9.283	-1.381	0.167
Period2:poly(Lat)2	**17.403**	**8.751**	**1.989**	**0.047**
Period2:Lon	*0.096*	*0.052*	*1.837*	*0.066*
Zero-inflation model				
Intercept	-17.55	446.14	-0.039 0.969	0.969

oligotrophic habitats (Table 1). In addition, surface feeders were more abundant towards southern latitudes and western longitudes, while a positive interaction between period and latitude as well as period and longitude indicated that declines became milder northwards and eastwards (Fig. A1). Surface feeder association with whooper swan-occupied sites (pp and ap) was significantly positive compared to sites that never had whooper swans (Fig. 2.). Furthermore, the coefficient of whooper swan change was positive, indicating that the abundance of surface feeders was positively associated with swan occurrence. Lakes occupied by Canada goose in the second period (ap) had more surface feeders compared to lakes never occupied by the goose, but the change in goose occurrence was not significant (Table A7).

Invertivorous diving ducks were more abundant in the eutrophic habitat classes compared with oligotrophic habitats, but their populations had also declined more steeply in these core habitats (Table 2). Overall, diving ducks were more abundant towards western longitudes and southern latitudes. The positive interaction between period and latitude suggested that the declines were weaker towards northern latitudes. Diving ducks were more abundant at whooper swan sites (pp and ap, Fig. 2.) and positively associated with whooper swan change. Canada goose showed no association with the diving ducks (Table A8).

Piscivore abundances were higher in the eutrophic habitat classes compared with the oligotrophic class, but the mesotrophic class showed significant negative abundances compared with the oligotrophic class (Table 3). The positive interaction connection between period and latitude was also found for piscivores. Piscivore abundance was higher in the whooper swan occurrence category ap (Fig. 2) compared with the absence sites, while swan occurrence change had no effect on it. Canada goose occurrence ap showed positive association with piscivorus ducks (Table A9).

4. Discussion

Despite the strong increase in both whooper swan and Canada goose populations, we did not detect any of the hypothesised negative effects of these species on smaller waterbirds. On the contrary, for the first time, we not only found that the overall abundances of all foraging guilds were positively associated with whooper swan presence at sites, but also that the numbers of surface feeders and diving ducks, were positively associated with whooper swan colonisation. While Canada goose sites had an overall positive association with surface feeders and piscivores, we did not detect an effect of goose colonisation on other waterbirds. Our results indicate that although smaller waterbirds have been commonly declining, the decrease has not been as strong on sites colonised by whooper swans between 1980 s and 2020 s. These associations may be explained by two mutually non-exclusive mechanisms: the whooper swan may act as a habitat quality indicator and/or a facilitator in the boreal wetlands affected by anthropogenic-driven changes.

Herbivory is an important factor in freshwater ecosystems, affecting plant abundance and diversity, modifying habitats for other organisms and influencing the cycling of nutrients (Bakker et al., 2016b). For example, swans have been found to affect the structure

Table 2
Parameters of the best-fitting model explaining diving duck abundances in 942 sites in Finland in relation to whooper swan occurrence (conditional and zero-inflation model parameters). Variable Period$_i$ is period 2 (2020 s) compared with period 1 (1980 s represented by intercept). Hab = Habitat class (S-Meso-Lake = semi mesotrophic lake, Meso-Lake = mesotrophic lake, Eu-Lake = eutrophic lake and Eu-Shore = eutrophic seashore. Oligotrophic lake class represented by intercept). Swan is a four-level factor describing whooper swan occurrence (ap = absent–present, pp = present–present, pa = present–absent; aa = absent–absent represented by the intercept). Swan change is a change in swan occupancy (continuous). Lat is centred latitude (including a second-order polynomial) and Lon is centred longitude. Parameters that are statistically significantly different from zero ($P < 0.05$) are bolded, and trend-setting values ($P < 0.1$) are shown in italics. Dispersion parameter for nbinom2 family = 0.865. Random effect variances: fPeriod=SiteID intercept 0.67, Period 1.0.

	Estimate	SE	z-value	P
Intercept	**-0.975**	**0.084**	**-11.561**	**< 0.001**
Period2	**-0.365**	**0.088**	**-4.150**	**< 0.001**
Hab (S-Meso-Lake)	**0.816**	**0.122**	**6.691**	**< 0.001**
Hab (Meso-Lake)	**0.552**	**0.122**	**4.506**	**< 0.001**
Hab (Eu-Lake)	**1.147**	**0.120**	**9.587**	**< 0.001**
Hab (Eu-Shore)	**1.820**	**0.294**	**6.190**	**< 0.001**
Swan (ap)	**0.596**	**0.082**	**7.249**	**< 0.001**
Swan (pp)	**0.800**	**0.215**	**3.728**	**< 0.001**
Swan (pa)	0.080	0.267	0.298	0.766
Swan change	**0.301**	**0.100**	**3.017**	**0.003**
poly(Lat)1	**24.478**	**5.539**	**4.419**	**< 0.001**
poly(Lat)2	**-16.600**	**5.534**	**-3.000**	**0.003**
Lon	**-0.114**	**0.041**	**-2.790**	**0.005**
Period2:Hab (S-Meso-Lake)	**-0.349**	**0.167**	**-2.086**	**0.037**
Period2:Hab (Meso-Lake)	-0.033	0.150	-0.219	0.827
Period2:Hab (Eu-Lake)	-0.239	0.151	-1.577	0.115
Period2:Hab (Eu-Shore)	-0.593	0.379	-1.565	0.118
Period2:poly(Lat)1	7.324	6.766	1.082	0.279
Period2:poly(Lat)2	**17.197**	**6.579**	**2.614**	**0.009**
Period2:Lon	-0.048	0.050	-0.951	0.342
Zero-inflation model				
Intercept	0.039	0.104	0.376	0.707

Table 3

Parameters of the best-fitting model explaining the abundance of piscivore ducks in 942 sites in Finland in relation to whooper swan occurrence (conditional and zero-inflation model parameters). Variable Period$_i$ is period 2 (2020 s) compared with period 1 (1980 s represented by intercept). Hab = Habitat class (S-Meso-Lake = semi mesotrophic lake, Meso-Lake = mesotrophic lake, Eu-Lake = eutrophic lake and Eu-Shore = eutrophic seashore. Oligotrophic lake class represented by intercept). Swan is a four-level factor describing whooper swan occurrence (ap = absent–present, pp = present–present, pa = present–absent; aa = absent–absent represented by the intercept). Swan change is a change in swan occupancy (continuous). Lat is centred latitude (including a second-order polynomial) and Lon is centred longitude. Parameters that are statistically significantly different from zero ($P < 0.05$) are bolded, and trend-setting values ($P < 0.1$) are shown in italics. Dispersion parameter for nbinom2 family = 0.698. Random effect variances: fPeriod=sp intercept= 0.40, Period2 = 0.11; fPeriod=SiteID intercept = 1.71, Period2 = 0.29.

	Estimate	SE	*z*-value	*P*
Intercept	**-2.696**	**0.311**	**-8.656**	**< 0.001**
Period2	-0.121	0.187	-0.643	0.520
Hab (S-Meso-Lake)	**1.304**	**0.159**	**8.190**	**< 0.001**
Hab (Meso-Lake)	**-0.512**	**0.199**	**-2.577**	**0.010**
Hab (Eu-Lake)	**0.729**	**0.165**	**4.409**	**< 0.001**
Hab (Eu-Shore)	**2.849**	**0.422**	**6.747**	**< 0.001**
Swan (ap)	**0.572**	**0.115**	**4.983**	**< 0.001**
Swan (pp)	0.254	0.347	0.734	0.463
Swan (pa)	0.149	0.398	0.376	0.707
Swan change	0.106	0.117	0.902	0.367
poly(Lat)1	*-16.179*	*9.353*	*-1.730*	*0.084*
poly(Lat)2	-11.696	8.988	-1.301	0.193
Lon	0.094	0.059	1.593	0.111
Period2:Hab (S-Meso-Lake)	*-0.320*	*0.179*	*-1.788*	*0.074*
Period2:Hab (Meso-Lake)	0.255	0.222	1.149	0.250
Period2:Hab (Eu-Lake)	-0.098	0.178	-0.548	0.584
Period2:Hab (Eu-Shore)	**-1.000**	**0.393**	**-2.543**	**0.011**
Period2:poly(Lat)1	*-19.049*	*10.007*	*-1.904*	*0.057*
Period2:poly(Lat)2	**17.640**	**8.896**	**1.983**	**0.047**
Period2:Lon	-0.022	0.056	-0.393	0.694
Zero-inflation model				
Intercept	**-0.837**	**0.282**	**-2.969**	**0.03**

and functioning of aquatic communities and ecosystems (Bakker et al., 2016a; 2016b; Wood et al., 2017). They can cause strong habitat modification by reducing aquatic plant cover and standing crop (Sandsten and Klaassen, 2008; Gayet et al., 2011; Wood et al., 2012) not only through direct grazing, but also by trampling vegetation during foraging (Lodge, 1991).

However, the negative effects of these actions for the other waterbirds are not evident. For example, whooper swans feed on *Equisetum* stands, which form the preferred foraging habitats of Eurasian wigeon broods (*Mareca penelope*, Nummi et al., 2013; Pöysä et al., 2017). *Equisetum* has decreased drastically in Fennoscandia during past decades, however, no relationship has been found between whooper swan occurrence and the observed *Equisetum* decrease, nor between the decrease of the Eurasian wigeon and the *Equisetum* decrease (Pöysä et al., 2018). On the contrary, Eurasian wigeon abundance was found to be positively associated with whooper swan occurrence at breeding lakes while reasons for the *Equisetum* loss remain unclear (Pöysä et al., 2018). Also, Pöysä and Sorjonen (2000) found that recolonising whooper swans had no negative effect on the breeding densities of dabbling duck species.

Positive heterospecific attraction effects may arise when species use the presence of other species as an indicator of habitat quality (Elmberg et al., 1997). For example, Eurasian wigeons and coots (*Fulica atra*) can be more abundant in wetlands where mute (*Cygnus olor*) or whooper swans are present (Broyer, 2009; Gayet et al., 2011; Pöysä et al., 2018). Our results support this conclusion: waterbird populations were more abundant in lakes occupied by the whooper swan, and furthermore, surface feeders and diving ducks declined less at sites that had become occupied by whooper swans since the 1980 s. However, we found no association between swan colonization and piscivore abundance. This indicates that the positive effect of whooper swan colonization on other waterbird species is indeed foraging niche specific. Interestingly, however, even piscivore species were more abundant at sites occupied by the whooper swan since the 1980 s, compared with sites never occupied by swans.

In addition to indicating habitat quality, the presence of large herbivorous waterbirds, may also facilitate the feeding of other waterbirds when they dig into the substrate, trample the benthos and expose tubers and roots (Källander, 2005). It has been shown that several waterbirds associate commensally with whooper swans at autumn stop-over site by utilising the vegetation exposed by the swans (Merilä and Ohtonen, 1987). For example, common pochards (*Aythya ferina*) have been found to double their instantaneous feeding rate when foraging in company with Bewick's swans (*Cygnus bewickii*) (Gyimesi et al., 2012). Moreover, some smaller waterfowl can benefit from coprophagy and have been observed to feed directly on swan faeces, presumably because swans' relatively poor digestive capabilities means that their faeces is relatively energy rich (Vogrin, 1997; Shimada, 2012).

Our findings suggest that the presence of large herbivorous waterbirds do not hamper other species, but may facilitate their presence and abundance also in breeding sites. For instance, it is possible that biotic disturbance caused by grazing swans actually facilitates ducks due to vegetation structure fragmentation (e.g., by creating open patches within over-grown vegetation). For example, a study by Nummi et al. (2006) showed that the indirect effects of non-native muskrat (*Ondatra zibethica*) herbivory mediated aquatic invertebrates through changes to vegetative habitat structure. Ducklings may find suitable feeding patches and edges within muskrat-created patch mosaics rich in invertebrates (Danell, 1977; Nummi et al., 2006).

One mechanism by which the presence of whooper swans benefit other waterbirds may be to provide an early warning system for other waterbirds. Whooper swans are highly visible and respond to various disturbances by swimming to open water and making alarm calls (H. Pöysä and V.-M. Väänänen, unpublished data). By doing so, whooper swans possibly provide an early warning system and alert other waterbirds of approaching predators, an idea that deserves further research. For comparison, breeding colonies of small gulls, such as the black-headed gull (*Chroicocephalus ridibundus*), maintain an early warning system and also provide defence against predators (Pöysä, 1988; Väänänen, 2000; Pöysä et al., 2019).

We also found that waterbird abundances declined less in the north than in the south, leading to an overall northward shift in abundance. Whether this is caused by climate change or is a land-use and/or habitat-related effect remains uncertain; it has recently been demonstrated that climate-driven changes may be thwarted by changes in habitat quality (Öst et al., 2021). Nevertheless, our results indicate that waterbirds have declined more in their eutrophic core habitats, where their abundances have been higher than in less valuable habitats. In support of this assertion, Pöysä and Paasivaara (2021) found that the distribution of breeding pairs of Eurasian wigeon and tufted duck (*Aythya fuligula*) had shifted toward lakes with sparser emergent vegetation, i.e. from eutrophic to oligotrophic lakes. These eutrophic wetlands may suffer from increased predator pressure, degraded water quality and overgrowth (Nilsson, 1978; Lehikoinen et al., 2016; Pöysä and Linkola, 2021; Holopainen and Lehikoinen, 2022). Our survey lakes exhibit a decreasing trend in water clarity and an increasingly darker colour, and eutrophic lakes in particular have become more turbid (Holopainen and Lehikoinen, 2022). Farming and forest ditching practices around lakes seem to associate with the state of the survey lakes, with possible ecological impacts due to intensified turbidity and brownification in wetland ecosystems (Blanchet et al., 2021). High turbidity and brownification impact the composition, structure and function of aquatic food webs via light conditions that govern important processes such as photosynthesis, system productivity, predator–prey interactions (Ranåker et al., 2012; Lehtovaara et al., 2014) and invertebrate production (Arzel et al., 2020). All these factors may negatively affect waterbird abundances. Lakes occupied by the whooper swan since the 1980 s may not have suffered as much from physio-chemical changes in water quality, thus maintaining higher waterbird abundances.

We acknowledge that while our data are large and geographically extensive, they are comprised of 1–4 years in the late 1980 s and 1–2 years in the early 2020 s, and are thereby potentially sensitive to observation error and random annual fluctuations in population sizes and environmental conditions. Occurrence of the large herbivore birds is not observed through the study period, and our approach does not necessarily consider carry-over effects (e.g., long-term effects of grazing). However, based on ringing recoveries, whooper swans have strong nesting site fidelity (Saurola et al., 2013; Pöysä et al., 2018). The herbivore impact on macrophytes depends on consumer density, especially on the biomass density of consumers (Wood et al., 2012, 2017). Our data are collected during the early breeding season, when whooper swans are territorial, and therefore their density in boreal lakes is low, usually with only one pair and family per lake, causing possible low lake-level grazing pressure. With these data, we cannot evaluate the possible pressure caused by the large herbivores during other stages of the life cycle, in particular during the brood rearing or migration periods, which may be even more important in demographical terms.

4.1. *Conservation aspects*

The numbers of several swan and especially goose species have increased enormously in Europe and North America during the past decades due to conservation measures and farmland practices, leading to conflicts with humans (Conover and Chasko, 1985; Abraham et al., 2005; Fox et al., 2017) and other species (Peterson et al., 2013). Based on our results, the growth of the whooper swan and Canada goose populations has not, at least so far, resulted in asymmetric competition at the breeding grounds in Finland. Therefore, research and management should be targeted towards anthropogenic changes in wetland habitat quality, ranging from water quality to non-native predator communities. Even so, we emphasise the importance of taking species interactions into account when designing and implementing management and conservation actions. The whooper swan is a large and visible bird that, as shown in the current study, exhibits positive associations with other waterbirds in boreal freshwater habitats. Due to these features, and the species' potential for attracting public attention to conservation programmes, we call for an evaluation of the possibility and utility of considering the whooper swan as a flagship umbrella species (Caro and O'Doherty, 1999; Kalinkat et al., 2016). We wish to echo the conclusions of Caro and O'Doherty (1999): indicator species usually act as representatives of other species in the community, and the best surrogate species are those that can be easily monitored. We therefore suggest that the whooper swan may indeed function well as a proxy for overall waterbird biodiversity and habitat quality, and can thus be used also as indicator of the outcomes of implemented conservation and management practices.

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Declaration of Competing Interest

The authors declare the following financial interests/personal relationships which may be considered as potential competing interests:Aleksi Lehikoinen reports financial support was provided by Ministry of Agriculture and Forestry of Finland. Kim Jaatinen (Nature and Game Management Trust Finland) reports financial support was provided by Sophie von Julins Stiftelse.

Data Availability

The waterfowl survey data used in this study are available at the open access data repository maintained by the Finnish Biodiversity Information Facility (FinBIF).

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Appendix A. Supporting information

Supplementary data associated with this article can be found in the online version at doi:10.1016/j.gecco.2022.e02144.

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