


Changes in waterbird occurrence and abundance at their northern range boundaries in response to climate warming: importance of site area and protection status

E. Gaget^{1,2} , O. Ovaskainen^{3,4,5}, U. Bradter⁶, F. Haas⁷, L. Jonas^{1,2}, A. Johnston⁸, T. Langendoen⁹, A. S. Lehtikainen¹⁰, T. Pärt¹¹, D. Pavón-Jordán⁶, B. K. Sandercock⁶, A. Soutan¹¹ & J. E. Brommer¹

1 Department of Biology, University of Turku, Turku, Finland

2 Tour du Valat, Research Institute for the Conservation of Mediterranean Wetlands, Arles, France

3 Department of Biological and Environmental Science, University of Jyväskylä, Jyväskylä, Finland

4 Research Centre for Ecological Change, Organismal and Evolutionary Biology Research Programme, Faculty of Biological and Environmental Sciences, University of Helsinki, Helsinki, Finland

5 Centre for Biodiversity Dynamics, Department of Biology, Norwegian University of Science and Technology, Trondheim, Norway

6 Department of Terrestrial Ecology, Norwegian Institute for Nature Research, Trondheim, Norway

7 Department of Biology, Lund university, Lund, Sweden

8 CREEM, School of Mathematics and Statistics, University of St. Andrews, St. Andrews, UK

9 Wetlands International, Ede, The Netherlands

10 The Finnish Museum of Natural History, University of Helsinki, Helsinki, Finland

11 Department of Ecology, The Swedish University of Agricultural Sciences, Uppsala, Sweden

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Correspondence

Elie Gaget, Tour du Valat, Research Institute for the Conservation of Mediterranean Wetlands, Arles, France.

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Abstract

Climate warming is driving changes in species distribution, but habitat characteristics can interact with warming temperatures to affect populations in unexpected ways. We investigated wintering waterbird responses to climate warming depending on habitat characteristics, with a focus on the northern boundary of their non-breeding distributions where winter climatic conditions are more extreme. At these Nordic latitudes, climate warming is expected to drive positive changes in species occurrence and abundance, with likely differences in species-specific responses. We analyzed the occurrence and abundance of 18 species of waterbirds monitored over 2,982 surveys at 245 inland wetlands over a 25-year period in Sweden. We used hierarchical modeling of species communities (HMSC) which enabled us to relate species-specific changes to both functional traits and phylogenetic relatedness. We investigated occurrence and abundance changes in response to average temperature, temperature anomalies, site area, site protection status (Natura 2000), and land use in agricultural and urban surfaces. Unsurprisingly, both average temperatures and temperature anomalies were the most important variables influencing positively waterbird occurrence and abundance. For 60% of the species, the effect of temperature anomalies was even stronger in large or protected wetlands. Geese and mallard occurred more often at sites surrounded by agricultural and urban surfaces, respectively, but their occurrence in these habitats was not affected by interactive effects with climate warming. Species abundance was greater inside protected areas only for 11% of the species, but occurrence probability was higher inside protected areas for 44% of the species. Overall, we observed that species thermal affinity was a strong predictor for positive species response to temperature anomalies, and that species sharing similar phylogenetic history had similar relationships with environmental variables. Protection of large wetlands and restoration of the surrounding habitats are two targets for climate change adaptation strategies to facilitate future responses of waterbirds to climate warming.

Introduction

Climate and habitat changes are two major drivers of biodiversity change, but can also interact to create more complex impacts on species distributions. In a direct response to increases in temperature, species distributions may shift poleward or to higher elevations (Lenoir *et al.*, 2020). However, species dispersal and establishment may be influenced by other environmental parameters, such as habitat suitability and connectivity among patches. Habitat suitability for a species can result in interactive effects between temperature change and habitat characteristics, for example when the availability of resources or refugia vary according to temperatures. Changes in species distributions are facilitated by availability of protected areas (Thomas *et al.*, 2012), such that the protective role of a protected area might improve with climate warming (Gaget *et al.*, 2021). On the other hand, an interaction between habitat degradation and climate warming may hamper changes in species distributions (Gaget *et al.*, 2020; Lenoir *et al.*, 2020). A better understanding of species responses to climate warming and interactions with habitat conditions is required to devise effective strategies for climate change adaptation (Schuurman *et al.*, 2022).

Waterbirds are highly mobile species, particularly during the non-breeding season, and can adjust their distributions to spatiotemporal variation in climatic conditions (Sauter, Korner-Nievergelt, & Jenni, 2010; Meehan *et al.*, 2021). During the winter season in Eurasia and North America, the northern boundary of the range distribution is typically constrained by cold temperatures, ice cover, access to open water, and limited daylight, which lead to reduced food availability and foraging time, and increased metabolic costs of thermoregulation (Schummer *et al.*, 2010). Large-bodied waterbird species may persist longer under cold temperatures due to greater body reserves and lower mass-specific basal metabolic rates (e.g. goosander *Mergus merganser*, Marchowski *et al.*, 2017). On the other hand, small-bodied waterbirds and species adapted to warmer conditions are predicted to show greater changes in occurrence in response to climate warming (Dalby *et al.*, 2013).

Species diet may explain some of the variation in species sensitivity to cold climatic conditions, with terrestrial foragers being less impacted by ice cover than aquatic species dependent on open water (Pavón-Jordán *et al.*, 2019). Terrestrial grazers, such as geese and some swans, may be dependent on the presence of agricultural land and benefit from climate warming (Fox & Abraham, 2017; Nilsson & Kampe-Persson, 2018). Man-made wetlands, such as in urban context, mostly result in a lower niche diversity compared to natural wetlands, but they can also provide a refuge that shelters species during cold spells with areas of open water (Adam *et al.*, 2015; Avilova, 2018).

Here, we investigated the occurrence and abundance of non-breeding waterbirds in response to variation in site temperatures and habitat characteristics in Sweden. Our data consisted of detections and counts of 18 species monitored at 245 Swedish inland wetlands over a 25-year period (2,982 surveys). The survey data were collected as part of the

International Waterbird Census (IWC), taking place each year in mid-January (Nilsson & Haas, 2016). In Sweden, average winter temperatures range from 0°C in the South to −15°C in the North, with intra and inter-annual variations affecting ice and snow conditions (Lussana, Tveito, & Uboldi, 2018). Local temperatures influence individual bird's thermoregulation costs and access to feeding resources, such as aquatic plants, fishes, or agricultural crops, resulting in spatio-temporal variation in wintering waterbird distributions and abundance in Sweden (Nilsson & Kampe-Persson, 2000; Nilsson, 2013, 2020; Nilsson & Haas, 2016). Historically, the Baltic Sea provided a refuge for waterbirds, with coastal wetlands being among the last sites to freeze. However, since the 1990s, rapid warming of temperatures has led to reductions in ice and subsequent increases in waterbird species richness and abundance, along with a spatial redistribution toward inland wetlands that were previously frozen during winter (Nilsson & Haas, 2016; Nilsson, 2020). The spatial redistribution was expected to be positively influenced by the Natura 2000 protected area network, as the main infrastructure for habitat and species conservation in Europe (Pavón-Jordán *et al.*, 2015; Pavón-Jordán *et al.*, 2017; Gaget *et al.*, 2021).

Our study objective was to test the interactive effects of habitat characteristics and temperature increase on wintering waterbird population changes at their northern range boundaries. In a context of fast climate warming, we were interested in documenting habitat characteristics facilitating or limiting population changes in response to temperature increase, at both species-specific and multi-species levels. We used a Bayesian joint-species distribution framework (HMSC; Ovaskainen *et al.*, 2017) which allowed us to examine the drivers of species occurrence and abundance changes, while relating the species-specific changes to variations in functional traits and phylogenetic relatedness. We predicted that warm temperatures should lead to positive changes in occurrence and abundance, and that large and protected sites should host more species and individuals during warm winters than small or unprotected sites because of greater food resources and higher ecosystem quality. Moreover, we predicted that agricultural and urban surfaces surrounding monitoring sites might filter species depending on their habitat preferences, which could be exacerbated in response to temperature increases.

Materials and methods

Waterbird monitoring

We examined changes in the occurrence and abundance of 18 species of non-breeding waterbirds in Sweden (Table 1). Bird surveys were conducted at 245 inland wetlands over a 25-year period (1993–2017, Fig. 1a). Surveys were conducted once a year in January by skilled ornithologists participating in the International Waterbird Census (IWC, Wetlands International, www.wetlands.org, Delany, 2010). The IWC is a global scheme but we focused on Sweden because (1) spatial polygons of most Swedish survey sites

Table 1 Functional traits per 18 species of waterbirds, including species thermal affinity in the nonbreeding range (°C), category of habitat preference and body mass ($\log_{(e)}$ -transformed, grams)

| Common name | Scientific name | $\log_{(e)}$ mass (g) | Habitat preference | Thermal affinity (°C) |
|-----------------------------|----------------------------|-----------------------|--------------------|-----------------------|
| Great crested grebe | <i>Podiceps cristatus</i> | 6.51 | Deep water | 3.25 |
| Eurasian coot | <i>Fulica atra</i> | 6.60 | Deep water | 5.86 |
| Gray heron | <i>Ardea cinerea</i> | 7.27 | Shallow water | 4.32 |
| Great cormorant | <i>Phalacrocorax carbo</i> | 7.72 | Deep water | 3.70 |
| Whooper swan | <i>Cygnus cygnus</i> | 9.15 | Farmland | -1.49 |
| Mute swan | <i>Cygnus olor</i> | 9.32 | Shallow water | 1.27 |
| Barnacle goose | <i>Branta leucopsis</i> | 7.47 | Farmland | 1.69 |
| Bean goose | <i>Anser fabalis</i> | 7.93 | Farmland | -2.51 |
| Greater white-fronted goose | <i>Anser albifrons</i> | 7.95 | Farmland | 2.53 |
| Greylag goose | <i>Anser anser</i> | 8.12 | Farmland | 4.47 |
| Tufted duck | <i>Aythya fuligula</i> | 6.64 | Deep water | 10.45 |
| Common pochard | <i>Aythya ferina</i> | 6.90 | Deep water | 11.34 |
| Eurasian wigeon | <i>Anas penelope</i> | 6.59 | Shallow water | 16.53 |
| Mallard | <i>Anas platyrhynchos</i> | 7.02 | Shallow water | -0.02 |
| Eurasian teal | <i>Anas crecca</i> | 5.91 | Shallow water | 12.72 |
| Common goldeneye | <i>Bucephala clangula</i> | 6.73 | Deep water | -1.11 |
| Goosander | <i>Mergus merganser</i> | 7.27 | Deep water | -0.40 |
| Smew | <i>Mergellus albellus</i> | 6.47 | Deep water | -1.58 |

were available allowing accurate assessment of the size and habitat of each site; (2) data collection was consistent over time and (3) the sampling region covered a northern country where the cold range margins of many waterbird species' winter ranges were located.

The national waterbird surveys were coordinated by the University of Lund and consistently performed within a delimited area at each survey site (Nilsson & Haas, 2016). Geese observations from outside of the delimited area were added to include feeding areas adjacent to the survey sites (Nilsson, 2013). The minor adaptation of the IWC protocol returns more robust numbers for geese, feeding on land and roosting at the survey site. We focused on wetlands at inland sites, that is, not reaching the sea, to exclude the possible influence of marine conditions on changes in waterbird distributions. We identified a total of 245 sites with ≥ 5 years of data (12 surveys on average) for which a clear delimitation of the surveyed area was provided (see Appendix S1 for further information on survey time series). We removed species with a total abundance over the 25-year study period of less than 500 individuals (e.g. northern pintail *Anas acuta*), to avoid rare species that result in limited information gain (Ovaskainen & Abrego, 2020). The survey design lacked repeated surveys within years which did not allow for estimation of the probability of detection (see Discussion). The dataset used for the analysis included 2982 independent surveys, with a cumulative record of 815,409 counted birds and 8612 species occurrences within a given site and year.

Species traits and phylogeny

We assessed multispecies distribution changes by accounting for species phylogeny (extracted from BirdTree, <https://birdtree.org>, Jetz *et al.*, 2012, 2014) and three functional traits (Table 1). Waterbird functional traits include the habitat

preferences for feeding activities: shallow water, deep water, or farmland (Pavón-Jordán *et al.*, 2019); the ($\log_{(e)}$ -transformed) mean body mass (g) for pooled sexes (Dunning Jr, 2007); and a species-specific estimate of thermal affinity during winter (°C). Thermal affinity was estimated for each species as the long-term mean temperature in January (1950–2000, www.worldclim.org) averaged over the species distribution area during the non-breeding period (BirdLife International and HBW, 2017; Gaget *et al.*, 2021).

Environmental variables

At each site, we considered both average winter temperatures during the study period and winter temperature anomalies. Winter temperatures were defined as the average of the minimum temperatures during November, December, and January each winter, which is the 3-month period most likely to influence migration behavior after the breeding season (Nilsson & Kampe-Persson, 2000) (Fig. 1b). We calculated temperatures per site and per winter from the daily minimum temperatures of the Nordic Gridded Climate Dataset (NGCD) (Lussana *et al.*, 2018). The NGCD layers had a spatial resolution of 1 km² and we extracted temperatures from the grid cells where the centroids of wetland sites were located. Temperature anomalies were annual variations in winter temperatures, calculated at site level by subtracting site average temperature over the study period to the temperature of the surveyed year. Inclement winter conditions can reduce site accessibility and potentially impact the estimation of waterbird population changes in response to temperature (Laubek *et al.*, 2019), so we checked whether the missing surveys were related to colder winter temperatures (Appendix S1). We found that indeed, mean winter temperatures were significantly ($P < 0.001$) colder for years with a missing survey compared to years when surveys were completed, with a

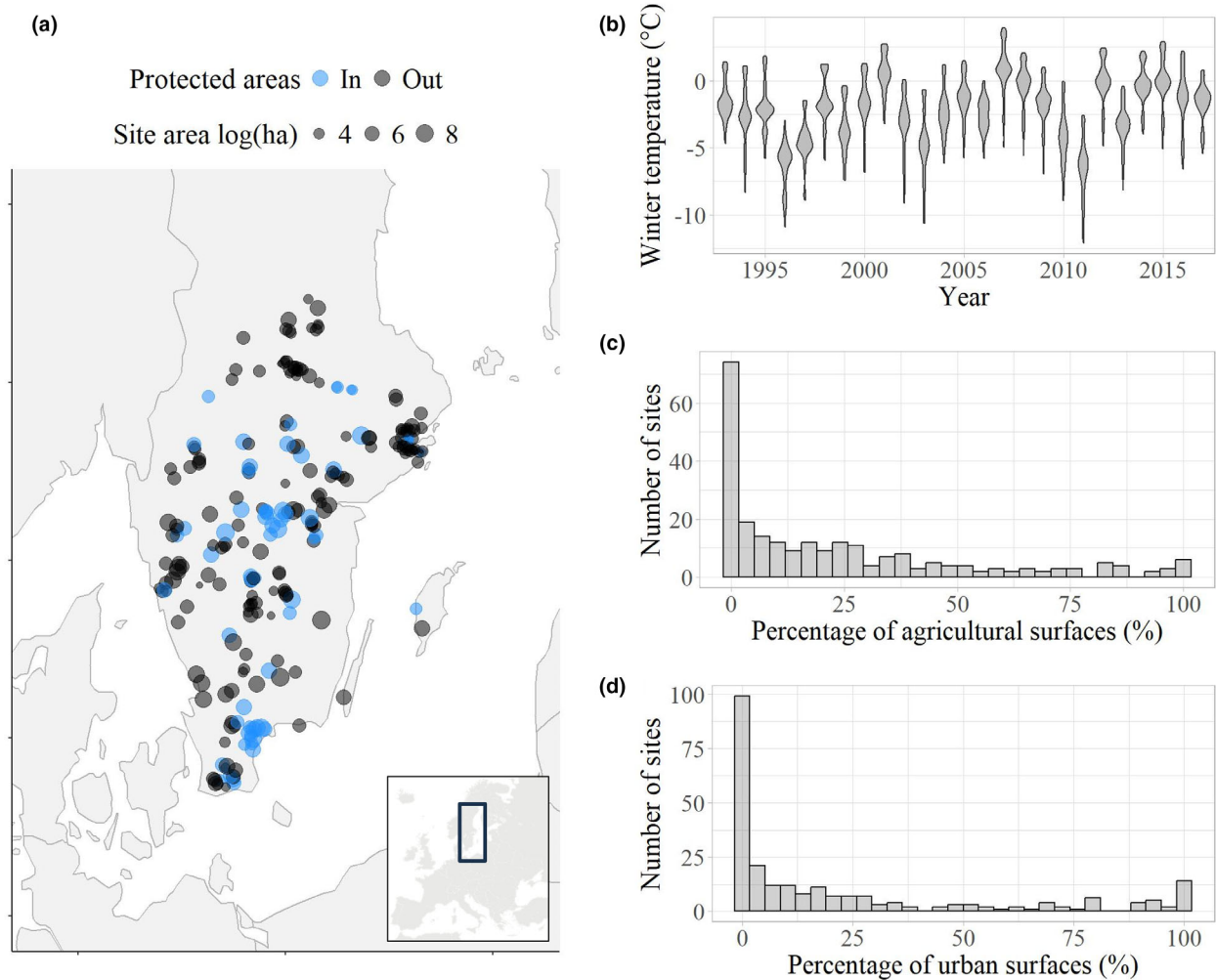


Figure 1 (a) Map of the study area located in southern Sweden in northern Europe (inset), on 245 wetland sites (area \log_{10}) transformed) located inside or outside protected areas, (b) violin plots of the range in winter temperatures over 1993–2017, and histograms of the proportion of land cover in either (c) agricultural and (d) urban surfaces in a 1 km buffer zone around monitored sites.

difference of $0.36 \pm 0.05^\circ\text{C}$. Consequently, despite small differences in temperature, estimated parameters for the effect of temperature on waterbird occurrence and abundance might be slightly underestimated.

To assess the possible interaction between temperature anomalies and habitat characteristics, we used the site area and the surface areas in agricultural and urban land cover surrounding the monitoring sites (Fig. 1c,d). We extracted the site area from the site polygons by delimiting the area monitored during the surveys (ha). Site area was used both as a variable reflecting the extent of the monitored area and as a proxy for habitat areas favorable to waterbirds. Indeed, we found a positive correlation between site area and wetland surfaces ($r_{\text{Pearson}} = 0.90$, $P < 0.001$). We assessed the proportion of urban surfaces and the proportion of agricultural surfaces within a buffer of 1 km around the borders of the site polygon. The extent of the buffer was arbitrarily assumed as reasonable to assess land cover around the

studied wetlands. The site polygon corresponds to the monitored wetland, and the 1 km buffer covers most, but not necessarily all, the surrounded lands monitored for geese. The landcover classes were identified from the Corine Land Cover assessment (www.land.copernicus.eu) using the 2006 assessment and at a spatial resolution of 100 m. Urban surfaces were defined following the Corine Land Cover thematic including: urban, industrial, constructed and non-agricultural – non-natural vegetated areas. Agricultural surfaces included arable lands, permanent crops, and heterogeneous agricultural surfaces. Using broad categorical land cover thematic resolution might increase uncertainty in parameter estimation (Liang *et al.*, 2013). We made the choice to limit model complexity, assuming that waterbirds would be equally affected by land cover sublevels that we combined together. Before running the models, we tested to ensure that the proportions of urban and agricultural surfaces were not strongly correlated. The correlation between the

proportions of urban and agricultural surfaces was $r_{\text{Pearson}} = -0.36$, $P < 0.001$ ($n = 245$). Correlations between site area and agricultural surfaces and site area and urban surfaces were $r_{\text{Pearson}} = -0.03$, $P = 0.7$ ($n = 245$) and $r_{\text{Pearson}} = -0.36$, $P < 0.001$ ($n = 245$), respectively.

We considered 64 wetland sites that were within the boundaries of a protected area separately from 181 sites that were located in areas without protection (Fig. 1a). Sites were considered to be inside a protected area if the site's centroid fell within the polygon of a protected area of the Natura 2000 network or the Common Database on Designated Areas (downloaded from www.eea.europa.eu). Designation of protected areas was not necessarily specific to waterbirds and the level of protection was not filtered from the IUCN protected area management categories, such that effective protection of waterbirds and their habitats can range from weak to strong. We did not consider the time since designation as a proxy for conservation effectiveness to avoid additional model complexity (but see Gaget *et al.*, 2022). All species of waterbirds have been recorded at sites inside and outside of protected areas.

Statistical analyses

We assessed changes in waterbird populations by using hierarchical modeling of species communities (HMSC), which is a multivariate hierarchical generalized linear mixed model fitted in a Bayesian framework (Ovaskainen *et al.*, 2017; Tikhonov *et al.*, 2019). The HMSC is a joint species distribution modeling approach that is valuable for describing multispecies occurrence and abundance changes in response to environmental variables while allowing parameter estimation for how species responses to environmental variation might be shared depending on similar functional traits and levels of phylogenetic relatedness. The HMSC returns parameter estimation per environmental variables per species, as well as the multi-specific patterns captured by functional traits or phylogenetic relatedness.

We used a hurdle approach to assess the effect of winter temperature and habitat characteristics on species occurrence (use or nonuse) and species abundance conditional on presence (nonzero counts, hereafter abundance). The hurdle approach was useful for dealing with the zero-inflation that is common in count data due to an excess of sites without birds, which also allowed us to compare parameters related to species occurrence and abundance. We used a binomial and a Gaussian error distribution for occurrence and \log_{10} abundance, respectively. We used a Gaussian distribution on \log_{10} transformed count data in order to reduce the computation time. We used the same fixed effects for both occurrence and abundance: site area (\log_{10}), urban surfaces (%), agricultural surfaces (%), site protection status (protected vs. not protected), average temperatures, temperature anomalies, and the two-way interactions between temperature anomalies and all of the habitat variables. Habitat variables and temperature anomalies were mean-centered to allow the interpretation of both main and interaction effects. Spatial autocorrelation was accommodated with a random effect on

site spatially structured from the geographical coordinates of each site (Tikhonov *et al.*, 2020) and an unstructured random effect of year. Functional traits for habitat preference, body mass and thermal affinity, and phylogenetic relatedness were added to the models to evaluate their importance for structuring species niches.

We assumed the default prior distribution and sampled the posterior distribution with 37,500 iterations from 4 MCMC chains. We considered the first 12,500 iterations as burn-in, and thinned the remaining iterations by 100, resulting in a total of 1000 posterior samples pooled over the four chains. The MCMC chains were well mixed and reached a reasonable stationary distribution (Appendix S2). We evaluated the occurrence and abundance model fits in terms of area under the curve (AUC) and R^2 , respectively. The predictive power was assessed by a two-fold cross validation, in which half of the data were randomly selected, following Ovaskainen & Abrego (2020). The effects were considered to be supported when the 95% Bayesian credible intervals did not overlap zero. We reported the modeling protocol following a standard protocol based on the ODMAP framework (Overview, Data, Model, Assessment and Prediction, Zurell *et al.*, 2020, see Supporting Information).

Results

The hierarchical model was a good fit to the occurrence data with high explanatory (AUC = 0.91 ± 0.04 SD) and predictive power (AUC = 0.87 ± 0.60) (Appendix S3). The model fit for abundance was moderate for explanatory ($R^2 = 0.48 \pm 0.11$) and predictive power ($R^2 = 0.30 \pm 0.14$) across all 18 species (Appendix S3). Thus, we concluded our results were robust for species occurrence but less so for abundance. Nevertheless, the environmental predictors resulted mostly in consistent effects on occurrence and on abundance among species (Fig. 2). We present only statistically supported effects unless explicitly stated.

Functional traits and phylogenetic patterns

Species occurrence was positively related to body mass ($\beta = 0.486$) and large-bodied species of waterbirds were more widely distributed in our study area (Appendix S4). In addition, species with cold thermal affinities had higher occurrence ($\beta = 0.079$) and were more abundant than species having warm thermal affinities ($\beta = 0.058$) (Appendix S4).

Species thermal affinity was positively related to both average temperatures ($\beta = 0.016$) and temperature anomalies for species occurrence ($\beta = 0.011$). The main effects, or interactions between environmental variables on the other functional traits (body mass and habitat preferences), were not statistically supported (Appendix S4).

The phylogenetic structure of the residual variation that was not explained by functional traits, was positive and strong for both species occurrence (95%CI: [0.87;1.00]) and abundance (95%CI [0.94;1.00]). Species sharing the same phylogenetic history had similar relationships with environmental variables (Fig. 2). For instance, a clade with four

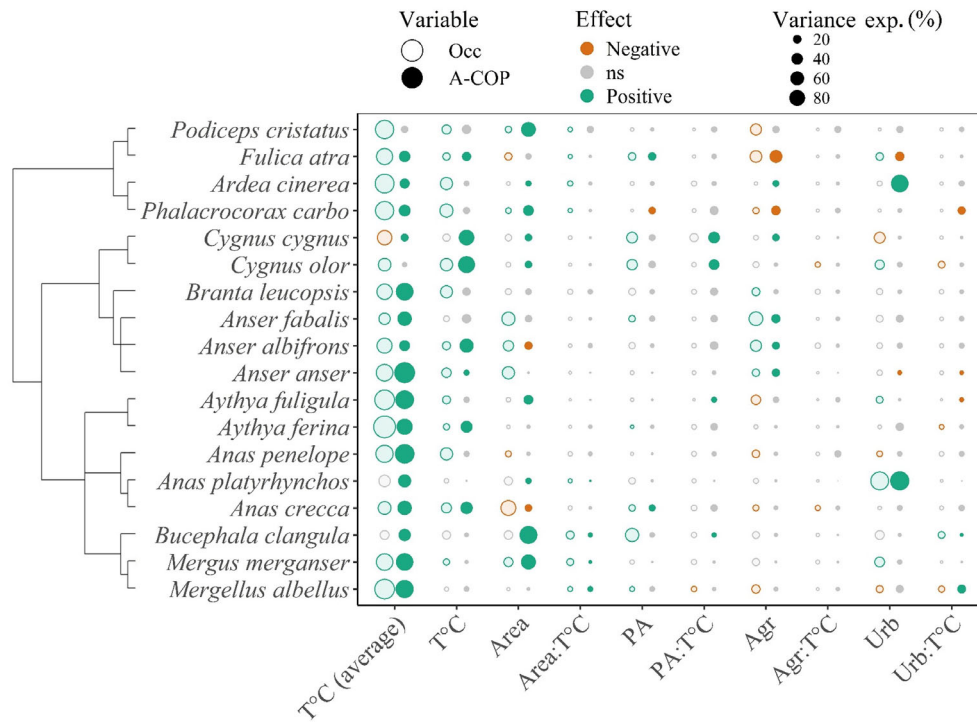


Figure 2 Effects of temperature and habitat characteristics on species occurrence (Occ) and abundance conditional upon presence (A-COP). Species are ordered phylogenetically. Explanatory variables include average temperature at site level (T°C average), temperature anomalies (T°C), site area (Area), proportion of urban surfaces (Urb), proportion of agricultural surfaces (Agr), and site protection (PA, inside compared to outside). Interacting effects are denoted by ‘:’. Variance is represented from the variance explained by fixed effects only. The effects were considered as statistically supported (i.e. colored dots) when 95% CI did not overlap zero.

species of geese was similarly linked to agricultural surfaces (*B. leucopsis*, *A. fabalis*, *A. albifrons* and *A. anser*, Fig. 2).

Species-specific patterns

Overall, all fixed effects together contributed on average 37.0% and 67.5% of the variance explained by the occurrence and abundance models, respectively, while the rest of the variance was explained by the random effects of year and sites (Table 2, Fig. 2). Among the random effects, the large variance explained by sites compared to years underlines more spatial than temporal variation unexplained by the fixed effects. Among the fixed effects, most of the variance was explained by average temperature, for both occurrence and abundance, followed by temperature anomaly, site area, land cover in agricultural or urban surfaces and the site protection status (Table 2). Main fixed effects explained on average more variance than interaction effects between temperature and other predictors (Table 2).

Unsurprisingly, the main effect of average temperature was positive on the occurrence or abundance of all species (Fig. 2, T°C average). Whooper swan (*C. cygnus*) was a large-bodied species with a contrasting pattern: average temperature was negatively related to occurrence and positively related to abundance. Temperature anomalies, used as a proxy for climate warming, resulted in positive effect on

Table 2 Variance explained across 18 species of waterbird per variable and per model fitted on species occurrence and abundance (mean ± SD). Marginal variance includes main effects and interactions (denoted by ‘:’) of the six explanatory variables; average temperatures in degrees Celsius (T°C (average)), temperature anomalies (T°C), site area (Area), proportion of urban surfaces (Urb), proportion of agricultural surfaces (Agr), and site protection (PA). Conditional variance includes the random effect of site and year, and the fixed effects

| Variable | Variance | Occurrence | Abundance |
|---------------|-------------|-------------|-------------|
| T°C (average) | Marginal | 43.2 ± 18.5 | 34.4 ± 21.1 |
| T°C | Marginal | 12.5 ± 8.3 | 14.2 ± 13.9 |
| Area | Marginal | 9.9 ± 10.0 | 13.0 ± 14.6 |
| Agr | Marginal | 9.7 ± 7.9 | 6.8 ± 6.5 |
| Urb | Marginal | 9.2 ± 12.1 | 11.3 ± 17.2 |
| PA | Marginal | 6.4 ± 7.4 | 4.1 ± 3.0 |
| PA:T°C | Marginal | 2.9 ± 2.1 | 7.2 ± 5.7 |
| Area:T°C | Marginal | 2.6 ± 2.2 | 2.4 ± 1.9 |
| Urb:T°C | Marginal | 2.2 ± 1.9 | 4.0 ± 3.0 |
| Agr:T°C | Marginal | 1.5 ± 1.2 | 2.6 ± 2.1 |
| Site | Conditional | 62.1 ± 21.4 | 28.4 ± 24.3 |
| Year | Conditional | 0.9 ± 0.6 | 4.2 ± 4.5 |
| Total fixed | Conditional | 37.0 ± 23.0 | 67.5 ± 23.0 |
| Total random | Conditional | 63.0 ± 21.1 | 32.5 ± 23.0 |

Winter temperatures have significantly increased by 1.29 ± 0.001°C over the 25 year period ($t = 50.20$, $P < 0.001$).

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either or both occurrence and abundance for 14 species. For 12 species, occurrence or abundance increased with site area. In addition, for eight species with a positive interaction between site area and temperature, the probability of occurrence or abundance were greater for large sites especially during warm winters (Fig. 2). For eight waterbird species occurrence or abundance were higher inside than outside protected areas. Only one species, the great cormorant (*Phalacrocorax carbo*), had an abundance that was negatively related to protected areas. We observed a positive interaction between site protection and temperature on the abundance of four species, suggesting that protected sites host more individuals of these waterbirds than unprotected sites especially during warm winters.

The occurrence or abundance of four species of geese, whooper swan and gray heron (*A. cinerea*) increased with the proportion of agricultural surfaces (Fig. 2). The interaction between agricultural surfaces and temperature was never positively supported. Conversely, the occurrence of seven species decreased with the proportion of agricultural surfaces, and both mute swan (*Cygnus olor*) and common teal (*Anas crecca*) occurred less at site surrounded by agricultural surfaces during warm winters. The occurrence or abundance of five species decreased with the proportion of urban surfaces (Fig. 2). Conversely, the occurrence or abundance of six species increased with the proportion of urban surface (Fig. 2). Mallards (*Anas platyrhynchos*) differed from other waterfowl because both occurrence and abundance were strongly positively related to urban surfaces. The interaction between urban surfaces and temperature was positive for two species but negative for six species. For the latter, during cold winters, the occurrence or abundance was higher at sites with a high proportion of urban surfaces.

Discussion

Our study resulted in four major findings documenting responses of nonbreeding waterbirds to climate warming and interactive effects with habitat characteristics, at both species-specific and multi-species levels. First, over the 25 year period, winter temperatures have increased by 1.29°C on the studied sites (Appendix S1). As a result, years warmer than the 25-year average were found to have higher probability of occurrence and higher species abundance for most waterbirds wintering in Sweden. The species responding the most to temperature increase were those having the warmest thermal niche. Our findings are consistent with the overall increases in nonbreeding waterbird populations in northern Europe that have been reported as a response to climate warming (Lehikoinen *et al.*, 2013; Pavón-Jordán *et al.*, 2020). Second, occurrence and abundance of waterbirds were positively related to both site area and site protection under the Natura 2000 network, with benefits that were even greater during warm winters for 60% of the species. Our results are consistent with previous evidence that large sites and protected areas might facilitate waterbirds' redistribution in response to climate warming during the non-breeding period (Pavón-Jordán *et al.*, 2015, 2020; Gaget

et al., 2022). Third, the interaction between urban surfaces and winter temperature was mainly negative when supported. Our findings could be explained by three non-exclusive hypotheses; 1) some species could benefit from urban surfaces during cold winters from an urban heat island effect (Chyb *et al.*, 2021), 2) running water could be over-represented in urban areas, if urban wetlands are less likely to freeze over, or 3) supplementary food may improve the availability of feeding resources for some dabbling ducks (Avilova, 2018). Last, the proportion of agricultural surfaces surrounding sites had benefits for terrestrial grazers known to feed on crop residue, including greylag goose (*Anser anser*), bean goose (*A. fabalis*), greater white-fronted goose (*A. albifrons*) and whooper swan (*Cygnus cygnus*). Taken together, our study demonstrates that warmer winters affect the occurrence and abundance of some phylogenetic species groups more than others and highlights that – as winter temperature increases – in particular larger and protected sites have a higher probability that waterbirds will overwinter there. In addition to our core four findings, the large proportion of variance captured by the spatial random effects suggests that waterbird occurrence and abundance may be influenced by other variables not included in our study, which include water depth or quality, exposure to harvest, regional population dynamics, or variation in the observation process (Johnston *et al.*, 2021).

The key motivation for our study was to explore the possible importance of interactions between winter temperature and site characteristics. Unsurprisingly, larger sites had a higher probability for occurrence and higher abundance of wintering waterbirds. However, we also found that in warmer winters, the probability of occurrence was even higher at large sites for most waterbird species. The interaction explained relatively little variance compared to the direct effects of average temperature or temperature anomalies alone, but was nevertheless supported for many species. Larger sites, therefore, experience substantially greater changes in community composition during warmer winters compared to small sites. One explanation for why large sites are used by more waterbirds during warmer winters in Sweden, is that large sites are likely to hold deep or running water that can remain open during mild winters when small sites might be ice covered (Nilsson & Haas, 2016). Larger sites may also offer more heterogeneous feeding or better quality habitats for waterbirds. Additional information on wetlands would have been likely beneficial to improve our understanding of species occurrence and abundance, such as the proportion of ice, water depth, surrounding vegetation or the amount of feeding resources. One puzzling finding was that the occurrence probability of common teal was lower in large sites. It is possible that this reflects feeding or roosting preference of the teal on small and shallow wetlands (Guillemain, Houte, & Fritz, 2000). To some extent, however, this finding could be due to methodology. Teal are a small-bodied duck and might remain undetected at large sites, because they often hide close to the edges and can be too far from the observer for detection. In general, it would be advantageous to correct for differences in detection across

species or due to site conditions (Vallecillo *et al.*, 2022). Unfortunately, we could not control for detection probability because the single visits under the survey protocol of the IWC framework do not have repeated visits needed for occupancy or N-mixture models. Also, the study design did not follow a random site selection, but was likely structured by birdwatcher preferences. For instance, wetlands traditionally without many waterbirds in winter might have been under-represented in the site selection. The consequence of this bias might be the underestimation of waterbird population changes along the diversity of Swedish landscapes.

Protected areas are not only important to support waterbirds (Guillemain, Fritz, & Duncan, 2002) but also to help some species to respond to climate warming (Pavón-Jordán *et al.*, 2020; Gaget *et al.*, 2022). Protected areas are designated on the basis of their ecological importance, and waterbirds are often directly targeted by the designation as a Natura 2000 protected area, or as a designated site under the Ramsar Convention on Wetlands. It is not surprising to observe more waterbirds inside than outside protected areas, but our results support in some extent that protected sites are also important for nonbreeding waterbirds in a context of winter warming. However, protected areas had a positive effect mainly on species occurrence (8 of 18 species) and more rarely on abundance (2 of 18 species), unless the interaction with winter temperature was considered. Thus, protected areas might be used as settlement areas by species moving their distribution northward (Thomas *et al.*, 2012; Lehikoinen *et al.*, 2019). A positive interaction between protected areas and winter temperature was however only observed for 4 of 18 species (Fig. 2) and was not related to species thermal affinities (Appendix S4). If protected areas improve waterbird distribution change in response to temperature increase, the phenomenon is likely to be heterogeneous among sites and species (Gaget *et al.*, 2022). One species, smew (*M. albellus*), had responses that were opposite to our predictions with protected sites becoming less attractive during warm winters. The result suggests possible overlooked interactions with underwater characteristics, such as depth, food availability, water quality, or ice condition. Alternatively, the unexpected patterns may be due to a regional context, where the network of protected area in northern Europe is in fact not enough to support rapid distribution changes of the species (Pavón-Jordán *et al.*, 2015).

Farmland species were positively affected by agricultural surfaces, but we did not find evidence for interactive effects with climate warming. For three species of geese (*A. albifrons*, *A. anser*, and *A. fabalis*) and whooper swans (*C. cygnus*), we observed associations with farmlands that were consistent with previous knowledge (Nilsson, 2013, 2014). The wintering populations of these four species have increased in southern Sweden over the last decades, due to conservation efforts protecting species against non-sustainable harvest, and changes in agricultural practices (Nilsson, 2013, 2014; Fox *et al.*, 2017; Montràs-Janer *et al.*, 2019). In Sweden, mechanical agriculture, compared to manual harvesting, produces large amounts of spill (e.g. cereal, potato, carrot, sugar beet, winter rape) which attract

geese and whooper swans during winter (Nilsson & Kampe-Persson, 2000; Nilsson, 2013, 2014). In addition, temperature increases have contributed to changes in the migratory behavior of these species (Nilsson, 2013; Nilsson & Kampe-Persson, 2018). A lack of information on land-use change over the study period is however a limitation to our study, potentially increasing parameter uncertainty on the effects of the surrounding farmland surfaces on farmland-dwellers population changes. Also, the thematic and spatial resolutions of land cover data we used might be too coarse, with respect of the 1 km buffer around sites, to fully capture the variation due to surrounding habitats. Nevertheless, our results are consistent with recent increases in wintering flocks of greater white-fronted goose in southwest Scania in Sweden, and also with the marked variations in number relative to inter-annual winter conditions (Nilsson & Kampe-Persson, 2020).

Sites surrounded by urban surfaces hosted waterbird species which can be considered urban dwellers, including mallard, tufted duck, goosander, mute swan, European coot, and gray heron. Species tolerant of human presence can benefit from nutrient-rich water and supplementary food from hand-feeding by visitors during winter inside or around cities (Avilova, 2018). Our finding of a negative interaction between urban surface and temperature is consistent with predictions of the heat island effect hypothesis (Chyb *et al.*, 2021). Species vulnerable to harsh winter may use urban wetlands as temporary refuges (Nilsson & Haas, 2016), limiting the effect of cold temperatures, ice or snow on their winter distribution changes (Schummer *et al.*, 2010; Meehan *et al.*, 2021).

We found that Mallard (*A. platyrhynchos*) shows patterns that are different compared to other waterbirds. Mallard is the most common waterbird species wintering in inland waters in Sweden, with a rapid increase in numbers since the 1990s (Nilsson & Haas, 2016). In contrast to most other waterbirds, Mallard occurrence and abundance were not affected by temperature anomalies, but the proportion of surrounding urban surfaces was the dominant factor explaining both occurrence and abundance, with a strong positive effect. The latter aspect is readily understood as Mallards are closely associated with human presence. In the absence of Mallard response to temperature anomalies, ongoing releases of captive-bred Mallards for hunting purposes might obscure the detection of population change in response to environmental conditions (Söderquist, Gunnarsson, & Elmberg, 2013). First because of the artificial changes in numbers, and second because captive-bred and wild Mallards have different movement patterns in winter (in Sweden wild Mallards migrate farther (Söderquist *et al.*, 2013)), potentially affecting movement patterns of hybrids of captive-bred and wild Mallards (Lavretsky & Sedinger, 2023).

Phylogeny was an important determinant of waterbird changes in occurrence and abundance. Related species with a shared evolutionary history were more likely to respond in the same way to winter temperature and habitat characteristics. By joint modeling of both phylogeny and functional traits we can therefore confidently conclude that among our sample of waterbirds, both geese and diving ducks responded differently to the

environmental changes. However, the strong phylogenetic signal, not explained by the functional traits based on habitat associations, raises questions about our classification of the functional traits. For instance, we considered the European wigeon and the common teal to be shallow-water dwellers after Pavón-Jordán *et al.* (2019), but the species are known to forage on farmlands as well in the study area. Alternatively, other functional traits with greater resolution might be useful, such as variation in trophic niche, bill or body morphology to characterize waterbird feeding ecology. Coarse resolution of functional traits can hide a gradient of habitat preferences, obscuring the estimation of relationships between functional groups and environmental predictors.

Loss and degradation of natural wetlands caused by anthropogenic activities can disrupt waterbird responses to climate warming and benefit generalist species (Gaget *et al.*, 2020). Our study showed that, in Sweden, waterbird occurrence and abundance changes in response to temperature increase were moderated by land cover, resulting in either higher or lower response to temperatures. We found that during warm winters, 14 of 18 species increased more at large sites or on sites protected by the Natura 2000 network, than on small or unprotected sites. Conservation strategies aiming at improving waterbird response to climate warming by facilitating distributional changes must address the protection of natural habitats, restoration of degraded wetlands, and rewilding of the surrounding or buffer areas.

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Authors' contributions

All authors have made a substantial contribution to the conception and design, or acquisition of data, or analysis and

interpretation of data, or drafting the article or revising it for intellectual content; have approved the final version for submission; have agreed to be accountable for the accuracy and integrity of the work that they conducted; have agreed to resolve queries relating to the work that they conducted and contributed to the study.

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Supporting information

Additional supporting information may be found online in the Supporting Information section at the end of the article.

Appendix S1. Relationship between missing surveys and winter temperatures.

Appendix S2. Model convergence, explanatory and predictive power.

Appendix S3. Explanatory and predictive power of the models. We evaluated the occurrence (Occ) and abundance conditional on presence (A-COP) model fits in term of area under the curve (AUC) and R^2 , respectively. The predictive power was assessed by a two-fold cross validation following Ovaskainen *et al.* (2017).

Appendix S4. Functional traits results.

Data S1. Supporting Information.