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Changes in wetland habitat use by waterbirds wintering in Czechia are related to diet and distribution changes

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Abstract

1. Understanding species habitat use and factors affecting changes in their distributions are necessary to promote the conservation of any biological community. We evaluated the changes in wetland use of the non-breeding waterbird community. Based on long-term citizen-science data (1988–2020), we tested the hypotheses that wetland use is associated with species diet and potential range-shift drivers (the tendency to occupy the same sites in consecutive years - site affinity and the species’ average temperature across its wintering range – STI).

2. We analysed species-specific wetland use of 25 species of waterbirds wintering in Czechia over a period of 33 years. The analyses explained variability in trends in numbers of the studied waterbird species across four inland wetland types: reservoirs, fishponds, industrial waters created by flooding of former mining sites, and running waters.

3. Trends in waterbird abundance positively correlated with species´ diet on fishponds, industrial and running waters. Among the diet groups, invertivores showed the largest increase in abundances on industrial waters, closely followed by herbivores. Herbivores showed the largest increase in abundances in fishponds, and piscivores did so in running waters. Regarding range-shift drivers, species with higher site affinity showed higher abundances on running waters, while species with low STI (i.e. wintering on average in sites with lower temperature) were more abundant on reservoirs. The abundance of both warm-dwelling and species with low site affinity increased on fishponds and industrial waters.

4. Our findings suggest that the increased importance of the wetland types considered here for wintering waterbirds is likely linked to diet related changes in habitat use and changes in species distributions; and highlight that wintering waterbirds are expected to select sites with higher availability of food, higher energy content and lower foraging cost.

5. Recent and rapid changes in species distributions may lead to a decrease in the effectiveness of national and international conservation efforts. When planning conservation measures, it should be kept in mind that, climate change does not only imply large-scale north/north-eastwards shifts of entire waterbird distributions, but can also modify the use of the habitats by waterbird species inside their traditional wintering range.

Introduction

Acquiring information regarding habitat use of different species (including temporal changes) is crucial for proposing effective conservation measures (Pullin, 2002; Angert *et al*., 2011; Dawson *et al*., 2011; Davis *et al*., 2014). Such information is especially relevant in the context of ongoing climate-driven changes in species distributions (Maclean *et al*., 2008; Chen *et al*., 2011; Podhrázský *et al*., 2017; Pavón-Jordán *et al*., 2019).

The non-breeding distribution and habitat use of many waterbirds have changed considerably during recent decades, with new important wintering areas being established in northern and eastern Europe (Lehikoinen *et al*., 2013; Nuijten *et al*., 2020). This phenomenon has been linked to climate-driven range changes and redistribution of abundances (Maclean *et al*., 2008; Thomas *et al*., 2012; Pavón-Jordán *et al*., 2015; Musilová, Musil, Zouhar & Adam, 2018a; Pavón-Jordán *et al*., 2019).

In addition to using newly available northern coastal areas around the Baltic Sea (Lehikoinen et al., 2013), many wintering waterbirds are progressively using inland waters in east and central Europe to a greater extent when compared to the 1990s (Musilová, Musil, Zouhar & Adam, 2018a; see also Guillemain & Hearn, 2017; Pavón-Jordán *et al*., 2020). Climate warming is shifting the zero-degree isotherm (i.e. average aerial temperature of 0 °C in January) and thus increasing also the availability of free-ice inland freshwater wetlands in this region (Pavón-Jordán *et al*., 2015, 2019, Musilová, Musil, Zouhar & Adam, 2018a). Some species are rapidly responding to this phenomenon and increasingly using the newly available wetlands in central and east Europe by altering their migratory behaviour (Sauter *et al*., 2010; Gunnarsson, Waldenström & Fransson, 2012; Adam *et al*., 2015, Podhrazský *et al*., 2017). This has several advantages - for example lowering the high mortality risk and energetic cost of a long migration (Newton, 2007) as well as reducing energy expenditure for thermoregulation in regions that were formerly hostile during winter (Ridgill & Fox, 1990; Musil *et al*., 2008; Dalby *et al*., 2013).

Although the most important wintering requirements of food resources and safety from predation are relatively well known (Snow & Perrins, 1998; Guillemain *et al*., 2000; Guillemain *et al.*, 2002; Schummer, Kaminski, Raedeke & Graber, 2010), long-term studies revealing the drivers of inland wetland use by waterbirds are absent in the literature, especially in the context of climate-driven changes in distributions. Food supply and availability of ice-free, open water in the wintering grounds are likely the most important limiting factors (Newton, 1998; Newton, 2013; Lewis *et al*., 2019) shaping waterbirds wintering distribution (Dalby *et al.*, 2013; Guillemain *et al*., 2015), followed by predation and air temperature (thermoregulation) (Ridgill & Fox, 1990; Maclean *et al.*, 2008; Adam *et al*., 2015). Hence, temperature alone does not simply explain the distribution pattern of wintering waterbirds (Dalby *et al*., 2013). The competition for food likely increases during winter, when individuals from low density breeding sites in the vast boreal and tundra areas in Fennoscandia and Russia congregate in their common wintering grounds further down the flyway (Guillemain *et al*., 2002; Brochet *et al.*, 2012). This behaviour, thus, presents an ideal opportunity to investigate how resource availability and competition for food and space drive habitat use by waterbirds during the wintering season.

In our study, we evaluate species-specific changes in the use of four different wetland types. We hypothesize that the habitat use of species among the investigated wetland types is driven by the species diet and that wetland types differ in their food supply (Kloskowski *et al*., 2009; Kameníková & Rajchard, 2013; Čížková *et al*.; 2013; Lewis *et al*., 2019). We expect a different speed of change in the use of fishponds by the different diet groups, because this particular type of wetland is characterised by high density of stocked fish. Thus, we expect a shift of invertivores from fishponds to other wetland types due to competition for invertebrates with a high density of fish (esp. Common Carp *Cyprinus Carpio*). On the other hand, fishponds constitute a food-rich habitat for piscivorous species (Musil, 2006; Nummi, Väänänen, Holopainen & Pöysä, 2016).

We also defined two species-specific determinants to outline the distribution of species regarding the four wetland types (later named range shift drivers): (a) a species' site affinity (the tendency to occupy the same sites in consecutive years) and (b) the species temperature index (STI) as a measure of the species thermal affinity (warm-dwelling or cold-dwelling species; see description below. See also Devictor *et al.*, 2008; Jiguet *et al.*, 2007). Based on these two species-specific traits and current climate warming (Hurrel & Deser, 2009), we predict increasing wintering abundances of species with low site affinity (i.e. species that show low site fidelity and thus show greater potential to change wintering sites) as well as species with high Species Temperature Index (STI; i.e. with high average winter temperature across its wintering distribution) as the winter weather conditions become more favourable for them to expand towards these previously unsuitable regions; see e.g. Gaget *et al.* 2021.

Methods

Study region

The study region covers the Czech Republic that lies in central Europe. In total, 1,169 monitored sites were classified according to the four wetland types considered: 68 reservoirs, 443 fishponds, 108 industrial waters and 550 running waters (Fig. 1).

Note that there are only a few small natural glacial lakes in the study region (Tucker & Evans, 1997; Chytil *et al.*, 1999) which are located in mountains; these are usually frozen in winter and are therefore not included in the monitoring scheme. Thus, the four types included in the analysis essentially cover all wetland sites available for wintering waterbirds (see Chytil *et al.*, 1999, Musil *et al.* 2001). The set of available sites in the study region remained unchanged throughout the whole study period (Fig. 2); all major changes in water bodies brought about by human activity in the study region had occurred before 1988, the beginning of the study period.

Waterbird monitoring data

Site-specific count data of waterbird abundances (in total 492,297 observations) were obtained from the results of the International Waterbird Census (IWC) in the Czech Republic between

1988 and 2020. IWC is a worldwide citizen-science census with a standardized methodology (see further details in Delany, 2005; Delany, 2010) managed by the national coordinator in each country and globally coordinated by Wetlands International (www.wetlands.org). Censuses are carried out in mid-January each winter because it is generally the coldest period of winter when the effect of food resources on waterbird distribution is considered most apparent due to limited site availability.

Waterbird counts were performed on a site during a day according to a complete and predefined list of species on predetermined dates and sites with the aim to maximize synchrony in the following years (Gilissen *et al.*, 2002). Census participants also recorded zero counts of individual species as well as zero counts of all species on a site. About 350 experienced volunteer birdwatchers contributed annually to the monitoring in Czechia. The most important element of IWC methodology is standardization: it requires a single count at each site each winter, optimally conducted by the same person in consecutive winters in order to make the comparisons between years straightforward and valid. Each site (up to a few km^2 of standing water or a few km of a course of running water) established on the list of sites was defined by boundaries (such as bridges, weirs or dam on rivers and streams) known by the census participants. Observers used a telescope or binoculars from the shoreline to look for flocks and/or individuals of waterbirds, usually moving from one observation site to another by foot. Running waters were monitored using line transects along the shore. The number of census participants per site (one, two or a group) and the duration of survey were designated according to bird abundance on each site, species and size of the water surface area, and weather (Bibby, Burgess & Hill, 2007; Sutherland, Pullin, Dolman & Knight, 2004). The counts at dawn were recommended for geese. Observations taken under extreme weather conditions (fog, rain, snow fall, strong wind) categorised as "strong effect" by the observer and incomplete observations were excluded from the dataset prior to the analysis.

A repeated scanning of the flocks and shoreline observations were used to increase the detectability of counted species. Census records were submitted to the national coordinator, who compiles the submitted records and checks their validity using the participants´ feedback if necessary. The quality of the IWC data has been verified in recently published studies (e.g. Fox *et al.,* 2010; Lehikoinen *et al.,* 2013; Amano *et al.,* 2018; Musilová, Musil, Zouhar & Adam, 2018a; Musilová *et al*., 2018b; Pavón-Jordán *et al*., 2019; Gaget *et al*., 2020; Pavón-Jordán *et al*., 2020). Monitoring methodology did not change over the study period.

The IWC targets all waterbirds, a group ecologically dependent on wetlands (Delany, 2010), i.e. swans, geese, ducks, grebes, cormorants, herons, rallids, waders and gulls. However, in this study, we only include 25 the most common wintering waterbird species, namely those exceeding 50 individuals in Czechia annually (see also Musil *et al*., 2011; Musilová *et al*., 2014; see Table 1 for an overview of the species). We followed Gill & Donsker (2018) for the species taxonomy.

Wetland types

The wetland types included in this study differ with regard to their origin, age and management practices (Chytil *et al*., 1999). *Fishponds* represent shallow water bodies with a small stream or canal for water inflow. As commercial subjects aimed at stocking and production of fish (mostly Carp), fishponds were formed in the Middle Ages (mostly in the 16th century), have artificially managed water levels, chemistry and nutrient input. *Reservoirs* have been built more recently (after 1900) and represent deep waterbodies with inflow from larger rivers (compared to fishponds). The fish stock in reservoirs are not managed for the purpose of commercial fisheries but rather managed by angling associations (recreation). The most recent wetland type are *industrial waters*, which were created by flooding of former mining, sand-pit or gravel-pit areas, or are sedimentary pools built in industrial areas since 1960s (Hrdinka, 2007). Among all standing water wetland types described above, there is a gradient of decreasing probability of complete ice-cover in winter with increasing depth: from fishponds (the shallowest) to industrial waters and finally to reservoirs (the deepest). High density fish stocks are most intensively managed in fishponds, followed by reservoirs and the least managed in industrial waters (Oertli *et al*., 2005; Musil, 2006, UNEP, 2017).

The trophic state of the wetland types ranges from oligotrophic waters (a low nutrient content), through mesotrophic and eutrophic waters to hypereutrophic waters, which present an extremely high nutrient content (Carlson, 1977). Among the four monitored wetland types, running waters contain the lowest content of nutrients, and fishponds are mostly eutrophic, sometimes hypertrophic (Chytil *et al*., 1999; Musil, 2006; Seiche *et al*., 2012; Čížková *et al*., 2013). The distribution of the monitored sites is shown in Fig. 1.

Species-specific variables

All 25 investigated waterbird species were described by the following three species-specific variables (*diet, species temperature index (STI)*, and *site affinity*), which could explain the temporal pattern in the wetland type use.

(i) All species were classified into *diet* groups based on their preferred food items in the wintering season: piscivorous, invertivorous, omnivorous and herbivorous (based on data and diet classification in Snow & Perrins, 1998; Kear, 2005; Šťastný & Hudec, 2016).

(ii) *Species temperature index (STI):* The STI (see Devictor *et al*., 2008; Jiguet *et al*., 2007 for detailes of STI calculation) reflects the long-term average January temperature (1950-2000) experienced by individuals of any given species across the species' entire wintering distribution. Species' distribution maps were downloaded from BirdLife International & HBW (2017) and all temperature data from the regions included in each species' wintering range (above) were downloaded from www.worldclim.org. For each species, all grid cells (5x5 degrees) with temperature data within a species' wintering range (BirdLife International & HBW 2017) were downloaded and averaged.

(iii) For each species, we calculated a measure of year-to-year variation in geographical distribution of the species across the study region (called *site affinity*). Thus, the species' fidelity to the wintering sites constitutes the basis of the covariate *site affinity*, which is bounded between 0 and 1, with the actual range of values being 0.14–0.82 in our data set. Values close to 1 indicate that the same sites are occupied in successive years, and with the same intensity; values close to zero imply large year-to-year variation in the selection of wintering sites. These values are based on Earth mover's distance (see Kranstauber, Smolla & Safi, 2017 for further details).

The pairwise correlation of continuous species-specific variables is 0.06, implying there is little collinearity (Hair, Anderson, Tatham & Black, 1995; Rogerson, 2001). The values of species-specific variables are listed in Table 1.

Statistical analysis

Our analyses proceeded in two stages, differing in the level of detail at which the count data were aggregated. In the first stage, we studied how trends in abundances of different species vary across wetland types. We first used a log-linear Poisson regression analysis to impute any missing waterbird count data from the long-term data series (in 1988–2020) using TRends and Indices for Monitoring data software (TRIM; Statistic Netherlands version 3.52, Pannekoek & Van Strien, 2005). Regression parameters were estimated using generalized estimating equations (GEE). Missing data were usually the result of incomplete coverage due to limited availability of observers in some years. The proportion of missing counts varied between 33% and 65% in the whole dataset, which is regarded as tolerable (Soldaat *et al*., 2017).

In this first stage, after imputing any missing data, we estimated the species-specific long-term trends in abundances (i.e. the change in abundance indices from one year to the next) at each of the four wetland types and assessed differences in these trends between the wetland types based on the rate of change: a strong increase or decrease (≥ 5% per year); a moderate increase or decrease (< 5% per year); a stable (trend was not significant and CIs were sufficiently narrow) or an uncertain trend (see also Fouque *et al*., 2009; Musil *et al*., 2011; Musilová *et al*., 2018b). Then, a Wald test was used to assess the significance of differences in the trends in the four wetland types. Furthermore, we used wetland type and site as covariates in the linear trend models (see also Pavón-Jordán *et al*., 2015; Musilová *et al*., 2018b).

In the second stage, we studied the effect of species-specific variables on population trends at different wetland types. As in the first step in this species-level analysis (above), we also used TRIM to fill the gaps in the data due to incomplete monitoring coverage. For each species, we obtained the TRIM-imputed *total abundance* by year and wetland type, producing a dataset of 3,267 observations (25 species, 33 years, 4 wetland types). Velvet Scoter (*Melanitta fusca*) was not recorded on fishponds and, therefore, excluded from the analyses.

Next, we explained these total abundances estimated with TRIM and their trends with species-specific variables in a regression approach. As the time abundances exhibited substantial overdispersion, we used negative binomial regression rather than the canonical Poisson distribution. The fact that observations for a species are repeated across years and wetland types led us to include species as a random effect in the model, meaning we fitted a Generalized Linear Mixed Model (GLMM). Moreover, to allow for (i) heteroskedasticity both between and within species, and (ii) arbitrary correlation within a species' values, we used a cluster-robust estimator of the standard errors in statistical inference, clustered at the species level (Cameron & Miller, 2015). To facilitate coefficient interpretation, all continuous variables were *z*-standardized (i.e. centred around the mean and divided by the standard deviation) prior to running the regressions.

For simplicity, our model specification assumes linear time trends in total abundances; we do nevertheless expect these trends to vary systematically with species-specific characteristics and across wetland types. Therefore, we included interactions of year and wetland types with all species-specific variables in our model. All regression models were estimated in Stata 16 (StataCorp, College Station, TX).

Results

492,297 observations from 25 species in 1,169 wetlands between 1988 and 2020 were included in this study. The mean annual abundance for four diet groups was the following: herbivores (23,467 ± 2,897 SE), omnivores (219,234 ± 3,264 SE), invertivores (6,295 ± 240 SE) and piscivores (15,136 ± 933 SE). The first stage of our analysis revealed significant differences in abundance trends between the four wetland types in 22 out of the 25 investigated species (Table 2). Prevailing decreasing (10 species) or stable trends (six species) were found in running waters while significant increasing trends in the abundance of 15 species were found in standing waters (reservoirs, fishponds and industrial waters). The significant differences (according to results of Wald test) in species trends among analysed wetland types were found in five of six herbivore species, in six of eight omnivore species, in all five invertivore species and in all six piscivore species. Increasing trend in abundances was found in all herbivores on reservoirs and in almost all species in industrial waters (Table 2).

The results from our GLMM showed that species exhibiting higher site affinity (i.e. low year-to-year variation in geographical distribution of the species across the study region) recorded the highest total abundances on running waters (Table 3). Similarly, cold-dwelling species (identified by a lower value of average temperature across its wintering range – STI) were more abundant in reservoirs (Table 3).

The effects of the interaction terms between species-specific variables and year showed the extent at which the trends in abundances on different wetland types varied with species-specific variables. For instance, the coefficient on year in the reservoirs column ($\beta = 0.056$) implied that the predicted yearly increase in total abundances in an omnivorous species (i.e. the reference diet group) with average values of site affinity and STI is about 5.6 per cent; the coefficient on herbivorous × year ($\beta = 0.022$) indicated that for a herbivorous species with average values of site affinity and STI, the annual increase was larger by ca. 2.2 per cent, i.e. about 8 per cent in total. The species' diet significantly affected the species trends on fishponds, industrial and running waters. On fishponds, herbivorous species showed the largest (positive) trend in total abundances (over 11 per cent per year at average values of site affinity and STI), followed closely by piscivores. On industrial waters, omnivores increased at the slowest pace by ca. 7–9 % slower than the other three diet groups. On running waters, piscivores increased at the fastest rate during the 1990s and early 2000s, followed closely by herbivores (Figures 3 and 4). Warm-dwelling and species with low site affinity showed the largest trend on fishponds and industrial waters.

The differences in trends and abundances across diet groups and wetland types are visualized in Figures 3 and 4. Figure 3 presents the underlying data on total abundances, along with trend curves obtained via scatterplot smoothing using LOESS. Figure 4 visualizes the trends predicted by the regression for different diet groups at different wetland types. The apparent discrepancies between Figure 3 and 4 are caused by the fact that in the regression that underlie Figure 4 (i) we estimate a (log-) linear for simplicity (while some trends in Figure 3 show a substantial degree of nonlinearity) and (ii) the predictions were obtained at fixed values of STI and site affinity, which otherwise vary between different diet groups. Figure 5 summarizes the findings in a graphical format.

Discussion

To promote the protection of wetland birds, the knowledge of species habitat use and facilitation of species distribution changes should be considered the cornerstones for effective adaptive management (Musilová *et al.*, 2018b; see also Pullin, 2002; Sutherland, Pullin, Dolman & Knight, 2004; Sinclair, Fryxell & Caughley, 2006; Musilová *et al.*, 2015; Holopainen *et al.*, 2015; Gaget *et al.*, 2020; Pavón-Jordán *et al.*, 2020). This study contributes to the identification of these cornerstones by demonstrating diet-specific changes in habitat use, and of species with high probability of range changes (summarized in Fig. 5), based on long-term nonbreeding data of wintering waterbirds.

Changes in habitat use in different diet groups

Generally, food supply is of high importance for waterbirds (Guillemain et al., 2015; Holopainen et al., 2015) due to its subsequent effect on breeding success, adult survival and also overall flyway population dynamics (Newton, 1998; Newton, 2013; Jørgensen *et al.*, 2016). Use of feeding habitat is a hierarchical process, influencing the species geographical distribution and the choice of a particular wetland (Green, 1998). Here, we demonstrated long-term changes in wetland type use among diet groups in fishponds, industrial and running waters, but not in reservoirs. Increased use of industrial waters was found in invertivore species, which predominantly used running waters in the beginning of the study period and progressively switch to industrial waters. Invertebrate biomass, which provides the majority of the food of invertivores, tend to be highest in early successional wetlands (Nummi & Holopainen, 2014; Petrie *et al.*, 2016), such are industrial waters. Furthermore, heterogeneity in the physical characteristics of foraging areas can affect foraging behaviour (Fernández & Lank, 2008) and therefore affect the species habitat use. Consistent with this, diving ducks represent most of the invertivore species; they feed at greater depths during the non-breeding period (Hughes & Green in Kear, 2005) and industrial waters likely provide favourable depths for their foraging behaviour. Lower foraging costs (Wood *et al.*, 2013a) in industrial waters compared to higher water velocities in running waters can make foraging more profitable for invertivores. The same effect could cause increased use of industrial waters in herbivores (almost in the same degree as in invertivores).

The *a priori* assumption of a low increase in abundances of invertivores in fishponds was confirmed. Invertebrates are fundamental to both terrestrial and aquatic food webs, and drastic decreases have been shown in terrestrial insects on a global level (Dirzo *et al.*, 2014;.Wagner *et al.*, 2021). Long-term studies on aquatic invertebrates are currently scarce (Gozlan *et al.*, 2019), but some indicate changes in aquatic invertebrate structure (Fried-Petersen *et al.*, 2020; Pilotto *et al.*, 2020; van der Lee, Aray-Ajoy, Futter & Angeler, 2021) associated with increasing levels of eutrophication and brownification as one of the most important driver of these changes (Jackson, Loewen, Vinebrooke & Chimimba, 2016; Lind *et al.*, 2018; Arzel *et al.*, 2020). Fishponds are commercial habitats with artificially managed nutrient input that increase the level of eutrophication (Roy *et al.*, 2020) and are aimed at stocking and breeding fish (mostly Carp). The artificial nutrient input have resulted in hypertrophy of fishponds, especially after the World War II (Pechar, 2000; Seiche *et al.*, 2012) and therefore these ponds exceed the nutrient level of other wetland types in the study region. It has been shown that high stocks of Carp in fishponds create an environment with extremely high competition for invertebrate food with invertivorous waterbird species during the breeding season (Musil, 2006). In this study, we show that this effect is also significant during the wintering season by a lower increase in the use of fishponds by invertivores.

Indeed, herbivores stood out as the most increasing diet group in fishponds, likely keeping outside the Carp-waterbird food competition. The importance of artificial fishponds as alternative sites for wintering herbivorous and omnivorous ducks was shown also in Doñana, Spain (Kloskowski *et al.*, 2009). However, some species of the herbivorous group (geese, Mute Swan and Eurasian Wigeon) are not strictly feeding inside of wetlands such as invertivores and piscivores and may feed both aquatically and terrestrially (Jacobsen & Ugelvik, 1994; Fox *et al*., 2005; Wood *et al*., 2013b). Therefore, the changes in wetland type use are less strongly related to wetland food supply in this group. Especially, due to the characteristics of the census protocol (dawn counts), variation in geese abundances are likely to be affected by this daily dynamic between the roosting and feeding sites. In the study region, geese have traditionally congregated in high numbers during winter and use reservoirs as a roosting sites and nearby fields as a dominant feeding sites, especially in south-Moravian lowland (Czech IWC data: http://www.waterbirdmonitoring.cz/vysledky/iwc20/). Conversely, other herbivorous species are counted during the daylight activities in the wetlands and thus do not include individuals that have left the wetlands (roosting sites) to forage in the fields. In addition, some waterbirds may often be feeding at different places during the night, such as omnivorous Mallards in the Netherlands (Kleyheeg *et al*., 2017) and granivorous dabbling ducks feeding on rice fields in the Mediterranean (Guillemain *et al.*, 2010; Brogi, Pernollet, Gauthier-Clerc & Guillemain, 2015; Parejo *et al*., 2019). Nevertheless, this nocturnal behaviour is likely difficult to quantify (Tourenq *et al.*, 2001) and any obvious suitable nocturnal feeding wetlands are not known from the study region.

On the species level, prevailing decreasing or stable trends in abundances were found in running waters, which represent the traditional wintering grounds in the study region (Adam *et al*., 2015; Musilová, Musil, Zouhar & Romportl, 2015; Musilová, Musil, Zouhar & Adam, 2018a). It is worth noting that running waters fulfil one of the most important habitat requirements for wintering waterbirds: to avoid unfavourable winter harshness and destructive winter extremes in the zero-degree-isotherm area (Musilová, Musil, Zouhar & Romportl, 2015; Musilová, Musil, Zouhar & Adam, 2018a). In recent decades, milder winter conditions in Central Europe (IPCC, 2014) likely provide an increased availability of new wintering areas, i.e. standing waters with reduced ice cover. Still, running waters still remain as suitable wintering sites, as revealed in this study, especially for piscivores and herbivorous. Recent climate and land use changes affect the fish assemblages, diversity and distribution (Comte *et al.*, 2013) as well as diversity and distribution of invertebrates (Haase *et al.*, 2019) with predicted up and downstream direction of shifts in the fish species in rivers (Radinger *et al.*, 2017), hence the use of rivers by piscivores is likely in accordance with these changes in fish distribution.

Wetland type use in species changing distribution

Generally, there is a trade-off between the cost and benefit of the wintering site use (Ridgill & Fox, 1990; Adam et al., 2015; Musilová, Musil, Zouhar & Romportl, 2015). Importantly, there is a gradient among the four investigated wetland types in the level of the winter harshness risk, i.e. the sensitivity to cold weather and freezing (running waters considered the most stable compared to standing waters, see above), in the level of habitat change risk (fishponds considered the most artificially affected), in the level of succession in freshwater communities (industrial waters considered as an early successional stages), trophic status (the highest nutrient content in fishponds); see the methods for details.

The nature of these differences reflected the use of wetland types in species with more or less probable range shifts and/or distribution changes. Species with high site affinity (i.e. species with low year-to-year variation in geographical distribution across the study region) revealed higher use of running waters. Higher stability in cold and extreme weather conditions, low level of habitat change risk caused by possible management of running waters are likely important for these species with lower probability of range changes. However, saturation of traditional wintering grounds was suggested to occur in Czech Republic (Musilová, Musil, Zouhar & Romportl, 2015) that could increase the competition for resources (Newton, 1998; Newton, 2013). In addition, higher water velocities in running waters compared to standing waters increase the foraging costs (Wood *et al.*, 2013a).

Furthermore, our study indicates the high importance of man-made standing wetlands (fishponds and industrial waters) for species more likely to undergo range shifts, i.e. species with low site affinity and warm-dwelling (higher average temperature across its wintering range – high STI –) species. Wintering waterbird populations are clearly changing their distribution (Lehikoinen *et al*,. 2013; Pavón-Jordán *et al*., 2015; Musilová, Musil, Zouhar & Adam, 2018a; Pavón-Jordán *et al*., 2019; Pavón-Jordán *et al*, 2020). These distribution changes could be associated with changes in ice cover, food availability, habitat and hunting pressure (Dalby *et al*., 2013; Newton, 2013; Guillemain *et al*., 2015; Pavón-Jordán *et al*, 2020; this study). Species with low site affinity increase the use of these newly available wetlands that are also considered less stable as wintering sites (higher winter harshness and habitat change risk, higher trophy in fishponds and lower succession in industrial waters). It seems that species with low site affinity grasp the benefits of milder climate in recent decades (Hurrel & Deser, 2009) and responded by increasingly use these alternative wetlands. The tendency of species with low site affinity to annually change the wintering sites implies they may be useful early-warning indicators of changing use of wintering sites (see also Green & Elmberg, 2014).

The thermal affinity was determined as an important trait explaining the species distribution and range changes leading by climate change (Gaget *et al*., 2020; Devictor *et a*l., 2008). The changes of nonbreeding distribution of waterbirds seems highly affected by climate warming (Pavón-Jordán *et al*., 2015; Gaget *et al*., 2018). Our study reveals the use of reservoirs by cold-dwelling species (mostly seaducks), while reservoirs represent deeper water bodies with inflow from larger rivers and have the lowest probability of complete ice-cover in winter among standing waters. In the light of climate warming, related northeastwards shifts of species distributions (Lehikoinen *et al*., 2013; Pavón-Jordán *et al*., 2015; Gaget *et al*., 2020; Pavón-Jordán *et al.*, 2020), and consequent decline and even local extinction of cold-dwelling species caused by distribution change (Devictor *et al*., 2008; Tayleur *et al*., 2016; Gaget *et al*., 2020), we assume that reservoirs could serve as a refuges for cold-dwelling species in the near future. Larger stochasticity and frequency of extreme weather events are also predicted by most climate change scenarios and thus such deep and large wetlands with stable temperature conditions suitable for benthic invertebrates will provide the resources required by these species. However, the overall increase in abundances of cold-dwelling species in the study region indicate that this issue could be much complex, as temperature is not the only driver of species distribution changes (Dalby *et al*., 2013). Conversely, warm-dwelling species increase the use of both fishponds and industrial waters. The availability of these shallower man-made wetlands may likely increase due to climate warming (Hurrel & Deser, 2010). The 'wintering strategy' of warm-dwelling species is driven by the geographic avoidance of the zero-degree isotherm to reduce winter harshness risk (Gaget *et al*., 2020), therefore warm-dwelling species likely do not reflect the difference in wetland types in terms of winter harshness risk and increase the use of industrial waters and fishponds with higher winter harshness risk. Increasing our knowledge of the habitat use of warm-dwelling species is of high importance since they are more likely to expand in the coming decades (Devictor *et al*., 2008; Tayleur *et al*., 2016; Gaget *et al*., 2020). Indeed, we can expect increasing concern of farmers and fishermen followed by the distribution changes of the warm-dwelling species, while some of them are already conflict species such as Greylag Goose or herons.

Conclusion

Our study highlight the general pattern that wintering waterbirds are expected to select sites with higher food availability (Fox *et al*., 1995; Green, 1998; Green, Fox, Hughes & Hilton, 1999; Guillemain, Fritz & Guillon *et al*. 2000; Chatterjee, Adhikari, Pal & Mukhopadhyay, 2020), higher energy content (van Eerden, 1984) and lower foraging cost (Wood *et al*., 2013a) to balance the costs and benefits of feeding site choice during wintering (Newton, 1998; Newton, 2013; Aharon-Rotman, Clark, Klaassen & Buttemer, 2016). The effort to meet these requirements resulted in a considerable change of the habitat use in the given species.

Understanding the role of habitat use in the context of changing distributions of different species is of high importance for conservation (see e.g. Janke *et al*., 2017), especially since the climate-driven range changes are already underway (e.g. Lehikoinen *et al*., 2013; Pavón-

Jordán *et al*., 2015, Musilová, Musil, Zouhar & Adam, 2018a; Pavón-Jordán *et al*., 2019; Pavón-Jordán *et al*, 2020) and may lead to the decrease of effectiveness of the conservation efforts (Musilová *et al*., 2018b). Consistent with this view, increasing use of industrial waters and fishponds for warm-dwelling and species with low site affinity exhibiting more probable range shifts and/or distribution changes, and conversely use of reservoirs by cold-dwelling species and running waters by species with high site affinity indicates importance of individual wetland types as wintering grounds, which should be considered in future conservation planning and effective management. The development and implementation of measures to increase the suitability of existing modified habitats for wildlife appears essential to conserve biodiversity (Sinclair, Fryxell & Caughley, 2006; Navedo, 2017). The implementation should be based on the core knowledge of the species habitat use and distribution changes (Musilová *et al*., 2018b). Climate-driven changes in species distributions should not necessarily have the north/eastwards direction (see e.g. Lehikoinen *et al*., 2013, 2016; Pavón-Jordán *et al*., 2015; Pavón-Jordán *et al*., 2020), but could also modify the use of habitats within species' current ranges.

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Data availability statement:

The data that support the findings of this study are available from the corresponding author upon reasonable request.

Additional Information:

The authors declare no competing interests.

Figure 1. Distribution of monitored wetland sites in the Czech Republic between 1988 and 2020

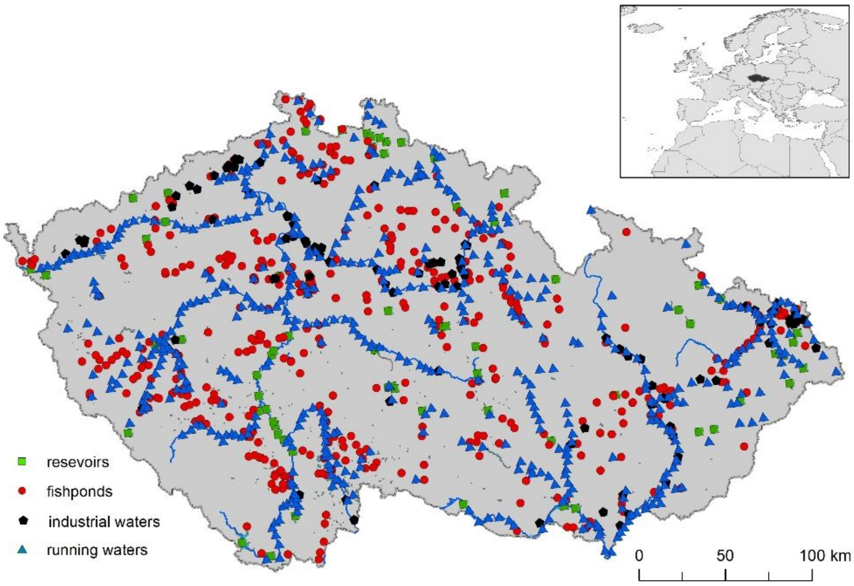


Figure 2. Proportion of monitored sites by wetland type and year. Transparent horizontal lines show the proportion of the given wetland type among all 1169 monitored sites.

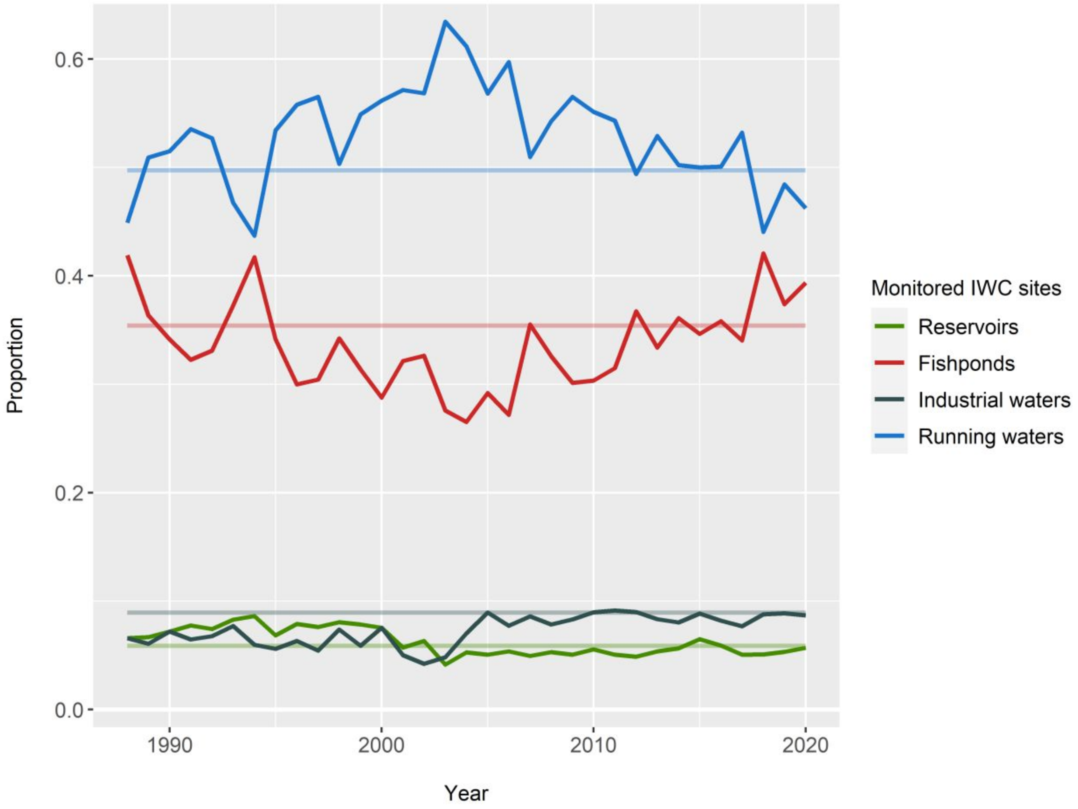


Figure 3. Yearly total abundances and their trends (obtained by LOESS smoothing) at individual wetland types, by diet group.

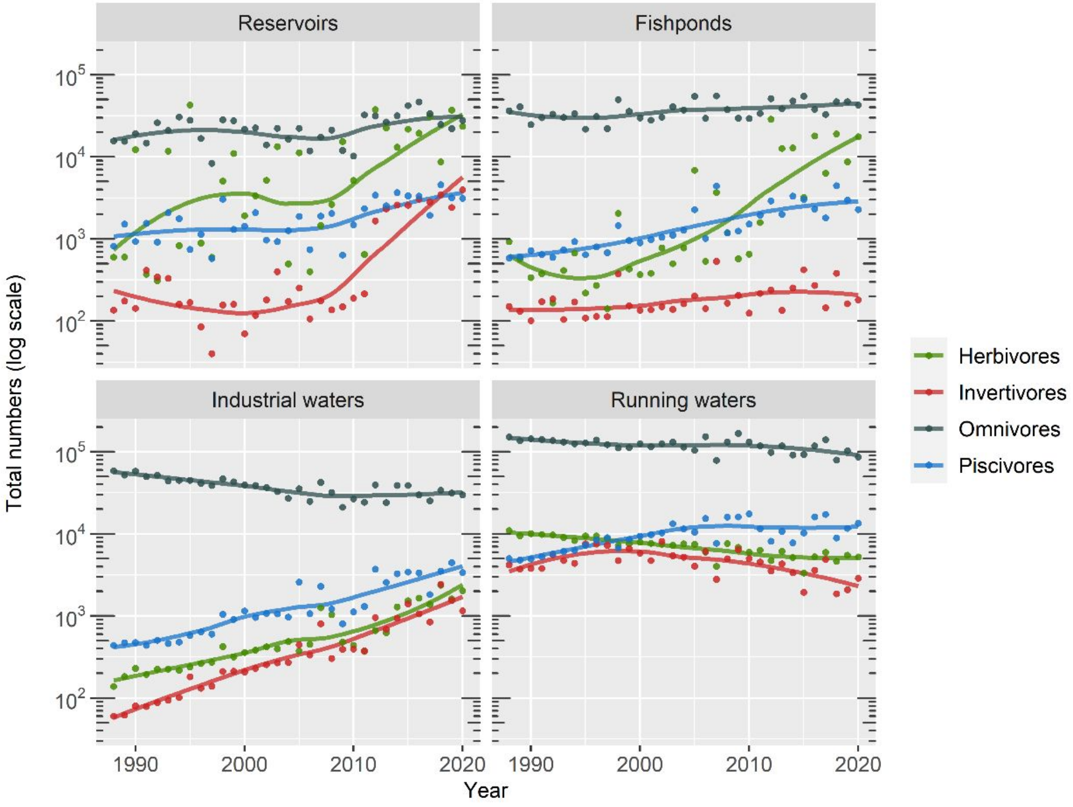


Figure 4. Predicted total abundances at individual wetland types and for different diet groups at mean values of STI and site affinity (based on the regression presented in Table 3).

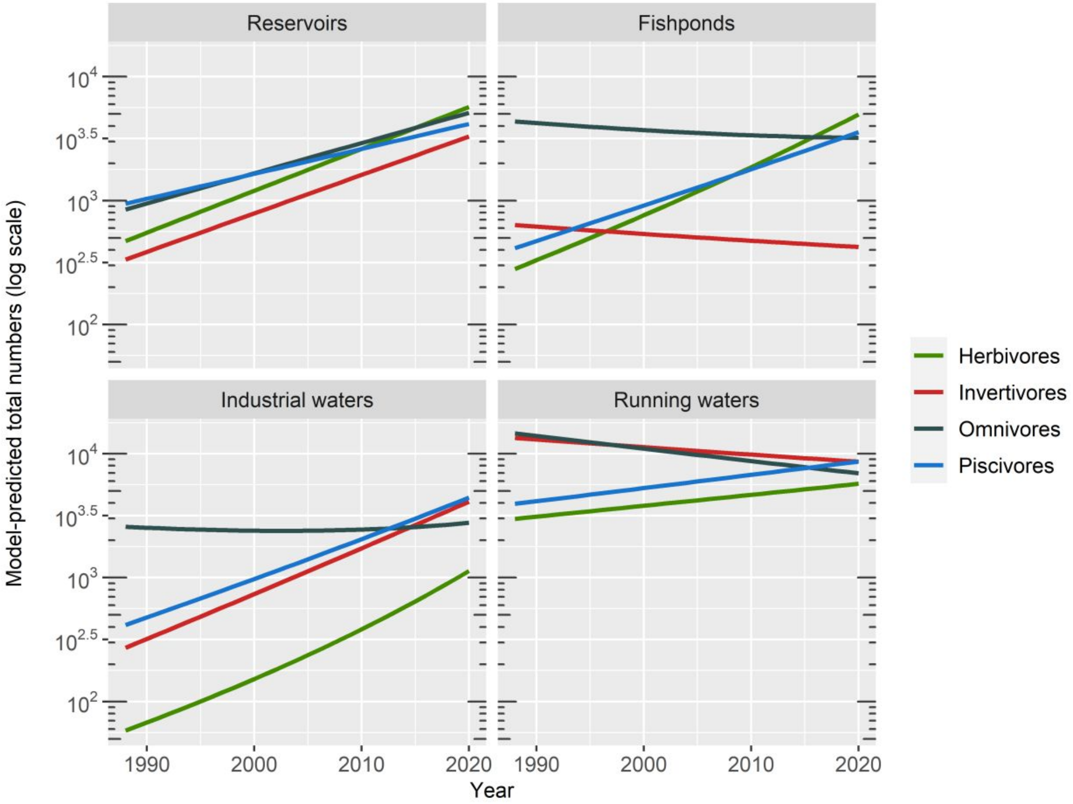


Figure 5. Wetland type use according to diet and range shift determinants of the species (graphical abstract).

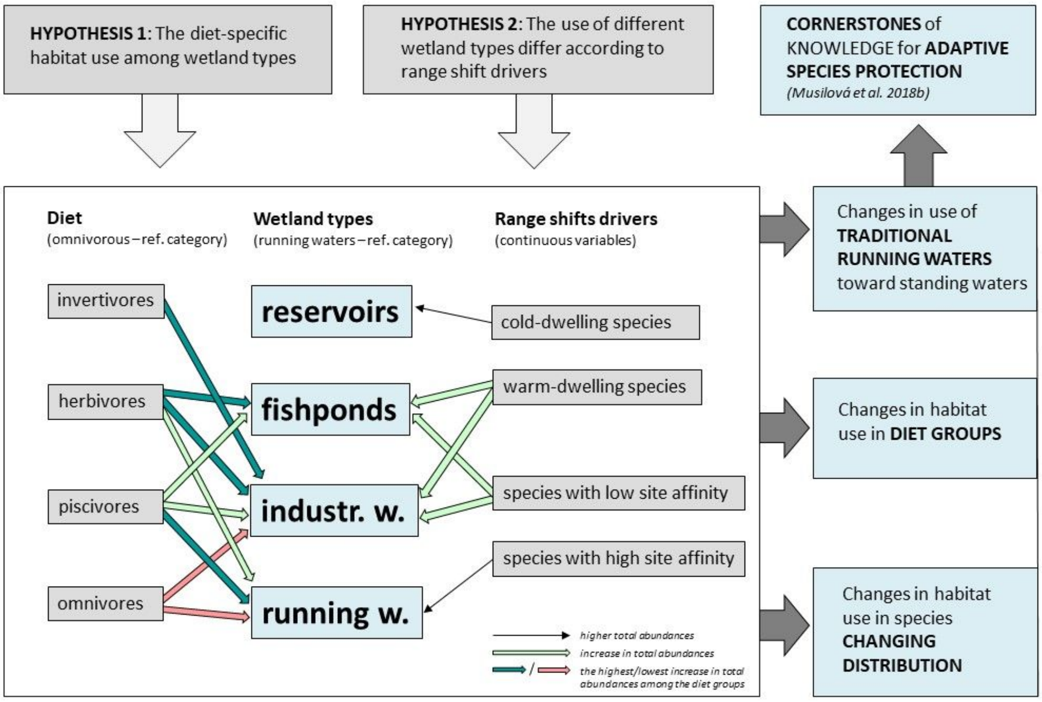


Table 1. List of investigated species and its species-specific variables (diet, species temperature index and site affinity)

Species		Diet	Species temperature index	Site affinity
Mute Swan	*Cygnus olor*	herbivore	1.27	0.771
Tundra Been Goose	*Anser serrirostris*	herbivore	-2.51	0.139
White-fronted Goose	*Anser albifrons*	herbivore	2.53	0.462
Greylag Goose	*Anser anser*	herbivore	4.47	0.516
Eurasian Wigeon	*Mareca penelope*	herbivore	16.53	0.468
Gadwall	*Mareca strepera*	herbivore	11.73	0.468
Eurasian Teal	*Anas crecca*	omnivore	12.72	0.572
Mallard	*Anas platyrhynchos*	omnivore	-0.02	0.747
Northern Pintail	*Anas acuta*	omnivore	16.9	0.412
Common Pochard	*Aythya ferina*	omnivore	11.34	0.576
Tufted Duck	*Aythya fuligula*	invertivore	10.45	0.816
Greater Scaup	*Aythya marila*	invertivore	0.43	0.487
Velvet Scoter	*Melanitta fusca*	invertivore	0.69	0.366
Common Goldeneye	*Bucephala clangula*	invertivore	-1.11	0.627
Smew	*Mergellus albellus*	piscivore	-1.58	0.515
Common Merganser	*Mergus merganser*	piscivore	-0.50	0.643
Little Grebe	*Tachybaptus ruficollis*	invertivore	3.54	0.689
Great Crested Grebe	*Podiceps cristatus*	piscivore	3.70	0.486
Great Cormorant	*Phalacrocorax carbo*	piscivore	3.25	0.612
Great Egret	*Ardea alba*	piscivore	5.41	0.543
Grey Heron	*Ardea cinerea*	piscivore	4.32	0.757
Common Moorhen	*Gallinula chloropus*	omnivore	5.61	0.775
Eurasian Coot	*Fulica atra*	omnivore	5.86	0.758
Black-headed Gull	*Chroicoceph. ridibundus*	omnivore	6.58	0.691
Mew Gull	*Larus canus*	omnivore	1.62	0.294

Notes: Species temperature index: the long-term average January temperature (1950–2000) experienced by individuals of any given species across the species' entire wintering distribution (Devictor *et al*., 2008; Jiguet *et al*., 2007). *Site affinity:* a measure of year-to-year variation in geographical distribution of the species across the study region. The measure is bounded between 0 and 1, with the actual range of values being 0.14–0.82 in our data set.See species-specific variables in methods for details.

Table 2. Changes in abundances of individual species in four wetland types (the overall area is also included)

Species	Reservoirs (overall slope±SE)	trend	Fishponds (overall slope±SE)	trend	Industrial waters (overall slope±SE)	trend	Running waters (overall slope±SE)	trend	All wetlands (overall slope±SE)	Trend	Difference in wetl.types trends (Wald test)
Mute Swan	0.04±0.01	MI**	-0.01±0.00	S	0.03±0.01	MI*	-0.04±0.00	MD**	-0.03±0.00	MD**	200.65***
Tundra Been Goose	0.01±62.66	U	0.09±0.11	U	-0.06±0.05	U	-0.04±0.02	MD*	0.02±0.02	S	0.00 ns.
White-fronted Goose	0.20±4.75	U	0.24±0.51	U	0.23±0.05	SI**	0.08±0.02	MI**	0.16±0.02	SI**	676.92***
Greylag Goose	0.16±0.44	U	0.19±0.06	SI*	0.09±0.03	MI**	0.01±0.01	S	0.13±0.00	SI**	334.18***
Eurasian Wigeon	0.07±0.07	U	0.14±0.09	U	0.16±0.03	SI**	0.02±0.018	MI**	0.07±0.01	SI**	170.32***
Gadwall	0.20±0.11	U	0.15±0.04	SI*	0.28±0.21	U	0.13±0.02	SI**	0.16±0.02	SI**	320.61***
Eurasian Teal	0.00±0.03	U	0.01±0.01	S	0.07±0.02	MI**	-0.01±0.01	MD*	0.00±0.00	S	2.24 ns.
Mallard	0.01±0.01	S	0.01±0.00	MI**	-0.04±0.01	MD**	-0.01±0.00	S	0.00±0.00	S	2.23 ns.
Northern Pintail	0.06±0.07	U	0.11±0.16	U	0.03±0.04	U	-0.01±0.02	S	0.04±0.01	MI*	19.85***
Common Pochard	0.03±0.07	U	-0.08±0.01	SD*	0.11±0.027	SI**	-0.14±0.02	SD**	-0.05±0.00	MD**	284.35***
Tufted Duck	0.11±0.03	SI*	0.00±0.01	S	0.10±0.02	SI**	-0.03±0.00	MD**	0.01±0.00	MI*	4.10*
Greater Scaup	0.17±0.13	U	0.01±0.09	U	0.13±0.08	U	-0.03±0.03	U	0.06±0.02	MI**	33.99***
Velvet Scoter	0.11±0.09	U	-		0.07±0.05	U	-0.10±0.20	U	0.06±0.02	MI**	31.97***
Common Goldeneye	0.09±0.02	SI**	0.05±0.02	MI**	0.11±0.02	SI**	-0.01±0.00	MD*	0.05±0.00	MI**	203.16***
Smew	0.05±0.07	U	0.03±0.07	U	0.13±0.04	MI**	0.00±0.01	S	0.03±0.01	MI**	18.18***
Common Merganser	0.03±0.01	MI**	0.07±0.01	SI*	0.07±0.01	MI**	0.02±0.00	MI**	0.03±0.00	MI**	151.26***
Little Grebe	0.03±0.02	U	-0.03±0.02	MD*	0.01±0.02	S	0.01±0.00	MI**	0.01±0.00	MI**	40.12***
Great Crested Grebe	0.05±0.01	MI**	0.08±0.04	MI*	0.07±0.02	MI**	-0.03±0.01	MD*	0.05±0.01	MI**	133.15***
Great Cormorant	0.04±0.01	MI**	0.08±0.01	SI*	0.08±0.01	SI*	0.04±0.00	MI**	0.05±0.00	MI**	296.69***
Great Egret	0.22±0.23	U	0.14±0.01	SI**	0.19±0.03	SI**	0.11±0.01	SI**	0.14±0.01	SI**	795.25***
Grey Heron	-0.02±0.01	MD**	0.03±0.00	MI**	0.02±0.01	S	-0.01±0.00	MD*	0.01±0.00	MI**	13.81***
Common Moorhen	0.02±0.04	U	0.02±0.01	MI*	0.05±0.02	MI*	-0.01±0.01	S	0.00±0.00	S	7.22**
Eurasian Coot	0.07±0.01	SI*	0.01±0.01	S	0.08±0.01	SI**	-0.07±0.00	SD**	-0.02±0.00	MD**	129.51***
Black-headed Gull	0.07±0.04	U	-0.01±0.01	S	-0.06±0.01	MD**	-0.02±0.002	MD**	-0.01±0.00	MD**	19.73***

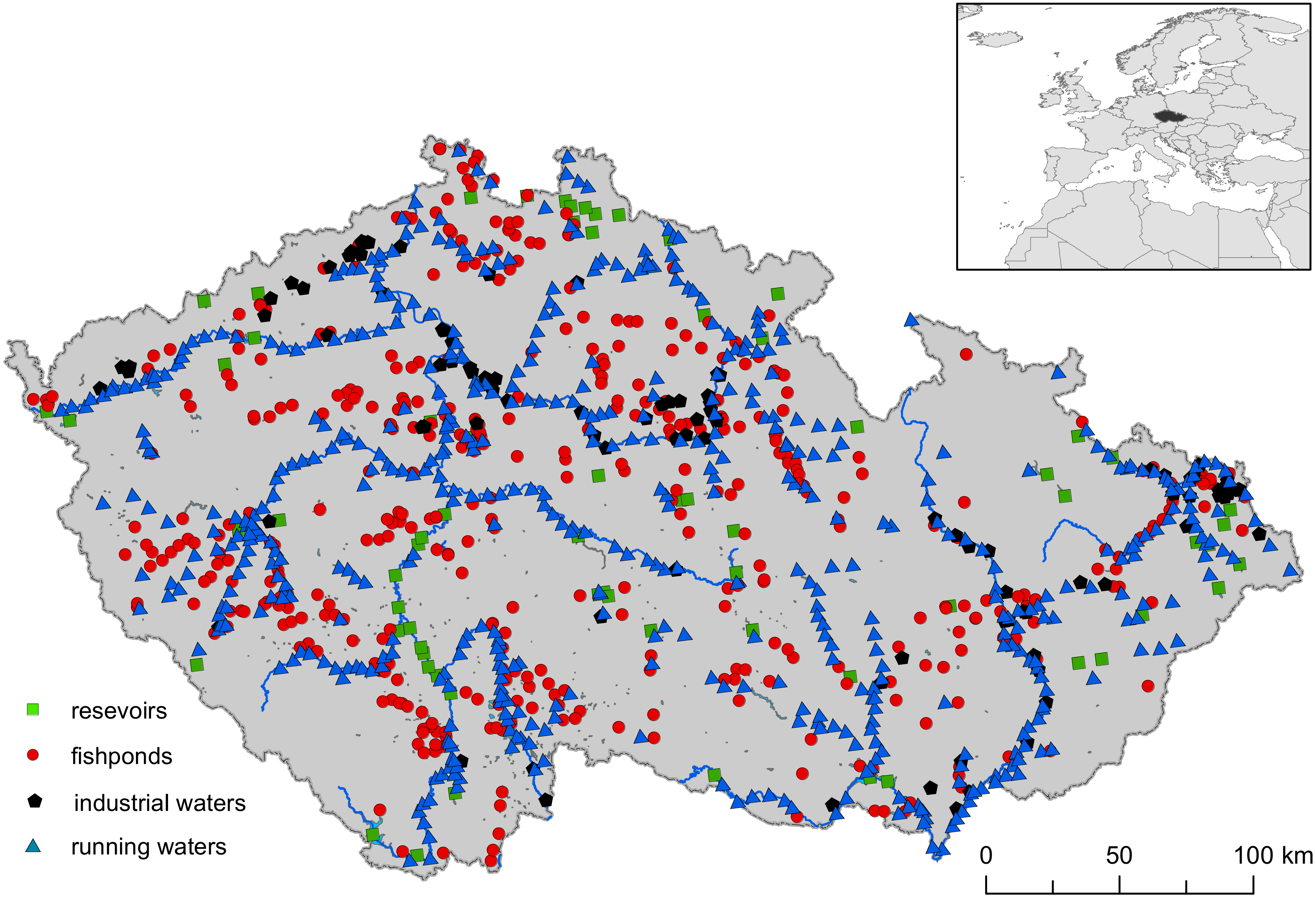
Mew Gull	0.06±0.07	U	0.01±0.02	U	0.02±0.01	S	0.02±0.01	S	0.04±0.01	MI**	85.90***

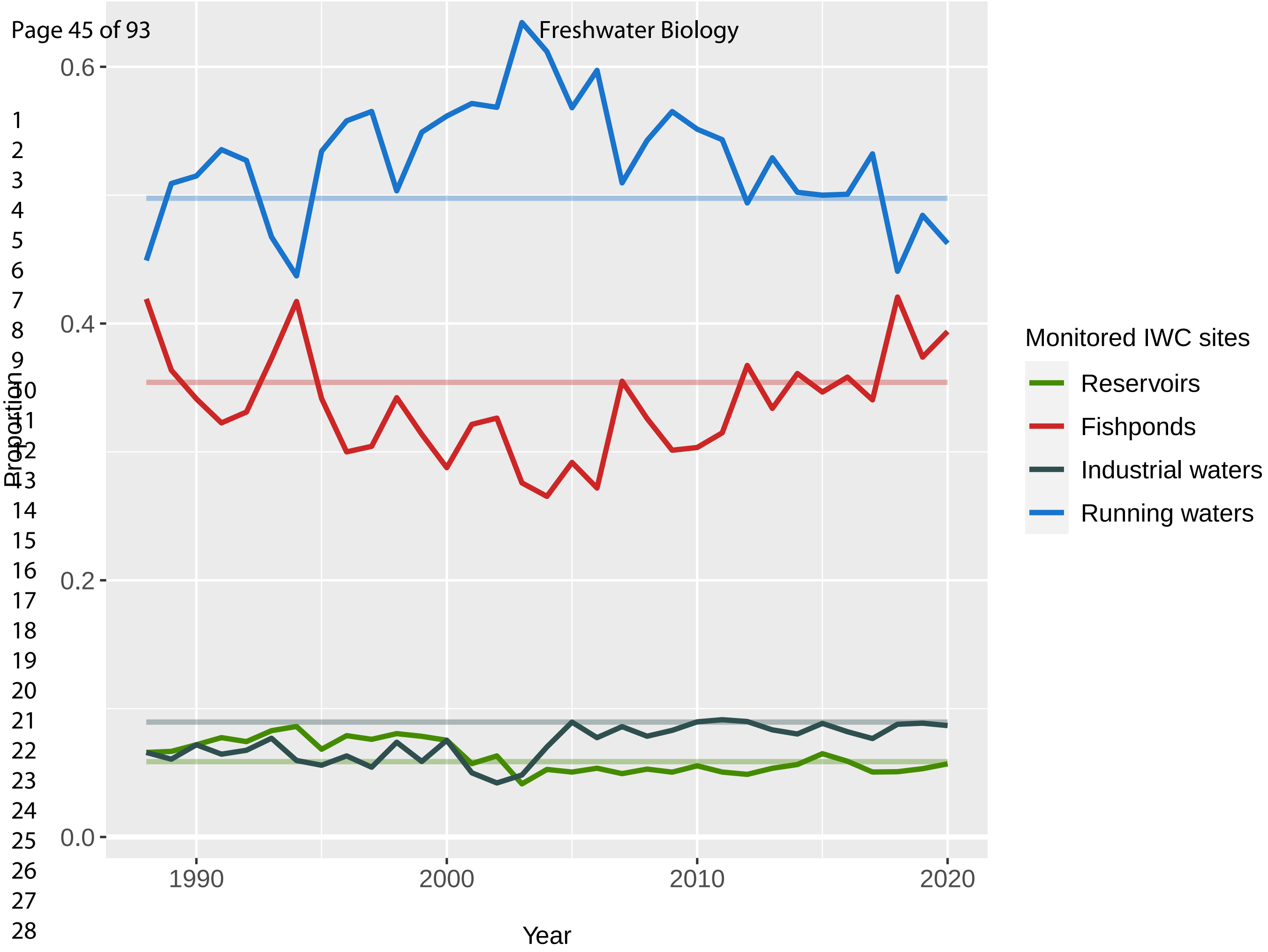
Notes: (i) * $p < 0.05$, ** $p < 0.01$, *** $p < 0.001$. (ii) Categories of trends: SI – strong increase, MI – moderate increase, S – stable, MD – moderate decrease, SD – strong decrease, U – uncertain.

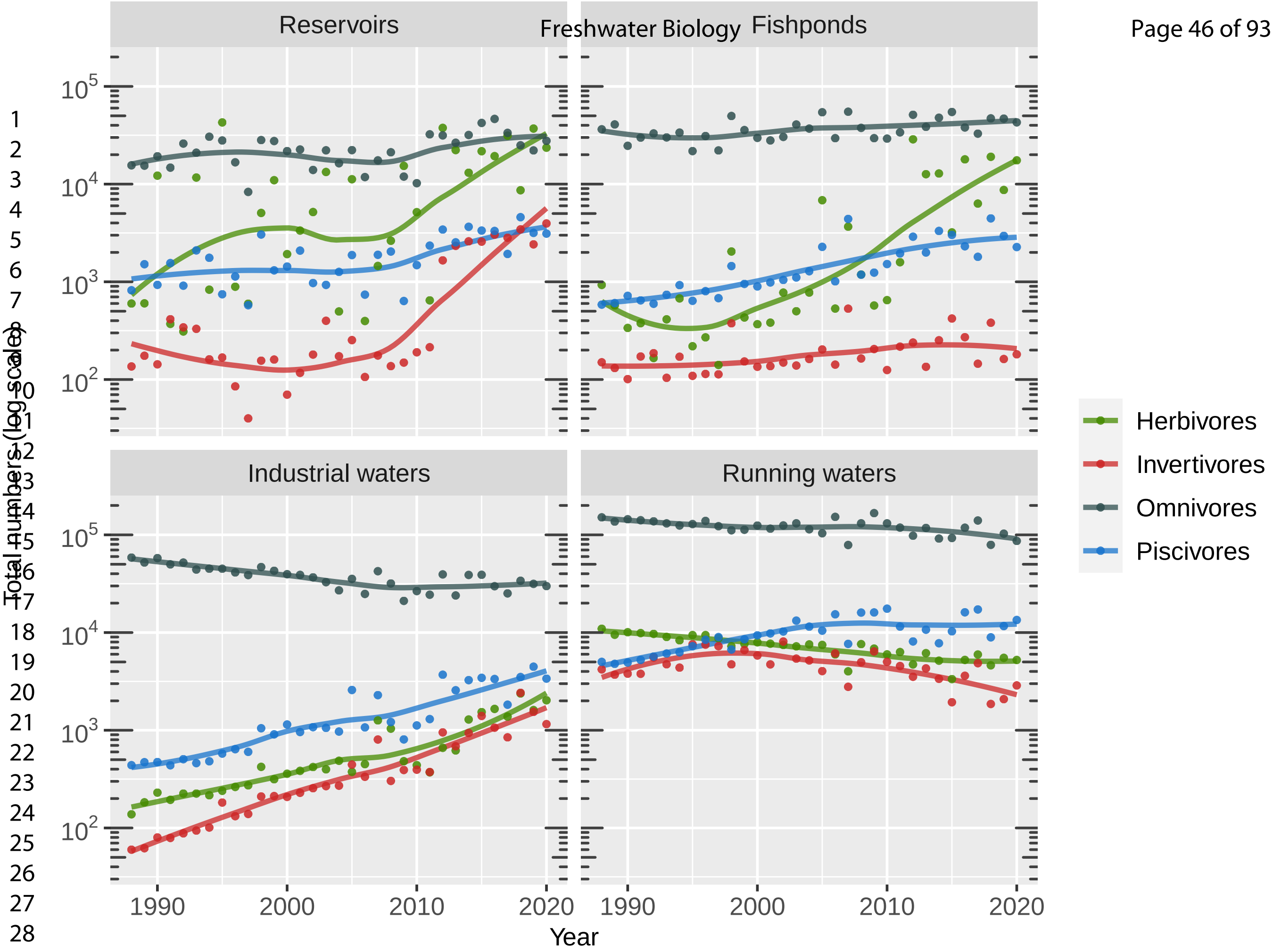
Table 3. Results of a random-effects negative binomial regression explaining total abundances.

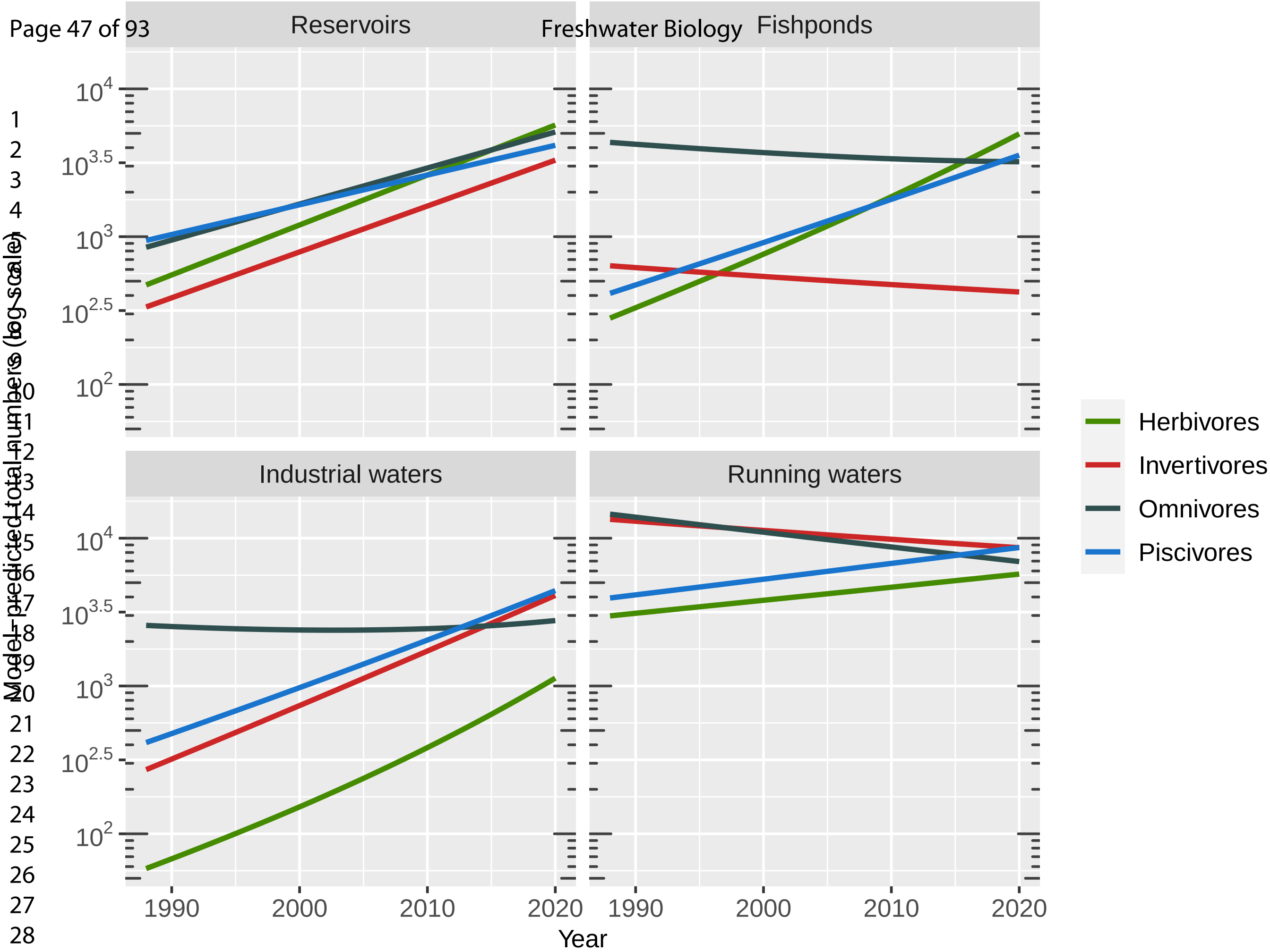
Diet	Reservoirs	Fishponds	Industrial	Running
Herbivores	–0.202	0.895	–0.635	0.370
	(0.866)	(1.227)	(1.118)	(0.928)
Omnivores	ref.	ref.	ref.	ref.
Invertivores	–0.898	–1.996**	0.282	0.113
	(0.731)	(0.740)	(0.570)	(0.725)
Piscivores	–0.597	0.172	0.549	0.593
	(0.746)	(1.138)	(1.059)	(0.978)
Site affinity (standardized)	0.206	0.627	0.360	1.290**
	(0.423)	(0.521)	(0.511)	(0.444)
STI (standardized)	–0.914*	–0.248	–0.0483	–0.415
	(0.370)	(0.485)	(0.447)	(0.352)
Year (base = 2020)	0.0557*	0.0147	0.0232	–0.0226
	(0.0270)	(0.0218)	(0.0199)	(0.0150)
Diet × year				
Herbivores × year	0.0220	0.0967*	0.0882**	0.0456
	(0.0357)	(0.0377)	(0.0280)	(0.0298)
Invertivores × year	0.0155	–0.0113	0.0847*	0.000531
	(0.0327)	(0.0225)	(0.0393)	(0.0172)
Piscivorous × year	–0.00951	0.0714*	0.0718**	0.0504*
	(0.0374)	(0.0308)	(0.0244)	(0.0222)
Site affinity × year	0.000514	–0.0204*	–0.0238*	0.00214
	(0.0171)	(0.0103)	(0.0114)	(0.0103)
STI × year	–0.000489	0.0198*	0.0275**	0.00853
	(0.0124)	(0.00967)	(0.0103)	(0.00814)
Constant	6.448***	5.694***	5.765***	5.918***
	(0.624)	(0.888)	(0.921)	(0.725)
log(α)	–0.0724	–0.0724	–0.0724	–0.0724
	(0.121)	(0.121)	(0.121)	(0.121)
var(species random effect)	4.088***	4.088***	4.088***	4.088***
	(1.041)	(1.041)	(1.041)	(1.041)
Observations	3267	3267	3267	3267
p(Different trends by diet)	0.63292	0.00002	0.00512	0.01802

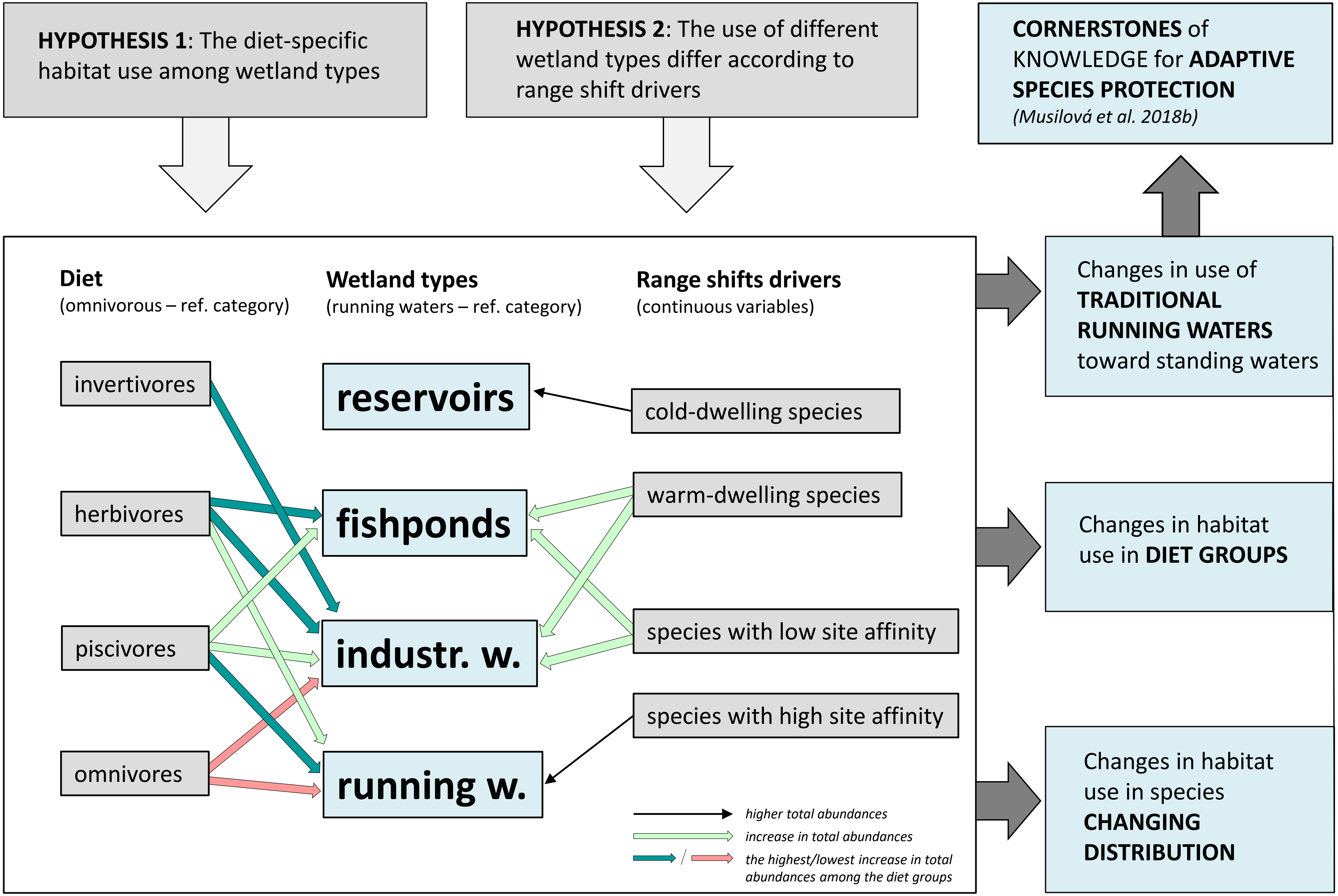
Notes: (i) The model specification contains the interactions of *wetland type* with all other covariates. To enhance readability, coefficients are presented in four columns, each related to one wetland type; moreover, the coefficients have been transformed to show the covariate effects *on the given wetland type*. (ii) Robust (Huber-White sandwich) standard errors in parentheses. (iii) * $p < 0.05$, ** $p < 0.01$, *** $p < 0.001$.


resevoirs
fishponds
industrial waters
running waters
0
50
100 km


0.6
0.4
0.2
0.0
Proportion
1990
2000
2010
2020
Year
Monitored IWC sites
Reservoirs
Fishponds
Industrial waters
Running waters


Reservoirs
Fishponds
Industrial waters
Running waters
Total numbers (log scale)
10^2
10^3
10^4
10^5
1990
2000
2010
2020
Year
Herbivores
Invertivores
Omnivores
Piscivores


Reservoirs
Fishponds
Industrial waters
Running waters
10^4
$10^{3.5}$
10^3
$10^{2.5}$
10^2
1990
2000
2010
2020
Year
Model−predicted total numbers (log scale)
Herbivores
Invertivores
Omnivores
Piscivores


HYPOTHESIS 1: The diet-specific habitat use among wetland types
HYPOTHESIS 2: The use of different wetland types differ according to range shift drivers
CORNERSTONES of KNOWLEDGE for ADAPTIVE SPECIES PROTECTION
(Musilová et al. 2018b)
Diet
(omnivorous – ref. category)
Wetland types
(running waters – ref. category)
Range shifts drivers
(continuous variables)
invertivores
herbivores
piscivores
omnivores
reservoirs
fishponds
industr. w.
running w.
cold-dwelling species
warm-dwelling species
species with low site affinity
species with high site affinity
higher total abundances
increase in total abundances
the highest/lowest increase in total abundances among the diet groups
Changes in use of TRADITIONAL RUNNING WATERS toward standing waters
Changes in habitat use in DIET GROUPS
Changes in habitat use in species CHANGING DISTRIBUTION

Changes in wetland habitat use by waterbirds wintering in Czechia are related to diet and distribution changes

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Abstract

1. Understanding species habitat use and factors affecting changes in their distributions are necessary to promote the conservation of any biological community. We evaluated the changes in wetland use of the non-breeding waterbird community. Based on long-term citizen-science data (1988–2020), we tested the hypotheses that wetland use is associated with species diet and potential range-shift drivers (the tendency to occupy the same sites in consecutive years - site affinity~~conservatism~~ and the species' average temperature across its wintering range – STI).

2. We analysed species-specific wetland use of 25 species of waterbirds wintering in Czechia over a period of 33 years. The analyses~~data~~ explained variability in trends in numbers of the studied waterbird species across four inland wetland types: reservoirs, fishponds, industrial waters created by flooding of former mining sites, and running waters.

3. Trends in waterbird abundance positively correlated with s~~S~~pecies´ diet ~~significantly correlated with their trends in numbers~~ on fishponds, industrial and running waters. Among the diet groups, i~~I~~nvertivores showed the largest increase in abundances~~numbers~~ ~~among the diet groups o~~in industrial waters, closely followed by herbivores. Herbivores showed the largest increase in abundances~~numbers~~ in fishponds, and piscivores did so in running waters. Regarding range-shift drivers, s~~S~~pecies with higher site affinity~~conservatism~~ showed higher abundances~~numbers~~ on running waters, while ~~cold-dwelling~~ species with low STI (i.e. wintering on average in sites with lower temperature) were more abundant on reservoirs. The abundance~~number~~ of both warm-dwelling and ~~less conservative~~ species with low site affinity increased on fishponds and industrial waters.

4. Our findings suggest that the increased importance of~~for~~ the ~~inland~~ wetland types~~s~~ considered here for wintering waterbirds is likely linked to diet related~~food-driven~~ changes in habitat use and changes in species distributions; and highlight ~~the general pattern~~ that wintering waterbirds are expected to select sites with higher availability of food, higher energy content and lower foraging cost.

Commented [ZM1]: AG2: data don't explain anything. Your analyses may.

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Commented [ZM3]: AG3: the reader cannot know what you mean, unless you define your measure properly above

Commented [DPJ4R4]: We have defined STI above, and it is also explained here again between brackets.

Commented [ZM5]: AG4: these seems wrong here. All your wetlands are "inland"?

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Commented [ZM7]: AG5: you don't study changes in food supply. Maybe "diet related changes"…

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5. Recent and rapid changes in species distributions may lead to a decrease in the effectiveness of national and international conservation efforts. When planning conservation measures, it should be kept in mind that, climate change does not only imply ~~only~~ large-scale north/north-eastwards shifts of entire waterbird distributions, but can also modify the use of the habitats ~~and their use~~ by waterbird species inside their ~~wintering~~ traditional wintering range.

Introduction

~~The extent of wetland habitats of natural origin has decreased worldwide, especially during the last century (Davidson, 2014; Kingsford, Basset & Jackson, 2016; O´Hare *et al.*, 2018). In Europe, for example, two thirds of all natural wetlands have disappeared in the past century (Čížková *et al.*, 2013). Although the loss of natural inland wetlands has been partially offset by the creation of man-made inland freshwater wetlands such as fishponds, reservoirs, and industrial waters (including gravel lakes, sandpit lakes, flooded areas after mining, and settling ponds), these differ in their physical and ecological characteristics (Tucker & Evans, 1997).~~

~~The importance of inland freshwater wetlands is increasing because climate warming is shifting the zero-degree isotherm (i.e. average aerial temperature of 0 °C in January) (Pavón-Jordán *et al.*, 2015, 2019, Musilová, Musil, Zouhar & Adam, 2018a). Some species are rapidly responding to this phenomenon by altering their migratory behaviour (Sauter *et al.*, 2010; Gunnarsson, Waldenström & Fransson, 2012; Podhrazský *et al.*, 2017, Adam *et al.*, 2015) to adjust to the new environmental conditions, consequently reducing the high mortality risk and energetic cost of a long migration (Newton, 2007) to minimise energy expenditure for thermoregulation during winter (Ridgill & Fox, 1990; Musil *et al.*, 2008; Dalby *et al.*, 2013a). This is especially evident in central European inland wetlands (both natural and of man-made origin), which have become increasingly important for wintering waterbirds in recent decades (Fox *et al.*, 2010; Musil, Musilová, Fuchs & Poláková, 2011; Beekman *et al.*, 2019), due to the redistribution of the abundance of many species (Ridgill & Fox 1990, Rainio *et al.*, 2006, Podhrázský *et al.*, 2017; Pavón-Jordán *et al.*, 2019) and range shifts (Lehikoinen *et al.*, 2013)~~

~~probably linked to the above-mentioned behavioural changes in response to climate change. These wetlands attract about four million waterbirds every winter (Wetlands International, 2018; see also http://iwc.wetlands.org). Moreover, wintering waterbird numbers have increased in this region in the past decades (Keller, 2011; Musil, Musilová, Fuchs & Poláková, 2011; Wetlands International, 2018). Hence, recent changes in central European winter weather creates favourable conditions that likely provide adequate foraging and safety opportunities throughout the wintering period (Švažas *et al*., 2001; Nilsson, 2008).~~

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in teh paragraph below, where they are easier to follow. I suggest you merge these paragraphs

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Acquiring ~~I~~information regarding habitat use of different species (including ~~and the~~ temporal changes) ~~taking place in the habitat use~~ is crucial for~~–~~ proposing effective conservation measures (Pullin, 2002; Angert *et al*., 2011; Dawson *et al*., 2011; Davis *et al*., 2014). Such information is especially ~~The~~ relevant~~ce~~ in the context of ongoing ~~of thise issue knowledge of habitat use increases, especially now when species are undergoing~~ climate-driven changes in species distributions ~~changes~~ (Maclean *et al*., 2008; Chen *et al*., 2011; Podhrázský *et al*., 2017; Pavón-Jordán *et al*., 2019).

The non-breeding distribution and habitat use of many waterbirds have changed considerably during recent decades, with new important wintering areas being established in northern and eastern Europe (Lehikoinen *et al*., 2013; Nuijten *et al*., 2020). ~~It is assumed that t~~This ~~development~~ phenomenon has been ~~is~~ linked to climate-driven range changes and redistribution of abundances (Maclean *et al*., 2008; Thomas *et al*., 2012; Pavón-Jordán *et al*., 2015; Musilová, Musil, Zouhar & Adam, 2018a; Pavón-Jordán *et al*., 2019).

In addition to using newly available northern coastal areas around the Baltic Sea (Lehikoinen et al., 2013), many wintering waterbirds are progressively using inland waters in east and central Europe to a greater extent when compared to the 1990s (Musilová, Musil, Zouhar & Adam, 2018a; see also Guillemain & Hearn, 2017; Pavón-Jordán *et al*., 2020). Climate warming is shifting the zero-degree isotherm (i.e. average aerial temperature of 0 °C in January) and thus increasing also the availability of free-ice ~~The increased use of importance of~~ inland freshwater wetlands ~~is now feasibleincreasing because~~ in this region ~~climate warming is shifting the zero-degree isotherm (i.e. average aerial temperature of 0 °C in~~

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in other countries?

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~~January)~~ (Pavón-Jordán *et al.*, 2015, 2019, Musilová, Musil, Zouhar & Adam, 2018a). Some species are rapidly responding to this phenomenon and increasingly using the newly available wetlands in central and east Europe by altering their migratory behaviour (Sauter *et al.*, 2010; Gunnarsson, Waldenström & Fransson, 2012; Adam *et al.*, 2015, Podhrazský *et al.*, 2017~~, Adam *et al.*, 2015~~). This has several advantages - for example lowering ~~to adjust to the new environmental conditions, consequently reducing~~ the high mortality risk and energetic cost of a long migration (Newton, 2007) as well as ~~to~~ reducing~~minimise~~ energy expenditure for thermoregulation ~~during winter~~ in regions that were formerly hostile during winter (Ridgill & Fox, 1990; Musil *et al.*, 2008; Dalby *et al.*, 2013~~a~~).

~~even~~ Although the most important wintering requirements of food resources and safety from predation are relatively well known (Snow & Perrins, 1998; Guillemain *et al.*, 2000; Guillemain *et al.*, 2002; Schummer, Kaminski, Raedeke & Graber, 2010), long-term studies revealing ~~. In spite of the rapidity of these distribution changes, Ddetailed long-term studies revealing~~ the drivers of inland wetland use by waterbirds ~~in light of their recent distribution change during the non-breeding season~~ are absent in the literature, especially in the context of climate-driven changes in distributions.~~remain scarceeven though the most important wintering requirements of food resources and safety from predation are relatively well known (Snow & Perrins, 1998; Guillemain *et al.*, 2000; Guillemain *et al.*, 2002; Schummer, Kaminski, Raedeke & Graber, 2010).~~

Food supply and availability of ice-free, open water in the wintering grounds are likely the most important limiting factors (Newton, 1998; Newton, 2013; Lewis *et al.*, 2019) shaping waterbirds wintering distribution (Dalby *et al.*, 2013; Guillemain *et al.*, 2015), followed by p~~.~~ ~~P~~redation and air temperature (thermoregulation) ~~are also be important factors affecting waterbird distribution~~ (Ridgill & Fox, 1990; Maclean *et al.*, 2008; Adam *et al.*, 2015). ~~However~~Hence, temperature alone does not simply explain the distribution pattern of wintering waterbirds (Dalby *et al.*, 2013~~a~~). The competition for food likely increases during winter, when individuals from low density breeding sites in the vast boreal and tundra areas in Fennoscandia and Russia congregate in their common wintering grounds further down the

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flyway (Guillemain *et al*., 2002; Brochet *et al*., 2012). This behaviour, thus, presents an ideal opportunity to investigate how resource availability and competition for food and space drive habitat use by waterbirds during the wintering season.

In our study, we evaluate species-specific changes in the use of four different wetland types.~~,~~ ~~including man-made wetlands. ~~We hypothesize that the habitat use ~~distribution ~~of species among the investigated wetland types is driven by the species diet and that wetland types differ in their food supply (Kloskowski *et al*., 2009; Kameníková & Rajchard, 2013; Čížková *et al*.~~,~~; 201~~9~~3; Lewis *et al*., 2019). We expect a different speed of change in the use of fishponds by ~~individual ~~the different diet groups, because this particular type of wetland~~ey~~ ~~which~~ is~~are~~ characterised by high density of stocked fish~~es~~ ~~stock~~.~~ Hence, with increasing fish density,~~ T~~In~~ ~~fishponds,~~hus, we expect a shift of invertivores from fishponds to other wetland types ~~habitats~~ due to ~~higher level of ~~competition for invertebrates with a high density of fish ~~stock ~~(esp. Common Carp *Cyprinus Carpio*). On the other hand, fishponds constitute a food-rich habitat ~~and on the contrary higher food availability ~~for piscivorous species (Musil, 2006; Nummi, Väänänen, Holopainen & Pöysä, 2016).

We also defined two species-specific determinants to outline the distribution of species ~~in regard to~~regarding ~~man-made~~the four wetland types (later named range shift drivers): (a) a species' site affinity~~conservatism~~ (the tendency to occupy the same sites in consecutive years) and (b) the species temperature index (STI) as a measure of the species thermal affinity (warm-dwelling or cold-dwelling species; see description below. See also Devictor *et al*., 2008; Jiguet *et al*., 2007)~~)~~. Based on these two species-specific traits and current climate warming (Hurrel & Deser, 20~~10~~09), w~~W~~e predict~~ed~~ ~~that the changes in use of different wetland types differ according to range shift drivers, i.e. an ~~increasing wintering abundances~~numbers~~ ~~probability of wintering in recently ice-free standing waters ~~of~~in~~ -species with low site affinity (i.e. species that show low site fidelity and thus show greater potential to change wintering sites) ~~and~~as well as ~~warm-dwelling ~~ species with high Species Temperature Index (STI; i.e. with high average winter temperature across its wintering distribution) as the winter weather conditions become more favourable for them to expand towards these previously unsuitable regions; see

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improvements to the objectives and hypotheses

Commented [ZM16R16]: The paragraphs were amended.

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directly, so explain what you expect to see. A shift from ponds into other habitats...

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e.g. Gaget *et al.* 2021. ~~species species with more probable range shifts and/or distribution changes (i.e. low-conservative and warm-dwelling species) as a consequence of climate warming (Hurrel & Deser, 2010).~~ .

Commented [ZM19]: AG11: this is unclear. Why should warmdwelling species be shifting more, if you also have sites which are now ice free? It sounds like you already know that "warm-dwelling species" have expanded more in Czechia?

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Methods

Study region

The study region covers the Czech Republic that lies in central Europe. In total, 1,169 monitored sites were classified according to the four wetland types considered: 68 reservoirs, 443 fishponds, 108 industrial waters and 550 running waters (Fig. 1). ~~Running waters include rivers and streams; they were defined as river sections with well-defined boundaries, such as bridges, weirs or dams (see Chytil *et al.*, 1999, for the list of wetland habitats in the Czech Republic).~~

Note that there are only a few small natural glacial lakes in the study region~~area~~ (Tucker & Evans, 1997; Chytil *et al.*, 1999) which are located in mountains; these are usually frozen in winter and are therefore not included in the monitoring scheme. Thus, the four types included in the analysis essentially cover all wetland sites available for wintering waterbirds (see Chytil *et al.*, 1999, Musil *et al.* 2001). The set of available sites in the study ~~area~~region remained unchanged throughout the whole study period (Fig. 2); all major changes in water bodies brought about by human activity in the study region~~area~~ had occurred before 1988, the beginning of the study period.

Waterbird monitoring data

Site-specific count data of waterbird abundances~~numbers~~ (in total 492,297 observations) were obtained from the results of the International Waterbird Census (IWC) in the Czech Republic between 1988 and 2020. IWC is a worldwide citizen-science census with a standardized methodology (see further details in Delany, 2005; Delany, 2010) managed by the national coordinator in each country and globally coordinated by Wetlands International (www.wetlands.org). Censuses are carried out in mid-January each winter because it is generally the coldest period of winter when the effect of food resources on waterbird distribution is considered most apparent due to limited site availability.

~~The counts of w~~Waterbird ~~numbers~~ counts were~~are~~ performed on a site during a day according to a complete and predefined list of species on predetermined dates and sites with the aim to maximize synchrony in the following years (Gilissen *et al*., 2002). Census participants also recorded zero counts of individual species as well as zero counts of all species on a site. About 350 experienced volunteer birdwatchers contributed annually to the monitoring in Czechia. The most important element of IWC methodology is standardization: it requires a single count at each site each winter, optimally conducted by the same person in consecutive winters in order to make the comparisons between years straightforward and valid. Each site (up to a few km^2 of standing water or a few km of a course of running water) established on the list of sites ~~is~~was defined by boundaries (such as bridges, weirs or dam on rivers and streams) known by the census participants. Observers used a telescope or binoculars from the shoreline to look for flocks and/or individuals of waterbirds, usually moving from one observation site to another by foot. Running waters we~~a~~re monitored using line transects along the shore. The number of census participants per site (one, two or a group) and the duration of survey ~~ar~~were designated according to bird abundance on each site, species and size of the water surface area, and weather (Bibby, Burgess & Hill, 2007; Sutherland, Pullin, Dolman & Knight, 2004). The counts at dawn ~~ar~~were~~e~~ recommended for geese. Observations taken under extreme weather conditions (fog, rain, snow fall, strong wind) categorised as “strong effect” by the observer and incomplete observations were excluded from the dataset prior to the analysis.

A repeated scanning of the flocks and shoreline observations ~~are~~were used to increase the detectability of counted species. Census records ~~are~~were submitted to the national coordinator, who compiles the submitted records and checks their validity using the participants´ feedback if necessary. The quality of the IWC data has been verified in recently published studies (e.g. Fox *et al.,* 2010; Lehikoinen *et al.,* 2013; Amano *et al.,* 2018; Musilová, Musil, Zouhar &

Adam, 2018a; Musilová *et al*., 2018b; Pavón-Jordán *et al*., 2019; Gaget *et al*., 2020; Pavón-Jordán *et al*., 2020). Monitoring methodology did not change over the study period.

The IWC targets all waterbirds, a group ecologically dependent on wetlands (Delany, 2010), i.e. ~~grebes, cormorants, herons,~~ swans, geese, ducks, grebes, cormorants, herons, rallids, waders and gulls. However, in this study, we only include 25 the most common wintering waterbird species, namely those exceeding 50 individuals in Czechia annually (see also Musil *et al*., 2011; Musilová *et al*., 2014; see Table 1 for an overview of the species). We followed Gill & Donsker (2018) for the species taxonomy.

Wetland types

The wetland types included in this study differ with regard to their origin, age and management practices (Chytil *et al*., 1999). *Fishponds* represent shallow water bodies with a small stream or canal for water inflow. As commercial subjects aimed at stocking and production of fish (mostly Carp ~~*Cyprinus carpio*~~), fishponds were formed in the Middle Ages (mostly in the 16th century), have artificially managed water levels, chemistry and nutrient input. *Reservoirs* have been built more recently (after 1900) and represent deep waterbodies with inflow from larger rivers (compared to fishponds). The fish stock in reservoirs are not managed for the purpose of commercial fisheries but rather managed by angling associations (recreation). The most recent wetland type are *industrial waters*, which were created by flooding of former mining, sand-pit or gravel-pit areas, or are sedimentary pools built in industrial areas since 1960s (Hrdinka, 2007). Among all standing water wetland types described above, there is a gradient of decreasing probability of complete ice-cover in winter with increasing depth: from fishponds (the shallowest) to industrial waters and finally to reservoirs (the deepest). High density f~~F~~ish stocks are most intensively managed in fishponds, followed by reservoirs and the least managed in industrial waters (Oert~~h~~li *et al*., 2005; Musil, 2006, UNEP, 2017). The trophic state of the wetland types ranges from oligotrophic waters (a low nutrient content), through mesotrophic and eutrophic waters to hypereutrophic waters, which present an extremely high nutrient content (Carlson, 1977). Among the four monitored wetland types,

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biomass, so talk about that

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running waters contain the lowest content of nutrients, and fishponds are mostly eutrophic, sometimes hypertrophic (Chytil *et al*., 1999; Musil, 2006; Seiche *et al*., 2012; Čížková *et al*., 201~~9~~3). The distribution of the monitored sites is shown in Fig. 1.

Species-specific variables

All 25 investigated waterbird species were described by the following three species-specific variables (*diet, species temperature index (STI)*, and *site affinity~~conservatism~~*), which could explain the temporal pattern in the wetland type use~~. The values of species-specific variables are listed in Table 1. We followed Gill & Donsker (2018) for the species taxonomy~~.

(i) All species were classified into *diet* groups based on their preferred food items in the wintering season: piscivorous, invertivorous, omnivorous and herbivorous (based on data and diet classification in Snow & Perrins, 1998; Kear, 2005; Šťastný & Hudec, 2016).

(ii) *Species temperature index (STI):* The STI (see Devictor *et al*., 2008; Jiguet *et al*., 2007 for detailes of STI calculation) reflects the long-term average January temperature (1950-2000) experienced by individuals of any given species across the species' entire wintering distribution. Species' distribution maps were downloaded from BirdLife International & HBW (2017) and all temperature data from the regions included in each species' wintering range (above) were downloaded from www.worldclim.org. For each species, all grid cells (5x5 degrees) with temperature data within a species' wintering range (BirdLife International & HBW 2017) were downloaded and averaged.

(iii) For each species, we calculated a measure of year-to-year variation in geographical distribution of the species across the study region~~area~~ (called *site affinity~~conservatism~~* ~~hereafter~~). ~~Considering the nature of this variable~~Thus, the species' fidelity to the wintering -sites ~~fidelity of individuals~~ constitutes the basis ~~serves as a main driver~~ of the covariate *site affinity*, which~~.~~ ~~The measure~~ is bounded between 0 and 1, with the actual range of values being 0.14–0.82 in our data set. Values close to 1 indicate that the same sites are occupied in successive years, and with the same intensity; values close to zero imply large year-to-year variation in ~~that~~ the selection of wintering sites ~~varies a lot over~~

Commented [ZM23]: AG13: but a basic question is if there are consistent patterns between species within each guild. E.g. do different herbivores behave in a similar way. Your paper seems to assume that, but not test it. You should discuss this somewhere. What evidence do you have that different guild members behave in a similar way?

Commented [MP24R24]: Trends in numbers were calculated for each species and wetland types. These are included in Table 2 together with the value of Wald test-testing differences in trends among analysed wetland types. The table shows e.g. positive trend in numbers in all herbivores on reservoirs, increasing trends in numbers in almost all species in industrial water.

~~time~~. These values are~~e calculation is~~ based on Earth mover's distance~~;~~ (see ~~(~~Kranstauber, Smolla & Safi, 2017~~see Zouhar, Musil, Musilová, in prep.)~~ for further details).

The ~~P~~pairwise correlation~~s~~ of continuous species-specific variables ~~were all below 0.30~~is 0.06, implying there is little collinearity (Hair, Anderson, Tatham & Black, 1995; Rogerson, 2001). ~~Hence all variables were included in our regression analysis (see e.g. Lehikoinen *et al*., 2016).~~ The values of species-specific variables are listed in Table 1.

Statistical analysis

Our analyses proceeded in two stages, differing in the level of detail at which the ~~monitoring~~ count data were aggregated. In the first stage, we studied how ~~the~~ trends in abundances~~number~~ of different species vary across wetland types. We first used a log-linear Poisson regression analysis to impute any missing waterbird count data from the long-term data series (in 1988–2020) using TRends and Indices for Monitoring data software (TRIM; Statistic Netherlands version 3.52, Pannekoek & Van Strien, 2005). Regression parameters were estimated using generalized estimating equations (GEE). Missing data were usually the result of incomplete coverage due to limited availability of observers in some ~~seasons~~years. The proportion of missing counts varied between 33% and 65% in the whole dataset, which is regarded as tolerable (Soldaat *et al*., 2017)~~. Consequently, we obtained the trend in numbers of adult individuals for each investigated species for each wetland type~~.

In this first stage, after imputing any missing data, we estimated the species-specific long-term trends in abundances~~numbers~~ (i.e. the change in abundance indices from one year to the next) at each of the four wetland types and assessed differences in these trends between the ~~four~~ wetland types based on the rate of change: a strong increase or decrease (≥ 5% per year); a moderate increase or decrease (< 5% per year); a stable (trend was not significant and CIs were sufficiently narrow) or an uncertain trend (see also Fouque *et al*., 2009; Musil *et al*., 2011; Musilová *et al*., 2018b). Then, a Wald test was used to assess the significance of differences in the trends ~~rate of changes in numbers~~ in the four wetland types. ~~We also used the imputed counts – referred to as *time totals* in TRIM – in our figures.~~ Furthermore, we used wetland

Commented [J25]: We replaced the citation of our unpublished manuscript – that focuses on the application of Earth mover's distance (EMD) specifically on the year-to-year changes in spatial distribution of waterbird species – with a citation of a more general (but published) paper that explains how EMD is applied in the comparison of spatial distributions in general.

Commented [ZM26]: AG14: This is not enough. You must provide a better explanation of this, since your other manuscript is not accessible

Commented [ZM27]: AG15: seems wrong, there are only two variables, conservatism and STI

Commented [MP28R28]: The value was changed.

type and site as covariates in the linear trend models (see also Pavón-Jordán *et al*., 2015; Musilová *et al*., 2018b).

In the second stage, we studied the effect of species-specific variables on population trends at different wetland types. As in the first step in this species-level analysis (above), we also used TRIM to fill the gaps in the data due to incomplete monitoring coverage. For each species, we obtained the TRIM-imputed *total abundance*~~*time totals* or yearly total abundance (later termed total numbers)~~ by year and wetland type, producing a dataset of 3,267 observations (25 species, 33 years, 4 wetland types). Velvet Scoter (*Melanitta fusca*) was not recorded on fishponds and, therefore, excluded from the analyses.

Next, we explained these total abundances~~numbers~~ estimated with TRIM and their trends with species-specific variables in a regression approach. As the time abundances ~~totals (i.e. total number of individuals)~~exhibited substantial overdispersion, we used negative binomial regression rather than the canonical Poisson distribution. The fact that observations for a species are repeated across years and wetland types led us to include species as a random effect in the model, meaning we fitted a Generalized Linear Mixed Model (GLMM). Moreover, to allow for (i) heteroskedasticity both between and within species, and (ii) arbitrary correlation within a species' values, we used a cluster-robust estimator of the standard errors in statistical inference, clustered at the species level (Cameron & Miller, 2015). To facilitate coefficient interpretation, all continuous variables were *z*-standardized (i.e. centred around the mean and divided by the standard deviation) prior to running the regressions.

For simplicity, our model specification assumes linear time trends in total abundances~~numbers~~; we do nevertheless expect these trends to vary systematically with species-specific characteristics and across wetland types. Therefore, we included interactions of year and wetland types with all species-specific variables in our model. All regression models were estimated in Stata 16 (StataCorp, College Station, TX).

Results

492,297 observations from 25 species in 1,169 wetlands between 1988 and 2020 were included in this study. The mean annual abundance for four diet groups was the following: herbivores (23,46~~6~~7~~.8~~ ± 2,897~~6.9~~ SE), omnivores (219,234~~.0~~ ± 3,264~~.4~~ SE), invertivores (6,295~~.2~~ ± 240~~.2~~ SE) and piscivores (15,136~~5.5~~ ± 933~~.2~~ SE). The first stage of our analysis revealed significant differences in abundance trends between the four wetland types in 22 out of the 25 investigated species (Table 2). Prevailing decreasing (10 species) or stable trends (six species) were found in running waters while significant increasing trends in the abundance of 15 species were found in standing waters (reservoirs, fishponds and industrial waters). The significant differences (according to results of Wald test) in species trends among analysed wetland types were found in five of six herbivore species, in six of eight omnivore species, in all five invertivore species and in all six piscivore species. Increasing trend in abundances was found in all herbivores on reservoirs and in almost all species in industrial waters (Table 2).

The results from our GLMM showed that species exhibiting higher site affinity~~conservatism~~ (i.e. low year-to-year variation in geographical distribution of the species across the study region) recorded the highest total abundances~~numbers~~ on running waters (Table 3). Similarly, cold-dwelling species (identified by a lower value of average temperature across its wintering range – STI~~species temperature index~~) were more abundant in reservoirs (Table 3).

The effects of the interaction terms between species-specific variables and year showed~~s~~ the extent at which the trends in abundances~~numbers~~ on different wetland types varied with species-specific variables. For instance, the coefficient on year in the reservoirs column (β = 0.056) implied~~s~~ that the predicted yearly increase in total abundances~~numbers~~ in an omnivorous species (i.e. the reference diet group) with average values of site affinity~~conservatism~~ and STI is about 5.6 per cent; the coefficient on herbivorous × year (β = 0.022) indicated~~s~~ that for a herbivorous species with average values of site affinity~~conservatism~~ and STI, the annual increase ~~is~~was larger by ca. 2.2 per cent, i.e. about 8 per cent in total. The species' diet significantly affected the species trends on fishponds, industrial and running waters. On fishponds, herbivorous species showed the largest (positive) trend in total abundances~~numbers~~ (over 11 per cent per year at average values of site affinity

~~conservatism~~ and STI), followed closely by piscivores. On industrial waters, omnivores increased at the slowest pace by ca. 7–9 % slower than the other three diet groups. On running waters, piscivores increased at the fastest rate during the 1990s and early 2000s, followed closely by herbivores (Figures 3 and 4). Warm-dwelling and ~~less conservative~~ species with low site affinity showed the largest trend on fishponds and industrial waters.

The differences in trends and abundances~~numbers~~ across diet groups and wetland types are visualized in Figures 3 and 4. Figure 3 presents the underlying data on total abundances~~numbers~~, along with trend curves obtained via scatterplot smoothing using LOESS. Figure 4 visualizes the trends predicted by the regression for different diet groups at different wetland types. The apparent discrepancies between Figure 3 and 4 are caused by the fact that in the regression that underlie Figure 4 (i) we estimate a (log-) linear for simplicity (while some trends in Figure 3 show a substantial degree of nonlinearity) and (ii) the predictions ~~are~~were obtained at fixed values of STI and site affinity~~conservatism~~, which otherwise vary between different diet groups. Figure 5 summarizes the findings in a graphical format.

Discussion

To promote the protection of wetland birds, the knowledge of species habitat use and facilitation of species distribution changes ~~are~~should be considered the cornerstones for effective adaptive management (Musilová *et al*., 2018b; see also Pullin, 2002; Sutherland, Pullin, Dolman & Knight, 2004; Sinclair, Fryxell & Caughley, 2006; Musilová *et al*., 2015; Holopainen *et al*., 2015; Gaget *et al*., 2020; Pavón-Jordán *et al*., 2020). This study contributes to the identification of these cornerstones by demonstrating diet-specific changes in habitat use, and of species with high probability of range changes (summarized in Fig. 5), based on long-term nonbreeding data of wintering waterbirds.

Commented [ZM29]: AG16: I don't see that as a consensus.
Many people just think about the need to conserve key sites with large numbers of waterbirds, e.g. Ramsar aites

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Changes in habitat use in different diet groups

Generally, food supply is of high importance for waterbirds (Guillemain et al., 2015; Holopainen et al., 2015) due to its subsequent effect on breeding success, adult survival and also overall flyway population dynamics (Newton, 1998; Newton, 2013; Jørgensen *et al.*, 2016). Use of feeding habitat is a hierarchical process, influencing the species geographical distribution and the choice of a particular wetland (Green, 1998). Here, we demonstrated long-term changes in wetland type use among diet groups in fishponds, industrial and running waters, but not in reservoirs. Increased use of industrial waters was ~~demonstrated~~ found in invertivore~~eous~~ species, which predominantly used running waters in the beginning of the study period and progressively switch to industrial waters. Invertebrate biomass, which provides the majority of the food of invertivores, tend to be highest in early successional wetlands (Nummi & Holopainen, 2014; Petrie *et al.*, 2016), such are industrial waters. Furthermore, heterogeneity in the physical characteristics of foraging areas can affect foraging behaviour (Fernández & Lank, 2008) and therefore affect the species habitat use. Consistent with this, diving ducks represent most of the invertivore~~eous~~ species; they feed at greater depths during the non-breeding period (Hughes & Green in Kear, 2005) and industrial waters likely provide favourable depths for their foraging behaviour. Lower foraging costs (Wood *et al.*, 2013a) in industrial waters compared to higher water velocities in running waters can make foraging more profitable for invertivores. The same effect could cause increased use of industrial waters in herbivores (almost in the same degree as in invertivores).

~~Assumed~~ The *a priori* assumption of a low increase in abundances~~numbers~~ of invertivores in fishponds was confirmed~~ in fishponds~~. In~~ in~~vertebrates are fundamental to ~~, an important element of~~ both terrestrial and aquatic food webs, and drastic decreases have been~~was~~ shown in terrestrial insects on a global level (Dirzo *et al.*, 2014;.Wagner *et al.*, 2021). Long-term studies on aquatic invertebrates are currently scarce (Gozlan *et al.*, 2019), but some indicate changes in aquatic invertebrate structure (Fried-Petersen *et al.*, 2020; Pilotto *et al.*, 2020; van der Lee, Aray-Ajoy, Futter & Angeler, 2021) associated with increasing levels of eutrophication and brownification as one of the most important driver of these changes (Jackson, Loewen, Vinebrooke & Chimimba, 2016; Lind *et al.*, 2018; Arzel *et al.*, 2020).

Fishponds are commercial habitats~~subjects~~ with artificially managed nutrient input that increase the level of eutrophication (Roy *et al*., 2020) and are aimed at stocking and breeding fish (mostly Carp). The artificial nutrient input have ~~been~~ resulted in hypertrophy of fishponds, especially after the World War II (Pechar, 2000; Seiche *et al*., 2012) and therefore these ponds exceed the nutrient level of other wetland types in the study region~~area~~. It ~~is noteworthy~~has been shown that high stocks of Carp in fishponds create an environment with extremely high competition ~~cause the competition~~ for invertebrate food with invertivorous waterbird species ~~in~~during the breeding season (Musil, 2006). In this study, we show that~~, whereas~~ this effect is also ~~noticeable~~ significant ~~in this study~~ during the wintering season by a lower increase in the use of fish~~-~~ponds by invertivores.

Indeed, herbivores stood out~~revealed~~ as the most increasing diet group in fishponds, likely keeping~~standing~~ outside the Carp-waterbird food competition. The ~~alternative~~ importance of artificial fishponds as alternative sites for wintering herbivorous and omnivorous ducks was shown also in Doñana ~~National Park~~, Spain (Kloskowski *et al*., 2009). However, some species of the herbivorous group (geese, Mute Swan and Eurasian Wigeon) are not strictly feeding inside of wetlands such as invertivores and piscivores and may feed both aquatically and terrestrially (Jacobsen & Ugelvik, 1994; Fox *et al*., 2005; Wood *et al*., 2013b). Therefore, the changes in wetland type use are less strongly~~accurate~~ related to wetland food supply in this group. Especially, due to the characteristics of the census protocol (dawn counts), variation in geese abundances~~numbers~~ are ~~more~~ likely to be affected by this daily dynamic ~~this issue due to dawn counts on~~between the roosting and feeding sites ~~the roost sites~~. In the study region~~area~~, geese have traditionally congregated in high numbers during winter and use ~~the traditional wintering grounds of high aggregations of geese are~~ reservoirs as a roosting sites and nearby fields as a dominant feeding sites, especially in south-Moravian lowland (Czech IWC data~~—~~: http://www.waterbirdmonitoring.cz/vysledky/iwc20/). Conversely, other herbivorous species are counted during the daylight activities in the wetlands and thus do not include individuals that ~~leave~~ have left the wetlands (roosting sites) to forage in the fields. In addition, some waterbirds may often be feeding at different places during the night, such as omnivorous

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Mallards in the Netherlands (Kleyheeg *et al*., 2017) and granivorous dabbling ducks feeding on rice fields in the Mediterranean (Guillemain *et al*., 2010; Brogi, Pernollet, Gauthier-Clerc & Guillemain, 2015; Parejo *et al*., 2019). Nevertheless, this nocturnal behaviour is likely difficult to quantify (Tourenq *et al.*, 2001) and any obvious suitable nocturnal feeding wetlands are not known from the study ~~area~~region.

On the species level, prevailing decreasing or stable trends in abundances~~numbers~~ were found in running waters, which represent the traditional wintering grounds in the study region~~area~~ (Adam *et al*., 2015; Musilová, Musil, Zouhar & Romportl, 2015; Musilová, Musil, Zouhar & Adam, 2018a). It is worth noting that running waters fulfil one of the most important habitat requirements for wintering waterbirds: to avoid unfavourable winter harshness and destructive winter extremes in the zero-degree-isotherm area (Musilová, Musil, Zouhar & Romportl, 2015; Musilová, Musil, Zouhar & Adam, 2018a). In recent decades, milder winter conditions in Central Europe (IPCC, 2014) likely provide an increased availability of new wintering areas, i.e. standing waters with reduced ice cover. ~~Conversely~~Still, running waters still remain as suitable wintering sites, as revealed in this study, especially for piscivores and herbivorous. Recent climate and land use changes affect the fish assemblages, diversity and distribution (Comte *et al*., 2013) as well as diversity and distribution of invertebrates (Haase *et al*., 2019) with predicted up and downstream direction of shifts in the fish species in rivers (Radinger *et al*., 2017), hence the use of rivers by piscivores is likely in accordance with these changes in fish distribution.

Wetland type use in species changing distribution

Generally, there is a trade-off between the cost and benefit of the wintering site use (Ridgill & Fox, 1990; Adam et al., 2015; Musilová, Musil, Zouhar & Romportl, 2015). Importantly, there is a gradient among the four investigated wetland types in the level of the winter harshness risk, i.e. the sensitivity to cold weather and freezing (running waters considered the most stable compared to standing waters, see above), in the level of habitat change risk (fishponds considered the most artificially affected), in the level of succession in freshwater communities (industrial waters considered as an early successional stages), trophic status~~y~~ (the highest nutrient content in fishponds); see the methods for details.

The nature of these differences reflected the use of wetland types in species with more or less probable range shifts and/or distribution changes. ~~High-conservative s~~Species with high site affinity (i.e. species with low~~er~~ year-to-year variation in geographical distribution across the study ~~area~~region) revealed higher use of running waters. Higher stability in cold and extreme weather conditions, low level of habitat change risk caused by possible management ~~and high level of succession~~ of running waters are likely important for these ~~conservative~~ species with lower probability of range changes. However, saturation of traditional wintering grounds was suggested to occur in Czech Republic (Musilová, Musil, Zouhar & Romportl, 2015) that could increase the competition for resources (Newton, 1998; Newton, 2013). In addition, higher water velocities in running waters compared to standing waters increase the foraging costs (Wood *et al*., 2013a).

~~Conversely~~Furthermore, our study indicates the high importance of man-made standing wetlands (fishponds and industrial waters) for species ~~with~~ more likely to undergo ~~probable~~ range shifts, i.e. species with low site affinity ~~low-conservative~~ and warm-dwelling (higher average temperature across its wintering range – high STI –) species. Wintering waterbird populations are clearly changing their distribution (Lehikoinen *et al*,. 2013; Pavón-Jordán *et al*., 2015; Musilová, Musil, Zouhar & Adam, 2018a; Pavón-Jordán *et al*., 2019; Pavón-Jordán *et al*, 2020). These distribution changes could be associated with changes in ice cover, food availability, habitat and hunting pressure (Dalby *et al*., 2013; Newton, 2013; Guillemain *et al*., 2015; Pavón-Jordán *et al*, 2020; this study). ~~Low-conservative s~~Species with low site affinity increase the use of these newly available wetlands that are also considered less stable as wintering sites (higher winter harshness and habitat change risk, higher trophy in fishponds and lower succession in industrial waters). It seems that ~~low conservative~~ species with low site affinity grasp the benefits of milder climate in recent decades (Hurrel & Deser, 2009) and responded by increasingly use these alternative wetlands. The tendency of ~~less conservative~~ species with low site affinity to annually change the wintering sites implies they may be useful

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mean by succession here

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early-warning indicators ~~as a pilot species to indicate~~of changing use of wintering sites (see also Green & Elmberg, 2014).

The thermal affinity was determined as an important trait explaining the species distribution and range changes leading by climate change (Gaget *et al*., 2020; Devictor *et al*., 2008). The changes of nonbreeding distribution of waterbirds seems highly affected by climate warming (Pavón-Jordán *et al*., 2015; Gaget *et al*., 2018). Our study reveals the use of reservoirs by cold-dwelling species (mostly seaducks), while reservoirs represent deeper water bodies with inflow from larger rivers and have the lowest probability of complete ice-cover in winter among standing waters. In the light of climate warming, related northeastwards shifts of species distributions (Lehikoinen *et al*., 2013; Pavón-Jordán *et al*., 2015; Gaget *et al*., 2020; Pavón-Jordán *et al*., 2020), ~~-~~and consequent decline and even local extinction of cold-dwelling species caused by distribution change (Devictor *et al*., 2008; Tayleur *et al*., 2016; Gaget *et al*., 2020), we assume that reservoirs could serve as a refuges for cold-dwelling species in the near future. Larger stochasticity and frequency of extreme weather events are also predicted by most climate change scenarios and thus such ~~as a~~ deep and large wetlands with stable temperature conditions suitable for~~for survival of~~ benthic invertebrates will provide the resources required by these species. However, the overall increase in abundances~~numbers~~ of cold-dwelling species in the study region~~area~~ indicate that this issue could be much ~~complicated~~complex, as temperature is not the only driver ~~hence the temperature do not simply explain the~~of species distribution changes (Dalby *et al*., 2013). Conversely, warm-dwelling species increase the use of both fishponds and industrial waters. The availability of these shallower man-made wetlands may likely increase ~~in recent years~~ due to climate warming (Hurrel & Deser, 2010). The 'wintering strategy' of warm-dwelling species is driven by the geographic avoidance of the zero-degree isotherm to reduce winter harshness risk (Gaget *et al*., 2020), therefore warm-dwelling species likely do not reflect the difference in wetland types in terms of winter harshness risk and increase the use of industrial waters and fishponds with higher winter harshness risk. Increasing our knowledge of the habitat use of warm-dwelling species ~~habitat use~~ is of high importance ~~due to its forecasted~~ since they are more likely to

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expand~~increase~~ in the coming decades (Devictor *et al*., 2008; Tayleur *et al*., 2016; Gaget *et al*., 2020). Indeed, we can expect increasing concern of farmers and fishermen followed by the distribution changes of the warm-dwelling species, while some of them are already conflict species such as Greylag Goose or herons.

Conclusion

Our study highlight the general pattern that wintering waterbirds are expected to select sites with higher food availability (Fox *et al*., 1995; Green, 1998; Green, Fox, Hughes & Hilton, 1999; Guillemain, Fritz & Guillon *et al*. 2000; Chatterjee, Adhikari, Pal & Mukhopadhyay, 2020), higher energy content (van Eerden, 1984) and lower foraging cost (Wood *et al*., 2013a) to balance the costs and benefits of feeding site choice during wintering (Newton, 1998; Newton, 2013; Aharon-Rotman, Clark, Klaassen & Buttemer, 2016). The effort to meet these requirements resulted in a considerable change of the habitat use in the given species. ~~Based on the flyway-level waterbird data, dramatic changes in relative abundances are expected (see e.g. Pavón-Jordán *et al*., 2020) with temperature-dependent inter-annual and long-term north-eastwards shift of the species distribution (Pavón-Jordán *et al*., 2019).~~ Understanding the role of habitat use in the~~is~~ context of changing distributions of different species is of high importance for conservation (see e.g. Janke *et al*., 2017), especially since the climate-driven range changes are already underway (e.g. Lehikoinen *et al*., 2013; Pavón-Jordán *et al*., 2015, Musilová, Musil, Zouhar & Adam, 2018a; Pavón-Jordán *et al*., 2019; Pavón-Jordán *et al*, 2020) and may lead to the decrease of effectiveness of the conservation efforts (Musilová *et al*., 2018b). Consistent with this view, increasing use of industrial waters and fishponds for warm-dwelling and ~~low-conservative~~ species with low site affinity ~~with~~exhibiting more probable range shifts and/or distribution changes, and conversely use of reservoirs by cold-dwelling species and running waters by ~~high-conservative~~ species with high site affinity indicates importance of individual wetland types as wintering grounds, which should be considered in future conservation planning and effective management. The development and implementation of measures to increase the suitability of existing modified

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habitats for wildlife appears essential to conserve biodiversity (Sinclair, Fryxell & Caughley, 2006; Navedo, 2017). The implementation should be based on the core knowledge of the species habitat use and distribution changes (Musilová *et al*., 2018b). C~~The c~~limate-driven changes in ~~the~~ species distributions should not necessarily have the north/eastwards direction (see e.g. Lehikoinen *et al*., 2013, 2016; Pavón-Jordán *et al*., 2015; Pavón-Jordán *et al*., 2020), but ~~climate changes~~ could also modify the use of habitats ~~and their use~~ within~~inside the~~ species’ current ranges.

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results on changes within each of the four habitats

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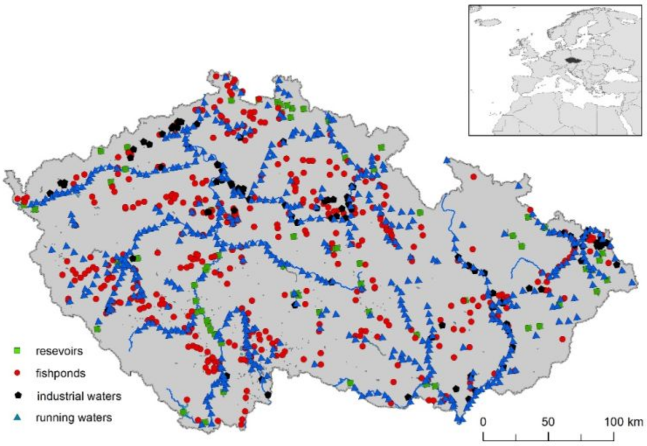
Data availability statement:

The data that support the findings of this study are available from the corresponding author upon reasonable request.

Additional Information:

The authors declare no competing interests.

Figure 1. Distribution of monitored wetland sites in the Czech Republic between 1988 and 2020



954 Figure 2. Proportion of monitored sites by wetland type and year. Transparent horizontal lines 955 show the proportion of the given wetland type among all 1169 monitored sites.

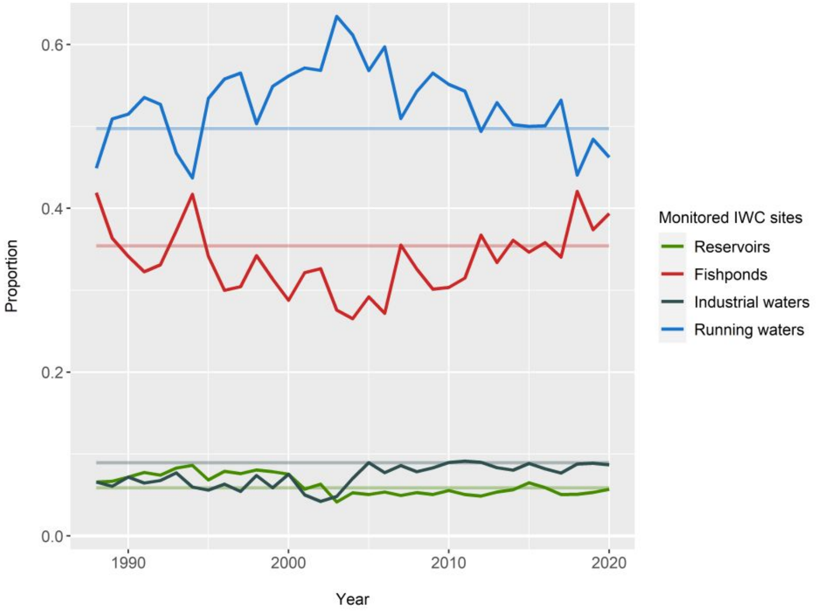


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Figure 3. Yearly total abundances and their trends (obtained by LOESS smoothing) at individual wetland types, by diet group.

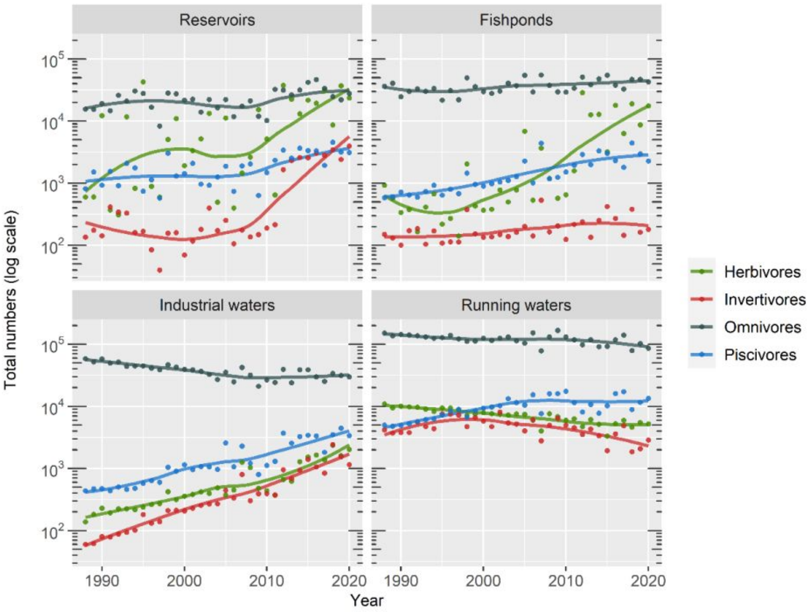

Figure 4. Predicted ~~time~~ totals abundances at individual wetland types and for different diet groups at mean values of STI and site affinity~~conservatism~~ (based on the regression presented in Table 3).

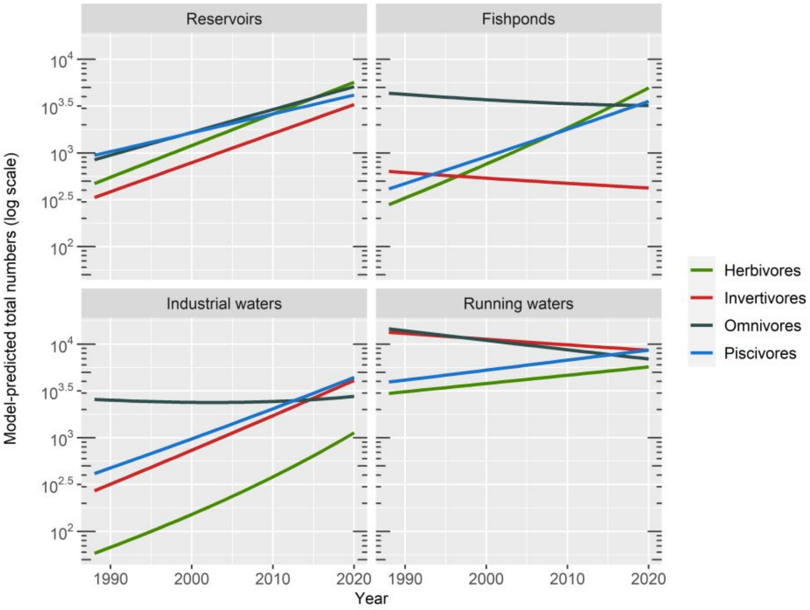

Figure 5. Wetland type use according to diet and range shift determinants of the species (graphical abstract).

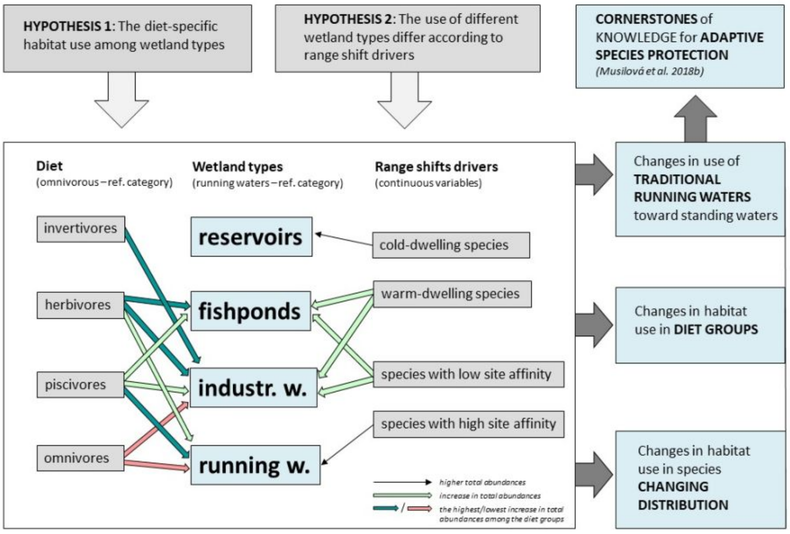

Table 1. List of investigated species and its species-specific variables (diet, species temperature index and site affinity ~~conservatism~~)

Species		Diet	Species temperature index	Site affinity~~conservatism~~
Mute Swan	*Cygnus olor*	herbivore	1.27	0.771
Tundra Been Goose	*Anser serrirostris*	herbivore	-2.51	0.139
White-fronted Goose	*Anser albifrons*	herbivore	2.53	0.462
Greylag Goose	*Anser anser*	herbivore	4.47	0.516
Eurasian Wigeon	*Mareca penelope*	herbivore	16.53	0.468
Gadwall	*Mareca strepera*	herbivore	11.73	0.468
Eurasian Teal	*Anas crecca*	omnivore	12.72	0.572
Mallard	*Anas platyrhynchos*	omnivore	-0.02	0.747
Northern Pintail	*Anas acuta*	omnivore	16.9	0.412
Common Pochard	*Aythya ferina*	omnivore	11.34	0.576
Tufted Duck	*Aythya fuligula*	invertivore	10.45	0.816
Greater Scaup	*Aythya marila*	invertivore	0.43	0.487
Velvet Scoter	*Melanitta fusca*	invertivore	0.69	0.366
Common Goldeneye	*Bucephala clangula*	invertivore	-1.11	0.627
Smew	*Mergellus albellus*	piscivore	-1.58	0.515
Common Merganser	*Mergus merganser*	piscivore	-0.50	0.643
Little Grebe	*Tachybaptus ruficollis*	invertivore	3.54	0.689
Great Crested Grebe	*Podiceps cristatus*	piscivore	3.70	0.486
Great Cormorant	*Phalacrocorax carbo*	piscivore	3.25	0.612
Great Egret	*Ardea alba*	piscivore	5.41	0.543
Grey Heron	*Ardea cinerea*	piscivore	4.32	0.757
Common Moorhen	*Gallinula chloropus*	omnivore	5.61	0.775
Eurasian Coot	*Fulica atra*	omnivore	5.86	0.758
Black-headed Gull	*Chroicoceph. ridibundus*	omnivore	6.58	0.691
Mew Gull	*Larus canus*	omnivore	1.62	0.294

Notes: Species temperature index: the long-term average January temperature (1950–2000) experienced by individuals of any given species across the species' entire wintering distribution (Devictor *et al*., 2008; Jiguet *et al*., 2007). *Site affinity:* a measure of year-to-year variation in geographical distribution of the species across the study region. The measure is bounded between 0 and 1, with the actual range of values being 0.14–0.82 in our data set.See species-specific variables in methods for details.

Table 2. Changes in abundances~~numbers~~ of individual species in four wetland types (the overall area is also included)

Species	Reservoirs (overall slope±SE)	trend	Fishponds (overall slope±SE)	trend	Industrial waters (overall slope±SE)	trend	Running waters (overall slope±SE)	trend	All wetlands (overall slope±SE)	Trend	Difference in wetl.types trends (Wald test)
Mute Swan	0.04±0.01	MI**	-0.01±0.00	S	0.03±0.01	MI*	-0.04±0.00	MD**	-0.03±0.00	MD**	200.65***
Tundra Been Goose	0.01±62.66	U	0.09±0.11	U	-0.06±0.05	U	-0.04±0.02	MD*	0.02±0.02	S	0.00 ns.
White-fronted Goose	0.20±4.75	U	0.24±0.51	U	0.23±0.05	SI**	0.08±0.02	MI**	0.16±0.02	SI**	676.92***
Greylag Goose	0.16±0.44	U	0.19±0.06	SI*	0.09±0.03	MI**	0.01±0.01	S	0.13±0.00	SI**	334.18***
Eurasian Wigeon	0.07±0.07	U	0.14±0.09	U	0.16±0.03	SI**	0.02±0.018	MI**	0.07±0.01	SI**	170.32***
Gadwall	0.20±0.11	U	0.15±0.04	SI*	0.28±0.21	U	0.13±0.02	SI**	0.16±0.02	SI**	320.61***
Eurasian Teal	0.00±0.03	U	0.01±0.01	S	0.07±0.02	MI**	-0.01±0.01	MD*	0.00±0.00	S	2.24 ns.
Mallard	0.01±0.01	S	0.01±0.00	MI**	-0.04±0.01	MD**	-0.01±0.00	S	0.00±0.00	S	2.23 ns.
Northern Pintail	0.06±0.07	U	0.11±0.16	U	0.03±0.04	U	-0.01±0.02	S	0.04±0.01	MI*	19.85***
Common Pochard	0.03±0.07	U	-0.08±0.01	SD*	0.11±0.027	SI**	-0.14±0.02	SD**	-0.05±0.00	MD**	284.35***
Tufted Duck	0.11±0.03	SI*	0.00±0.01	S	0.10±0.02	SI**	-0.03±0.00	MD**	0.01±0.00	MI*	4.10*
Greater Scaup	0.17±0.13	U	0.01±0.09	U	0.13±0.08	U	-0.03±0.03	U	0.06±0.02	MI**	33.99***
Velvet Scoter	0.11±0.09	U	-		0.07±0.05	U	-0.10±0.20	U	0.06±0.02	MI**	31.97***
Common Goldeneye	0.09±0.02	SI**	0.05±0.02	MI**	0.11±0.02	SI**	-0.01±0.00	MD*	0.05±0.00	MI**	203.16***
Smew	0.05±0.07	U	0.03±0.07	U	0.13±0.04	MI**	0.00±0.01	S	0.03±0.01	MI**	18.18***
Common Merganser	0.03±0.01	MI**	0.07±0.01	SI*	0.07±0.01	MI**	0.02±0.00	MI**	0.03±0.00	MI**	151.26***
Little Grebe	0.03±0.02	U	-0.03±0.02	MD*	0.01±0.02	S	0.01±0.00	MI**	0.01±0.00	MI**	40.12***
Great Crested Grebe	0.05±0.01	MI**	0.08±0.04	MI*	0.07±0.02	MI**	-0.03±0.01	MD*	0.05±0.01	MI**	133.15***
Great Cormorant	0.04±0.01	MI**	0.08±0.01	SI*	0.08±0.01	SI*	0.04±0.00	MI**	0.05±0.00	MI**	296.69***
Great Egret	0.22±0.23	U	0.14±0.01	SI**	0.19±0.03	SI**	0.11±0.01	SI**	0.14±0.01	SI**	795.25***
Grey Heron	-0.02±0.01	MD**	0.03±0.00	MI**	0.02±0.01	S	-0.01±0.00	MD*	0.01±0.00	MI**	13.81***
Common Moorhen	0.02±0.04	U	0.02±0.01	MI*	0.05±0.02	MI*	-0.01±0.01	S	0.00±0.00	S	7.22**
Eurasian Coot	0.07±0.01	SI*	0.01±0.01	S	0.08±0.01	SI**	-0.07±0.00	SD**	-0.02±0.00	MD**	129.51***
Black-headed Gull	0.07±0.04	U	-0.01±0.01	S	-0.06±0.01	MD**	-0.02±0.002	MD**	-0.01±0.00	MD**	19.73***

Mew Gull	0.06±0.07	U	0.01±0.02	U	0.02±0.01	S	0.02±0.01	S	0.04±0.01	MI**	85.90***

Notes: (i) * $p < 0.05$, ** $p < 0.01$, *** $p < 0.001$. (ii) Categories of trends: SI – strong increase, MI – moderate increase, S – stable, MD – moderate decrease, SD – strong decrease, U – uncertain.

Table 3. Results of a random-effects negative binomial regression explaining total abundances~~numbers~~.

Diet	Reservoirs	Fishponds	Industrial	Running
Herbivores	–0.202	0.895	–0.635	0.370
	(0.866)	(1.227)	(1.118)	(0.928)
Omnivores	ref.	ref.	ref.	ref.
Invertivores	–0.898	–1.996**	0.282	0.113
	(0.731)	(0.740)	(0.570)	(0.725)
Piscivores	–0.597	0.172	0.549	0.593
	(0.746)	(1.138)	(1.059)	(0.978)
Site affinity~~conservatism~~ (standardized)	0.206	0.627	0.360	1.290**
	(0.423)	(0.521)	(0.511)	(0.444)
STI (standardized)	–0.914*	–0.248	–0.0483	–0.415
	(0.370)	(0.485)	(0.447)	(0.352)
Year (base = 2020)	0.0557*	0.0147	0.0232	–0.0226
	(0.0270)	(0.0218)	(0.0199)	(0.0150)
Diet ~~#~~ × year				
Herbivores ×# year	0.0220	0.0967*	0.0882**	0.0456
	(0.0357)	(0.0377)	(0.0280)	(0.0298)
Invertivores ×# year	0.0155	–0.0113	0.0847*	0.000531
	(0.0327)	(0.0225)	(0.0393)	(0.0172)
Piscivorous ×# year	–0.00951	0.0714*	0.0718**	0.0504*
	(0.0374)	(0.0308)	(0.0244)	(0.0222)
Site affinity~~conservatism~~ ×# year	0.000514	–0.0204*	–0.0238*	0.00214
	(0.0171)	(0.0103)	(0.0114)	(0.0103)
STI ×# year	–0.000489	0.0198*	0.0275**	0.00853
	(0.0124)	(0.00967)	(0.0103)	(0.00814)
Constant	6.448***	5.694***	5.765***	5.918***
	(0.624)	(0.888)	(0.921)	(0.725)
log(α)	–0.0724	–0.0724	–0.0724	–0.0724
	(0.121)	(0.121)	(0.121)	(0.121)
var(species random effect)	4.088***	4.088***	4.088***	4.088***
	(1.041)	(1.041)	(1.041)	(1.041)
Observations	3267	3267	3267	3267
p(Different trends by diet)	0.63292	0.00002	0.00512	0.01802

Notes: (i) The model specification contains the interactions of *wetland type* with all other covariates. To enhance readability, coefficients are presented in four columns, each related to one wetland type; moreover, the coefficients have been transformed to show the covariate effects *on the given wetland type*. (ii) Robust (Huber-White sandwich) standard errors in parentheses. (iii) * $p < 0.05$, ** $p < 0.01$, *** $p < 0.001$.