



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

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5 2 distribution changes
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3 20 Abstract
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5 21 1. Understanding species habitat use and factors affecting changes in their distributions are
6
7 22 necessary to promote the conservation of any biological community. We evaluated the changes
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9 23 in wetland use of the non-breeding waterbird community. Based on long-term citizen-science
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11 24 data (1988–2020), we tested the hypotheses that wetland use is associated with species diet
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13 25 and potential range-shift drivers (the tendency to occupy the same sites in consecutive years -
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15 26 site affinity and the species' average temperature across its wintering range – STI).

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18 27 2. We analysed species-specific wetland use of 25 species of waterbirds wintering in Czechia
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20 28 over a period of 33 years. The analyses explained variability in trends in numbers of the studied
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22 29 waterbird species across four inland wetland types: reservoirs, fishponds, industrial waters
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24 30 created by flooding of former mining sites, and running waters.

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26 31 3. Trends in waterbird abundance positively correlated with species' diet on fishponds,
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28 32 industrial and running waters. Among the diet groups, invertivores showed the largest increase
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30 33 in abundances on industrial waters, closely followed by herbivores. Herbivores showed the
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32 34 largest increase in abundances in fishponds, and piscivores did so in running waters. Regarding
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34 35 range-shift drivers, species with higher site affinity showed higher abundances on running
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36 36 waters, while species with low STI (i.e. wintering on average in sites with lower temperature)
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38 37 were more abundant on reservoirs. The abundance of both warm-dwelling and species with
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40 38 low site affinity increased on fishponds and industrial waters.

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43 39 4. Our findings suggest that the increased importance of the wetland types considered here for
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45 40 wintering waterbirds is likely linked to diet related changes in habitat use and changes in
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47 41 species distributions; and highlight that wintering waterbirds are expected to select sites with
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49 42 higher availability of food, higher energy content and lower foraging cost.

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51 43 5. Recent and rapid changes in species distributions may lead to a decrease in the effectiveness
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53 44 of national and international conservation efforts. When planning conservation measures, it
54
55 45 should be kept in mind that, climate change does not only imply large-scale north/north-
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57 46 eastwards shifts of entire waterbird distributions, but can also modify the use of the habitats
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59 47 by waterbird species inside their traditional wintering range.

48 Introduction

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50 Acquiring information regarding habitat use of different species (including temporal changes)
51 is crucial for proposing effective conservation measures (Pullin, 2002; Angert *et al.*, 2011;
52 Dawson *et al.*, 2011; Davis *et al.*, 2014). Such information is especially relevant in the context
53 of ongoing climate-driven changes in species distributions (Maclean *et al.*, 2008; Chen *et al.*,
54 2011; Podhrázský *et al.*, 2017; Pavón-Jordán *et al.*, 2019).

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

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

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3 75 Although the most important wintering requirements of food resources and safety from
4
5 76 predation are relatively well known (Snow & Perrins, 1998; Guillemain *et al.*, 2000;
6
7 77 Guillemain *et al.*, 2002; Schummer, Kaminski, Raedeke & Graber, 2010), long-term studies
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9 78 revealing the drivers of inland wetland use by waterbirds are absent in the literature, especially
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11 79 in the context of climate-driven changes in distributions. Food supply and availability of ice-
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13 80 free, open water in the wintering grounds are likely the most important limiting factors
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15 81 (Newton, 1998; Newton, 2013; Lewis *et al.*, 2019) shaping waterbirds wintering distribution
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17 82 (Dalby *et al.*, 2013; Guillemain *et al.*, 2015), followed by predation and air temperature
18
19 83 (thermoregulation) (Ridgill & Fox, 1990; Maclean *et al.*, 2008; Adam *et al.*, 2015). Hence,
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21 84 temperature alone does not simply explain the distribution pattern of wintering waterbirds
22
23 85 (Dalby *et al.*, 2013). The competition for food likely increases during winter, when individuals
24
25 86 from low density breeding sites in the vast boreal and tundra areas in Fennoscandia and Russia
26
27 87 congregate in their common wintering grounds further down the flyway (Guillemain *et al.*,
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29 88 2002; Brochet *et al.*, 2012). This behaviour, thus, presents an ideal opportunity to investigate
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31 89 how resource availability and competition for food and space drive habitat use by waterbirds
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33 90 during the wintering season.

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37 91 In our study, we evaluate species-specific changes in the use of four different wetland types.
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39 92 We hypothesize that the habitat use of species among the investigated wetland types is driven
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41 93 by the species diet and that wetland types differ in their food supply (Kloskowski *et al.*, 2009;
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43 94 Kameníková & Rajchard, 2013; Čížková *et al.*, 2013; Lewis *et al.*, 2019). We expect a
44
45 95 different speed of change in the use of fishponds by the different diet groups, because this
46
47 96 particular type of wetland is characterised by high density of stocked fish. Thus, we expect a
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49 97 shift of invertivores from fishponds to other wetland types due to competition for invertebrates
50
51 98 with a high density of fish (esp. Common Carp *Cyprinus Carpio*). On the other hand, fishponds
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53 99 constitute a food-rich habitat for piscivorous species (Musil, 2006; Nummi, Väänänen,
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55 100 Holopainen & Pöysä, 2016).

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58 101 We also defined two species-specific determinants to outline the distribution of species
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60 102 regarding the four wetland types (later named range shift drivers): (a) a species' site affinity

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3 103 (the tendency to occupy the same sites in consecutive years) and (b) the species temperature
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5 104 index (STI) as a measure of the species thermal affinity (warm-dwelling or cold-dwelling
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7 105 species; see description below. See also Devictor *et al.*, 2008; Jiguet *et al.*, 2007). Based on
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9 106 these two species-specific traits and current climate warming (Hurrell & Deser, 2009), we
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11 107 predict increasing wintering abundances of species with low site affinity (i.e. species that show
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13 108 low site fidelity and thus show greater potential to change wintering sites) as well as species
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15 109 with high Species Temperature Index (STI; i.e. with high average winter temperature across
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17 110 its wintering distribution) as the winter weather conditions become more favourable for them
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19 111 to expand towards these previously unsuitable regions; see e.g. Gaget *et al.* 2021.
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26 114 Methods

27 115 Study region

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30 116 The study region covers the Czech Republic that lies in central Europe. In total, 1,169
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32 117 monitored sites were classified according to the four wetland types considered: 68 reservoirs,
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34 118 443 fishponds, 108 industrial waters and 550 running waters (Fig. 1).

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37 119 Note that there are only a few small natural glacial lakes in the study region (Tucker & Evans,
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39 120 1997; Chytil *et al.*, 1999) which are located in mountains; these are usually frozen in winter
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41 121 and are therefore not included in the monitoring scheme. Thus, the four types included in the
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43 122 analysis essentially cover all wetland sites available for wintering waterbirds (see Chytil *et al.*,
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45 123 1999, Musil *et al.* 2001). The set of available sites in the study region remained unchanged
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47 124 throughout the whole study period (Fig. 2); all major changes in water bodies brought about
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49 125 by human activity in the study region had occurred before 1988, the beginning of the study
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51 126 period.
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55 128 Waterbird monitoring data

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58 129 Site-specific count data of waterbird abundances (in total 492,297 observations) were obtained
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60 130 from the results of the International Waterbird Census (IWC) in the Czech Republic between

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2
3 131 1988 and 2020. IWC is a worldwide citizen-science census with a standardized methodology
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5 132 (see further details in Delany, 2005; Delany, 2010) managed by the national coordinator in
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7 133 each country and globally coordinated by Wetlands International (www.wetlands.org).
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9 134 Censuses are carried out in mid-January each winter because it is generally the coldest period
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11 135 of winter when the effect of food resources on waterbird distribution is considered most
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13 136 apparent due to limited site availability.

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15 137 Waterbird counts were performed on a site during a day according to a complete and
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17 138 predefined list of species on predetermined dates and sites with the aim to maximize synchrony
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19 139 in the following years (Gilissen *et al.*, 2002). Census participants also recorded zero counts of
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21 140 individual species as well as zero counts of all species on a site. About 350 experienced
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23 141 volunteer birdwatchers contributed annually to the monitoring in Czechia. The most important
24
25 142 element of IWC methodology is standardization: it requires a single count at each site each
26
27 143 winter, optimally conducted by the same person in consecutive winters in order to make the
28
29 144 comparisons between years straightforward and valid. Each site (up to a few km² of standing
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31 145 water or a few km of a course of running water) established on the list of sites was defined by
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33 146 boundaries (such as bridges, weirs or dam on rivers and streams) known by the census
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35 147 participants. Observers used a telescope or binoculars from the shoreline to look for flocks
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37 148 and/or individuals of waterbirds, usually moving from one observation site to another by foot.
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39 149 Running waters were monitored using line transects along the shore. The number of census
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41 150 participants per site (one, two or a group) and the duration of survey were designated according
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43 151 to bird abundance on each site, species and size of the water surface area, and weather (Bibby,
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45 152 Burgess & Hill, 2007; Sutherland, Pullin, Dolman & Knight, 2004). The counts at dawn were
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47 153 recommended for geese. Observations taken under extreme weather conditions (fog, rain,
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49 154 snow fall, strong wind) categorised as “strong effect” by the observer and incomplete
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51 155 observations were excluded from the dataset prior to the analysis.

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55 156 A repeated scanning of the flocks and shoreline observations were used to increase the
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57 157 detectability of counted species. Census records were submitted to the national coordinator,
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59 158 who compiles the submitted records and checks their validity using the participants’ feedback
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3 159 if necessary. The quality of the IWC data has been verified in recently published studies (e.g.
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5 160 Fox *et al.*, 2010; Lehtikoinen *et al.*, 2013; Amano *et al.*, 2018; Musilová, Musil, Zouhar &
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7 161 Adam, 2018a; Musilová *et al.*, 2018b; Pavón-Jordán *et al.*, 2019; Gaget *et al.*, 2020; Pavón-
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9 162 Jordán *et al.*, 2020). Monitoring methodology did not change over the study period.

11 163 The IWC targets all waterbirds, a group ecologically dependent on wetlands (Delany, 2010),
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13 164 i.e. swans, geese, ducks, grebes, cormorants, herons, rallids, waders and gulls. However, in
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15 165 this study, we only include 25 the most common wintering waterbird species, namely those
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17 166 exceeding 50 individuals in Czechia annually (see also Musil *et al.*, 2011; Musilová *et al.*,
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19 167 2014; see Table 1 for an overview of the species). We followed Gill & Donsker (2018) for the
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21 168 species taxonomy.

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25 26 170 Wetland types

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28 171 The wetland types included in this study differ with regard to their origin, age and management
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30 172 practices (Chytil *et al.*, 1999). *Fishponds* represent shallow water bodies with a small stream
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32 173 or canal for water inflow. As commercial subjects aimed at stocking and production of fish
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34 174 (mostly Carp), fishponds were formed in the Middle Ages (mostly in the 16th century), have
35
36 175 artificially managed water levels, chemistry and nutrient input. *Reservoirs* have been built
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38 176 more recently (after 1900) and represent deep waterbodies with inflow from larger rivers
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40 177 (compared to fishponds). The fish stock in reservoirs are not managed for the purpose of
41
42 178 commercial fisheries but rather managed by angling associations (recreation). The most recent
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44 179 wetland type are *industrial waters*, which were created by flooding of former mining, sand-pit
45
46 180 or gravel-pit areas, or are sedimentary pools built in industrial areas since 1960s (Hrdinka,
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48 181 2007). Among all standing water wetland types described above, there is a gradient of
49
50 182 decreasing probability of complete ice-cover in winter with increasing depth: from fishponds
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52 183 (the shallowest) to industrial waters and finally to reservoirs (the deepest). High density fish
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54 184 stocks are most intensively managed in fishponds, followed by reservoirs and the least
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56 185 managed in industrial waters (Oertli *et al.*, 2005; Musil, 2006, UNEP, 2017).

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3 186 The trophic state of the wetland types ranges from oligotrophic waters (a low nutrient content),
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5 187 through mesotrophic and eutrophic waters to hypereutrophic waters, which present
6
7 188 an extremely high nutrient content (Carlson, 1977). Among the four monitored wetland types,
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9 189 running waters contain the lowest content of nutrients, and fishponds are mostly eutrophic,
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11 190 sometimes hypertrophic (Chytil *et al.*, 1999; Musil, 2006; Seiche *et al.*, 2012; Čížková *et al.*,
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13 191 2013). The distribution of the monitored sites is shown in Fig. 1.
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17 193 Species-specific variables

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20 194 All 25 investigated waterbird species were described by the following three species-specific
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22 195 variables (*diet*, *species temperature index (STI)*, and *site affinity*), which could explain the
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24 196 temporal pattern in the wetland type use.

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26 197 (i) All species were classified into *diet* groups based on their preferred food items in the
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28 198 wintering season: piscivorous, invertivorous, omnivorous and herbivorous (based on data
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30 199 and diet classification in Snow & Perrins, 1998; Kear, 2005; Šťastný & Hudec, 2016).

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32 200 (ii) *Species temperature index (STI)*: The STI (see Devictor *et al.*, 2008; Jiguet *et al.*, 2007
33
34 201 for details of STI calculation) reflects the long-term average January temperature (1950-
35
36 202 2000) experienced by individuals of any given species across the species' entire wintering
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38 203 distribution. Species' distribution maps were downloaded from BirdLife International &
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40 204 HBW (2017) and all temperature data from the regions included in each species'
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42 205 wintering range (above) were downloaded from www.worldclim.org. For each species,
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44 206 all grid cells (5x5 degrees) with temperature data within a species' wintering range
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46 207 (BirdLife International & HBW 2017) were downloaded and averaged.

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49 208 (iii) For each species, we calculated a measure of year-to-year variation in geographical
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51 209 distribution of the species across the study region (called *site affinity*). Thus, the species'
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53 210 fidelity to the wintering sites constitutes the basis of the covariate *site affinity*, which is
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55 211 bounded between 0 and 1, with the actual range of values being 0.14–0.82 in our data set.
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57 212 Values close to 1 indicate that the same sites are occupied in successive years, and with
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59 213 the same intensity; values close to zero imply large year-to-year variation in the selection

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3 214 of wintering sites. These values are based on Earth mover's distance (see Kranstauber,
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5 215 Smolla & Safi, 2017 for further details).

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7 216 The pairwise correlation of continuous species-specific variables is 0.06, implying there is
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9 217 little collinearity (Hair, Anderson, Tatham & Black, 1995; Rogerson, 2001). The values of
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11 218 species-specific variables are listed in Table 1.

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16 220 Statistical analysis

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18 221 Our analyses proceeded in two stages, differing in the level of detail at which the count data
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20 222 were aggregated. In the first stage, we studied how trends in abundances of different species
21
22 223 vary across wetland types. We first used a log-linear Poisson regression analysis to impute any
23
24 224 missing waterbird count data from the long-term data series (in 1988–2020) using TRends and
25
26 225 Indices for Monitoring data software (TRIM; Statistic Netherlands version 3.52, Pannekoek
27
28 226 & Van Strien, 2005). Regression parameters were estimated using generalized estimating
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30 227 equations (GEE). Missing data were usually the result of incomplete coverage due to limited
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32 228 availability of observers in some years. The proportion of missing counts varied between 33%
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34 229 and 65% in the whole dataset, which is regarded as tolerable (Soldaat *et al.*, 2017).

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36 230 In this first stage, after imputing any missing data, we estimated the species-specific long-term
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38 231 trends in abundances (i.e. the change in abundance indices from one year to the next) at each
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40 232 of the four wetland types and assessed differences in these trends between the wetland types
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42 233 based on the rate of change: a strong increase or decrease ($\geq 5\%$ per year); a moderate increase
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44 234 or decrease ($< 5\%$ per year); a stable (trend was not significant and CIs were sufficiently
45
46 235 narrow) or an uncertain trend (see also Fouque *et al.*, 2009; Musil *et al.*, 2011; Musilová *et al.*,
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48 236 2018b). Then, a Wald test was used to assess the significance of differences in the trends in
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50 237 the four wetland types. Furthermore, we used wetland type and site as covariates in the linear
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52 238 trend models (see also Pavón-Jordán *et al.*, 2015; Musilová *et al.*, 2018b).

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54
55 239 In the second stage, we studied the effect of species-specific variables on population trends at
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57 240 different wetland types. As in the first step in this species-level analysis (above), we also used
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59 241 TRIM to fill the gaps in the data due to incomplete monitoring coverage. For each species, we

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3 242 obtained the TRIM-imputed *total abundance* by year and wetland type, producing a dataset of
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5 243 3,267 observations (25 species, 33 years, 4 wetland types). Velvet Scoter (*Melanitta fusca*)
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7 244 was not recorded on fishponds and, therefore, excluded from the analyses.
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9 245 Next, we explained these total abundances estimated with TRIM and their trends with species-
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11 246 specific variables in a regression approach. As the time abundances exhibited substantial
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13 247 overdispersion, we used negative binomial regression rather than the canonical Poisson
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15 248 distribution. The fact that observations for a species are repeated across years and wetland
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17 249 types led us to include species as a random effect in the model, meaning we fitted a
18
19 250 Generalized Linear Mixed Model (GLMM). Moreover, to allow for (i) heteroskedasticity both
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21 251 between and within species, and (ii) arbitrary correlation within a species' values, we used
22
23 252 a cluster-robust estimator of the standard errors in statistical inference, clustered at the species
24
25 253 level (Cameron & Miller, 2015). To facilitate coefficient interpretation, all continuous
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27 254 variables were *z*-standardized (i.e. centred around the mean and divided by the standard
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29 255 deviation) prior to running the regressions.
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31 256 For simplicity, our model specification assumes linear time trends in total abundances; we do
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33 257 nevertheless expect these trends to vary systematically with species-specific characteristics
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35 258 and across wetland types. Therefore, we included interactions of year and wetland types with
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37 259 all species-specific variables in our model. All regression models were estimated in Stata 16
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39 260 (StataCorp, College Station, TX).
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263 Results

264 492,297 observations from 25 species in 1,169 wetlands between 1988 and 2020 were included
265 in this study. The mean annual abundance for four diet groups was the following: herbivores
266 ($23,467 \pm 2,897$ SE), omnivores ($219,234 \pm 3,264$ SE), invertivores ($6,295 \pm 240$ SE) and
267 piscivores ($15,136 \pm 933$ SE). The first stage of our analysis revealed significant differences
268 in abundance trends between the four wetland types in 22 out of the 25 investigated species
269 (Table 2). Prevailing decreasing (10 species) or stable trends (six species) were found in

1
2
3 270 running waters while significant increasing trends in the abundance of 15 species were found
4
5 271 in standing waters (reservoirs, fishponds and industrial waters). The significant differences
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7 272 (according to results of Wald test) in species trends among analysed wetland types were found
8
9 273 in five of six herbivore species, in six of eight omnivore species, in all five invertivore species
10
11 274 and in all six piscivore species. Increasing trend in abundances was found in all herbivores on
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13 275 reservoirs and in almost all species in industrial waters (Table 2).

14
15 276 The results from our GLMM showed that species exhibiting higher site affinity (i.e. low year-
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17 277 to-year variation in geographical distribution of the species across the study region) recorded
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19 278 the highest total abundances on running waters (Table 3). Similarly, cold-dwelling species
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21 279 (identified by a lower value of average temperature across its wintering range – STI) were
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23 280 more abundant in reservoirs (Table 3).

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25 281 The effects of the interaction terms between species-specific variables and year showed the
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27 282 extent at which the trends in abundances on different wetland types varied with species-
28
29 283 specific variables. For instance, the coefficient on year in the reservoirs column ($\beta = 0.056$)
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31 284 implied that the predicted yearly increase in total abundances in an omnivorous species (i.e.
32
33 285 the reference diet group) with average values of site affinity and STI is about 5.6 per cent; the
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35 286 coefficient on herbivorous \times year ($\beta = 0.022$) indicated that for a herbivorous species with
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37 287 average values of site affinity and STI, the annual increase was larger by ca. 2.2 per cent, i.e.
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39 288 about 8 per cent in total. The species' diet significantly affected the species trends on
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41 289 fishponds, industrial and running waters. On fishponds, herbivorous species showed the largest
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43 290 (positive) trend in total abundances (over 11 per cent per year at average values of site affinity
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45 291 and STI), followed closely by piscivores. On industrial waters, omnivores increased at the
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47 292 slowest pace by ca. 7–9 % slower than the other three diet groups. On running waters,
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49 293 piscivores increased at the fastest rate during the 1990s and early 2000s, followed closely by
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51 294 herbivores (Figures 3 and 4). Warm-dwelling and species with low site affinity showed the
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53 295 largest trend on fishponds and industrial waters.

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55 296 The differences in trends and abundances across diet groups and wetland types are visualized
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57 297 in Figures 3 and 4. Figure 3 presents the underlying data on total abundances, along with trend

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3 298 curves obtained via scatterplot smoothing using LOESS. Figure 4 visualizes the trends
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5 299 predicted by the regression for different diet groups at different wetland types. The apparent
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7 300 discrepancies between Figure 3 and 4 are caused by the fact that in the regression that underlie
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9 301 Figure 4 (i) we estimate a (log-) linear for simplicity (while some trends in Figure 3 show a
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11 302 substantial degree of nonlinearity) and (ii) the predictions were obtained at fixed values of STI
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13 303 and site affinity, which otherwise vary between different diet groups. Figure 5 summarizes the
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15 304 findings in a graphical format.
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22 307 Discussion

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24 308 To promote the protection of wetland birds, the knowledge of species habitat use and
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26 309 facilitation of species distribution changes should be considered the cornerstones for effective
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28 310 adaptive management (Musilová *et al.*, 2018b; see also Pullin, 2002; Sutherland, Pullin,
29
30 311 Dolman & Knight, 2004; Sinclair, Fryxell & Caughley, 2006; Musilová *et al.*, 2015;
31
32 312 Holopainen *et al.*, 2015; Gaget *et al.*, 2020; Pavón-Jordán *et al.*, 2020). This study contributes
33
34 313 to the identification of these cornerstones by demonstrating diet-specific changes in habitat
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36 314 use, and of species with high probability of range changes (summarized in Fig. 5), based on
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38 315 long-term nonbreeding data of wintering waterbirds.
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43 317 Changes in habitat use in different diet groups

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45 318 Generally, food supply is of high importance for waterbirds (Guillemain *et al.*, 2015;
46
47 319 Holopainen *et al.*, 2015) due to its subsequent effect on breeding success, adult survival and
48
49 320 also overall flyway population dynamics (Newton, 1998; Newton, 2013; Jørgensen *et al.*,
50
51 321 2016). Use of feeding habitat is a hierarchical process, influencing the species geographical
52
53 322 distribution and the choice of a particular wetland (Green, 1998). Here, we demonstrated long-
54
55 323 term changes in wetland type use among diet groups in fishponds, industrial and running
56
57 324 waters, but not in reservoirs. Increased use of industrial waters was found in invertivore
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59 325 species, which predominantly used running waters in the beginning of the study period and
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3 326 progressively switch to industrial waters. Invertebrate biomass, which provides the majority
4
5 327 of the food of invertivores, tend to be highest in early successional wetlands (Nummi &
6
7 328 Holopainen, 2014; Petrie *et al.*, 2016), such are industrial waters. Furthermore, heterogeneity
8
9 329 in the physical characteristics of foraging areas can affect foraging behaviour (Fernández &
10
11 330 Lank, 2008) and therefore affect the species habitat use. Consistent with this, diving ducks
12
13 331 represent most of the invertivore species; they feed at greater depths during the non-breeding
14
15 332 period (Hughes & Green in Kear, 2005) and industrial waters likely provide favourable depths
16
17 333 for their foraging behaviour. Lower foraging costs (Wood *et al.*, 2013a) in industrial waters
18
19 334 compared to higher water velocities in running waters can make foraging more profitable for
20
21 335 invertivores. The same effect could cause increased use of industrial waters in herbivores
22
23 336 (almost in the same degree as in invertivores).

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25
26 337 The *a priori* assumption of a low increase in abundances of invertivores in fishponds was
27
28 338 confirmed. Invertebrates are fundamental to both terrestrial and aquatic food webs, and drastic
29
30 339 decreases have been shown in terrestrial insects on a global level (Dirzo *et al.*, 2014; Wagner
31
32 340 *et al.*, 2021). Long-term studies on aquatic invertebrates are currently scarce (Gozlan *et al.*,
33
34 341 2019), but some indicate changes in aquatic invertebrate structure (Fried-Petersen *et al.*, 2020;
35
36 342 Pilotto *et al.*, 2020; van der Lee, Aray-Ajoy, Futter & Angeler, 2021) associated with
37
38 343 increasing levels of eutrophication and brownification as one of the most important driver of
39
40 344 these changes (Jackson, Loewen, Vinebrooke & Chimimba, 2016; Lind *et al.*, 2018; Arzel *et*
41
42 345 *al.*, 2020). Fishponds are commercial habitats with artificially managed nutrient input that
43
44 346 increase the level of eutrophication (Roy *et al.*, 2020) and are aimed at stocking and breeding
45
46 347 fish (mostly Carp). The artificial nutrient input have resulted in hypertrophy of fishponds,
47
48 348 especially after the World War II (Pechar, 2000; Seiche *et al.*, 2012) and therefore these ponds
49
50 349 exceed the nutrient level of other wetland types in the study region. It has been shown that
51
52 350 high stocks of Carp in fishponds create an environment with extremely high competition for
53
54 351 invertebrate food with invertivorous waterbird species during the breeding season (Musil,
55
56 352 2006). In this study, we show that this effect is also significant during the wintering season by
57
58 353 a lower increase in the use of fishponds by invertivores.

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3 354 Indeed, herbivores stood out as the most increasing diet group in fishponds, likely keeping
4
5 355 outside the Carp-waterbird food competition. The importance of artificial fishponds as
6
7 356 alternative sites for wintering herbivorous and omnivorous ducks was shown also in Doñana,
8
9 357 Spain (Kloskowski *et al.*, 2009). However, some species of the herbivorous group (geese,
10
11 358 Mute Swan and Eurasian Wigeon) are not strictly feeding inside of wetlands such as
12
13 359 invertivores and piscivores and may feed both aquatically and terrestrially (Jacobsen &
14
15 360 Ugelvik, 1994; Fox *et al.*, 2005; Wood *et al.*, 2013b). Therefore, the changes in wetland type
16
17 361 use are less strongly related to wetland food supply in this group. Especially, due to the
18
19 362 characteristics of the census protocol (dawn counts), variation in geese abundances are likely
20
21 363 to be affected by this daily dynamic between the roosting and feeding sites. In the study region,
22
23 364 geese have traditionally congregated in high numbers during winter and use reservoirs as a
24
25 365 roosting sites and nearby fields as a dominant feeding sites, especially in south-Moravian
26
27 366 lowland (Czech IWC data: <http://www.waterbirdmonitoring.cz/vysledky/iwc20/>).
28
29 367 Conversely, other herbivorous species are counted during the daylight activities in the
30
31 368 wetlands and thus do not include individuals that have left the wetlands (roosting sites) to
32
33 369 forage in the fields. In addition, some waterbirds may often be feeding at different places
34
35 370 during the night, such as omnivorous Mallards in the Netherlands (Kleyheeg *et al.*, 2017) and
36
37 371 granivorous dabbling ducks feeding on rice fields in the Mediterranean (Guillemain *et al.*,
38
39 372 2010; Brogi, Pernollet, Gauthier-Clerc & Guillemain, 2015; Parejo *et al.*, 2019). Nevertheless,
40
41 373 this nocturnal behaviour is likely difficult to quantify (Tourenq *et al.*, 2001) and any obvious
42
43 374 suitable nocturnal feeding wetlands are not known from the study region.
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46
47 375 On the species level, prevailing decreasing or stable trends in abundances were found in
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49 376 running waters, which represent the traditional wintering grounds in the study region (Adam
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51 377 *et al.*, 2015; Musilová, Musil, Zouhar & Romportl, 2015; Musilová, Musil, Zouhar & Adam,
52
53 378 2018a). It is worth noting that running waters fulfil one of the most important habitat
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55 379 requirements for wintering waterbirds: to avoid unfavourable winter harshness and destructive
56
57 380 winter extremes in the zero-degree-isotherm area (Musilová, Musil, Zouhar & Romportl,
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59 381 2015; Musilová, Musil, Zouhar & Adam, 2018a). In recent decades, milder winter conditions

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3 382 in Central Europe (IPCC, 2014) likely provide an increased availability of new wintering
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5 383 areas, i.e. standing waters with reduced ice cover. Still, running waters still remain as suitable
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7 384 wintering sites, as revealed in this study, especially for piscivores and herbivorous. Recent
8
9 385 climate and land use changes affect the fish assemblages, diversity and distribution (Comte *et*
10
11 386 *al.*, 2013) as well as diversity and distribution of invertebrates (Haase *et al.*, 2019) with
12
13 387 predicted up and downstream direction of shifts in the fish species in rivers (Radinger *et al.*,
14
15 388 2017), hence the use of rivers by piscivores is likely in accordance with these changes in fish
16
17 389 distribution.
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21 391 Wetland type use in species changing distribution

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24 392 Generally, there is a trade-off between the cost and benefit of the wintering site use (Ridgill &
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26 393 Fox, 1990; Adam *et al.*, 2015; Musilová, Musil, Zouhar & Romportl, 2015). Importantly, there
27
28 394 is a gradient among the four investigated wetland types in the level of the winter harshness
29
30 395 risk, i.e. the sensitivity to cold weather and freezing (running waters considered the most stable
31
32 396 compared to standing waters, see above), in the level of habitat change risk (fishponds
33
34 397 considered the most artificially affected), in the level of succession in freshwater communities
35
36 398 (industrial waters considered as an early successional stages), trophic status (the highest
37
38 399 nutrient content in fishponds); see the methods for details.
39

40
41 400 The nature of these differences reflected the use of wetland types in species with more or less
42
43 401 probable range shifts and/or distribution changes. Species with high site affinity (i.e. species
44
45 402 with low year-to-year variation in geographical distribution across the study region) revealed
46
47 403 higher use of running waters. Higher stability in cold and extreme weather conditions, low
48
49 404 level of habitat change risk caused by possible management of running waters are likely
50
51 405 important for these species with lower probability of range changes. However, saturation of
52
53 406 traditional wintering grounds was suggested to occur in Czech Republic (Musilová, Musil,
54
55 407 Zouhar & Romportl, 2015) that could increase the competition for resources (Newton, 1998;
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57 408 Newton, 2013). In addition, higher water velocities in running waters compared to standing
58
59 409 waters increase the foraging costs (Wood *et al.*, 2013a).
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3 410 Furthermore, our study indicates the high importance of man-made standing wetlands
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5 411 (fishponds and industrial waters) for species more likely to undergo range shifts, i.e. species
6
7 412 with low site affinity and warm-dwelling (higher average temperature across its wintering
8
9 413 range – high STI –) species. Wintering waterbird populations are clearly changing their
10
11 414 distribution (Lehikoinen *et al.*, 2013; Pavón-Jordán *et al.*, 2015; Musilová, Musil, Zouhar &
12
13 415 Adam, 2018a; Pavón-Jordán *et al.*, 2019; Pavón-Jordán *et al.*, 2020). These distribution
14
15 416 changes could be associated with changes in ice cover, food availability, habitat and hunting
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17 417 pressure (Dalby *et al.*, 2013; Newton, 2013; Guillemain *et al.*, 2015; Pavón-Jordán *et al.*, 2020;
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19 418 this study). Species with low site affinity increase the use of these newly available wetlands
20
21 419 that are also considered less stable as wintering sites (higher winter harshness and habitat
22
23 420 change risk, higher trophy in fishponds and lower succession in industrial waters). It seems
24
25 421 that species with low site affinity grasp the benefits of milder climate in recent decades (Hurrell
26
27 422 & Deser, 2009) and responded by increasingly use these alternative wetlands. The tendency
28
29 423 of species with low site affinity to annually change the wintering sites implies they may be
30
31 424 useful early-warning indicators of changing use of wintering sites (see also Green & Elmberg,
32
33 425 2014).

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35
36 426 The thermal affinity was determined as an important trait explaining the species distribution
37
38 427 and range changes leading by climate change (Gaget *et al.*, 2020; Devictor *et al.*, 2008). The
39
40 428 changes of nonbreeding distribution of waterbirds seems highly affected by climate warming
41
42 429 (Pavón-Jordán *et al.*, 2015; Gaget *et al.*, 2018). Our study reveals the use of reservoirs by cold-
43
44 430 dwelling species (mostly seaducks), while reservoirs represent deeper water bodies with
45
46 431 inflow from larger rivers and have the lowest probability of complete ice-cover in winter
47
48 432 among standing waters. In the light of climate warming, related northeastwards shifts of
49
50 433 species distributions (Lehikoinen *et al.*, 2013; Pavón-Jordán *et al.*, 2015; Gaget *et al.*, 2020;
51
52 434 Pavón-Jordán *et al.*, 2020), and consequent decline and even local extinction of cold-dwelling
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54 435 species caused by distribution change (Devictor *et al.*, 2008; Tayleur *et al.*, 2016; Gaget *et al.*,
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56 436 2020), we assume that reservoirs could serve as a refuges for cold-dwelling species in the near
57
58 437 future. Larger stochasticity and frequency of extreme weather events are also predicted by
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3 438 most climate change scenarios and thus such deep and large wetlands with stable temperature
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5 439 conditions suitable for benthic invertebrates will provide the resources required by these
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7 440 species. However, the overall increase in abundances of cold-dwelling species in the study
8
9 441 region indicate that this issue could be much complex, as temperature is not the only driver of
10
11 442 species distribution changes (Dalby *et al.*, 2013). Conversely, warm-dwelling species increase
12
13 443 the use of both fishponds and industrial waters. The availability of these shallower man-made
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15 444 wetlands may likely increase due to climate warming (Hurrell & Deser, 2010). The ‘wintering
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17 445 strategy’ of warm-dwelling species is driven by the geographic avoidance of the zero-degree
18
19 446 isotherm to reduce winter harshness risk (Gaget *et al.*, 2020), therefore warm-dwelling species
20
21 447 likely do not reflect the difference in wetland types in terms of winter harshness risk and
22
23 448 increase the use of industrial waters and fishponds with higher winter harshness risk.
24
25 449 Increasing our knowledge of the habitat use of warm-dwelling species is of high importance
26
27 450 since they are more likely to expand in the coming decades (Devictor *et al.*, 2008; Tayleur *et*
28
29 451 *al.*, 2016; Gaget *et al.*, 2020). Indeed, we can expect increasing concern of farmers and
30
31 452 fishermen followed by the distribution changes of the warm-dwelling species, while some of
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33 453 them are already conflict species such as Greylag Goose or herons.
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39 455 Conclusion

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41 456 Our study highlight the general pattern that wintering waterbirds are expected to select sites
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43 457 with higher food availability (Fox *et al.*, 1995; Green, 1998; Green, Fox, Hughes & Hilton,
44
45 458 1999; Guillemain, Fritz & Guillon *et al.* 2000; Chatterjee, Adhikari, Pal & Mukhopadhyay,
46
47 459 2020), higher energy content (van Eerden, 1984) and lower foraging cost (Wood *et al.*, 2013a)
48
49 460 to balance the costs and benefits of feeding site choice during wintering (Newton, 1998;
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51 461 Newton, 2013; Aharon-Rotman, Clark, Klaassen & Buttemer, 2016). The effort to meet these
52
53 462 requirements resulted in a considerable change of the habitat use in the given species.
54
55 463 Understanding the role of habitat use in the context of changing distributions of different
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57 464 species is of high importance for conservation (see e.g. Janke *et al.*, 2017), especially since the
58
59 465 climate-driven range changes are already underway (e.g. Lehtikoinen *et al.*, 2013; Pavón-

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3 466 Jordán *et al.*, 2015, Musilová, Musil, Zouhar & Adam, 2018a; Pavón-Jordán *et al.*, 2019;
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5 467 Pavón-Jordán *et al.*, 2020) and may lead to the decrease of effectiveness of the conservation
6
7 468 efforts (Musilová *et al.*, 2018b). Consistent with this view, increasing use of industrial waters
8
9 469 and fishponds for warm-dwelling and species with low site affinity exhibiting more probable
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11 470 range shifts and/or distribution changes, and conversely use of reservoirs by cold-dwelling
12
13 471 species and running waters by species with high site affinity indicates importance of individual
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15 472 wetland types as wintering grounds, which should be considered in future conservation
16
17 473 planning and effective management. The development and implementation of measures to
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19 474 increase the suitability of existing modified habitats for wildlife appears essential to conserve
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21 475 biodiversity (Sinclair, Fryxell & Caughley, 2006; Navedo, 2017). The implementation should
22
23 476 be based on the core knowledge of the species habitat use and distribution changes (Musilová
24
25 477 *et al.*, 2018b). Climate-driven changes in species distributions should not necessarily have the
26
27 478 north/eastwards direction (see e.g. Lehikoinen *et al.*, 2013, 2016; Pavón-Jordán *et al.*, 2015;
28
29 479 Pavón-Jordán *et al.*, 2020), but could also modify the use of habitats within species' current
30
31 480 ranges.
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42
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58
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494 “Waterbirds as bioindicators of wetlands health: food specialisation determines the waterbird’
495 response to climatic and environmental changes“.

Copy for Review

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49 861 Data availability statement:

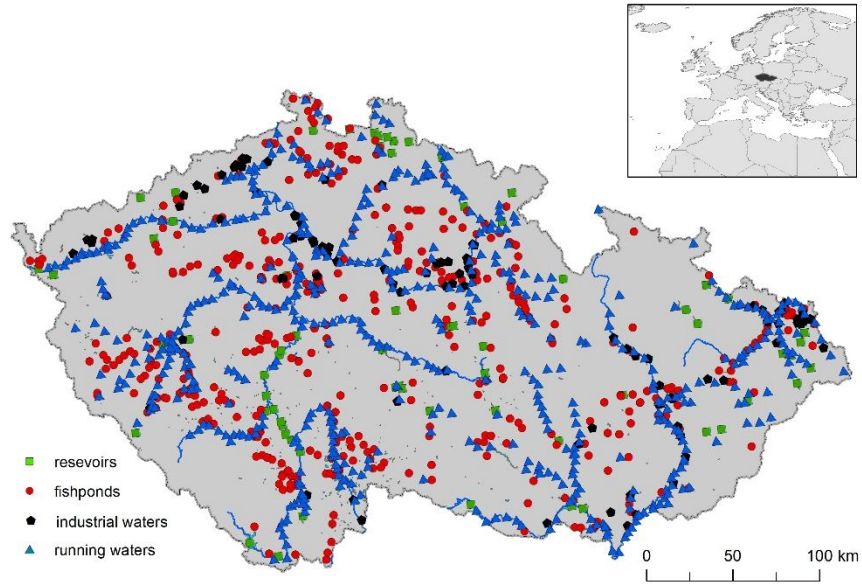
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51 862 The data that support the findings of this study are available from the corresponding author
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53 863 upon reasonable request.
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86 865 Additional Information:

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88 866 The authors declare no competing interests.
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868 Figure 1. Distribution of monitored wetland sites in the Czech Republic between 1988 and
869 2020

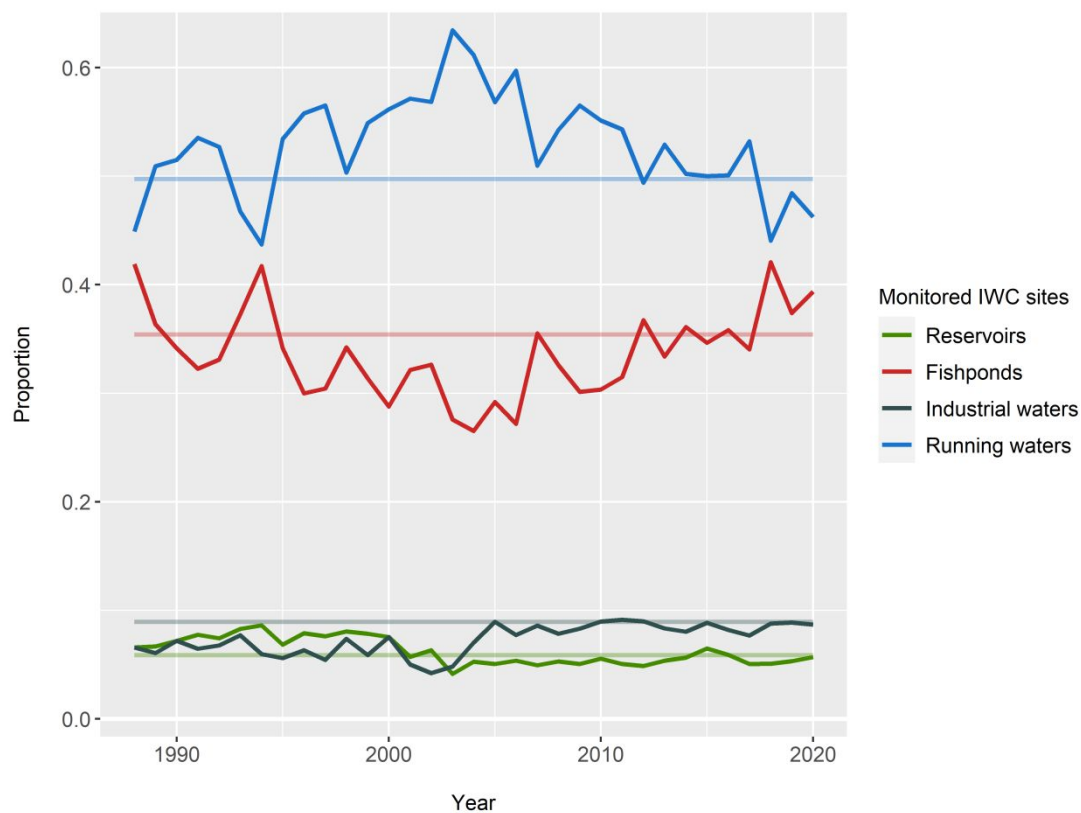


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Review

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

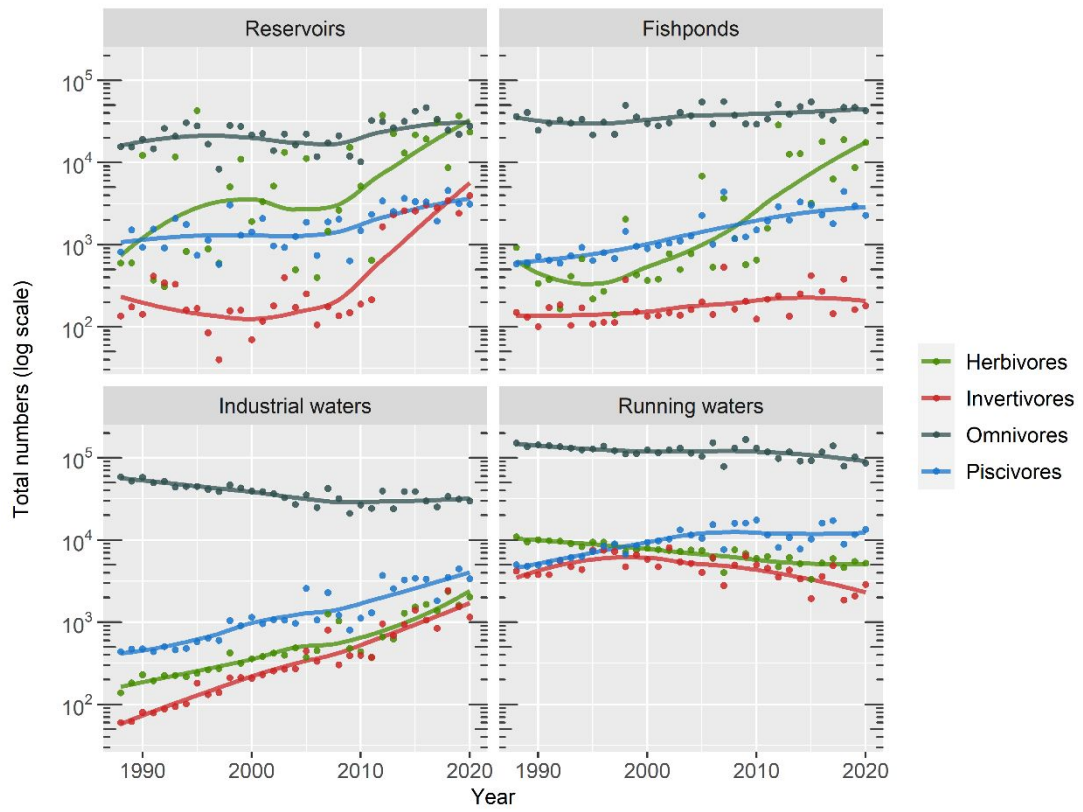


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878 Figure 3. Yearly total abundances and their trends (obtained by LOESS smoothing) at
879 individual wetland types, by diet group.

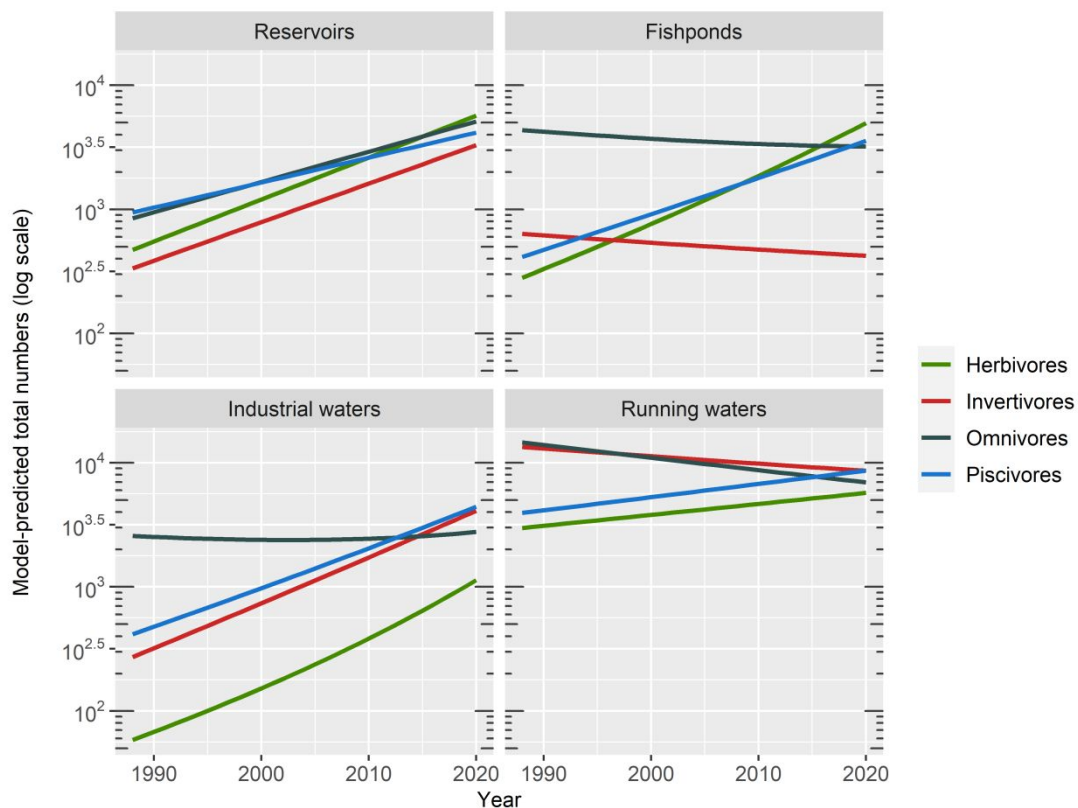


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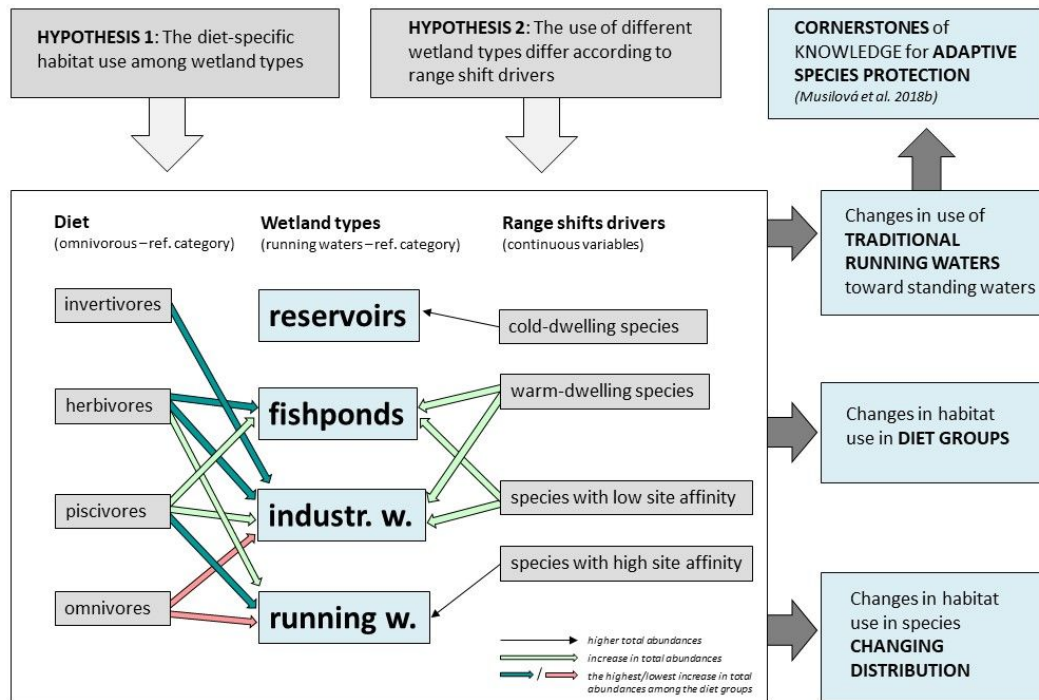
882 Figure 4. Predicted total abundances at individual wetland types and for different diet groups
 883 at mean values of STI and site affinity (based on the regression presented in Table 3).



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Review

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



887

Review

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

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

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

896 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 Bean 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***

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3 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***
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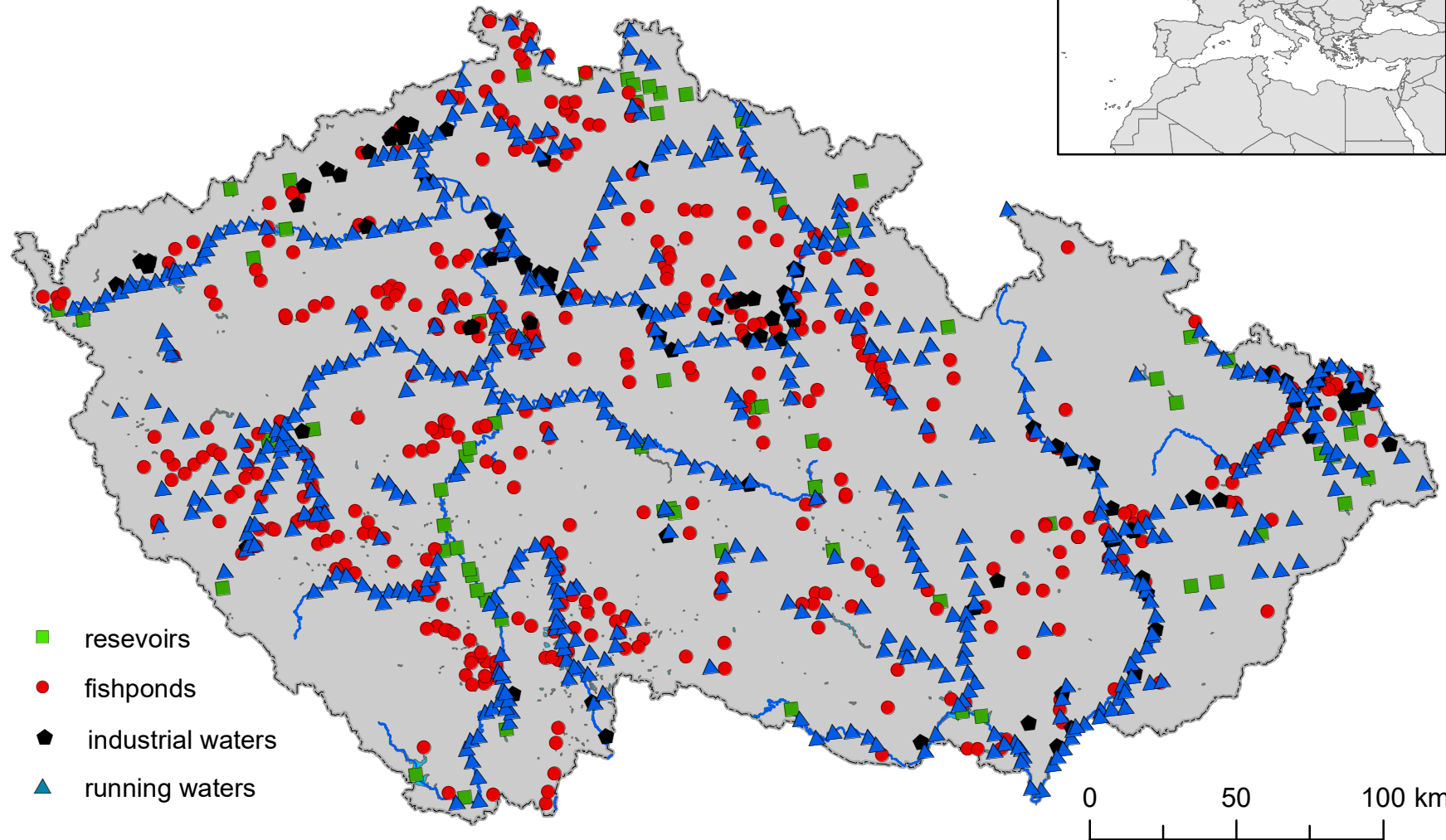
5 897 Notes: (i) * $p < 0.05$, ** $p < 0.01$, *** $p < 0.001$. (ii) Categories of trends: SI – strong increase, MI – moderate increase, S – stable, MD – moderate decrease,
6 898 SD – strong decrease, U – uncertain.
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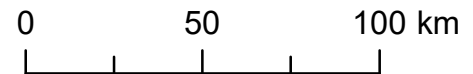
899 Table 3. Results of a random-effects negative binomial regression explaining total
 900 abundances.

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

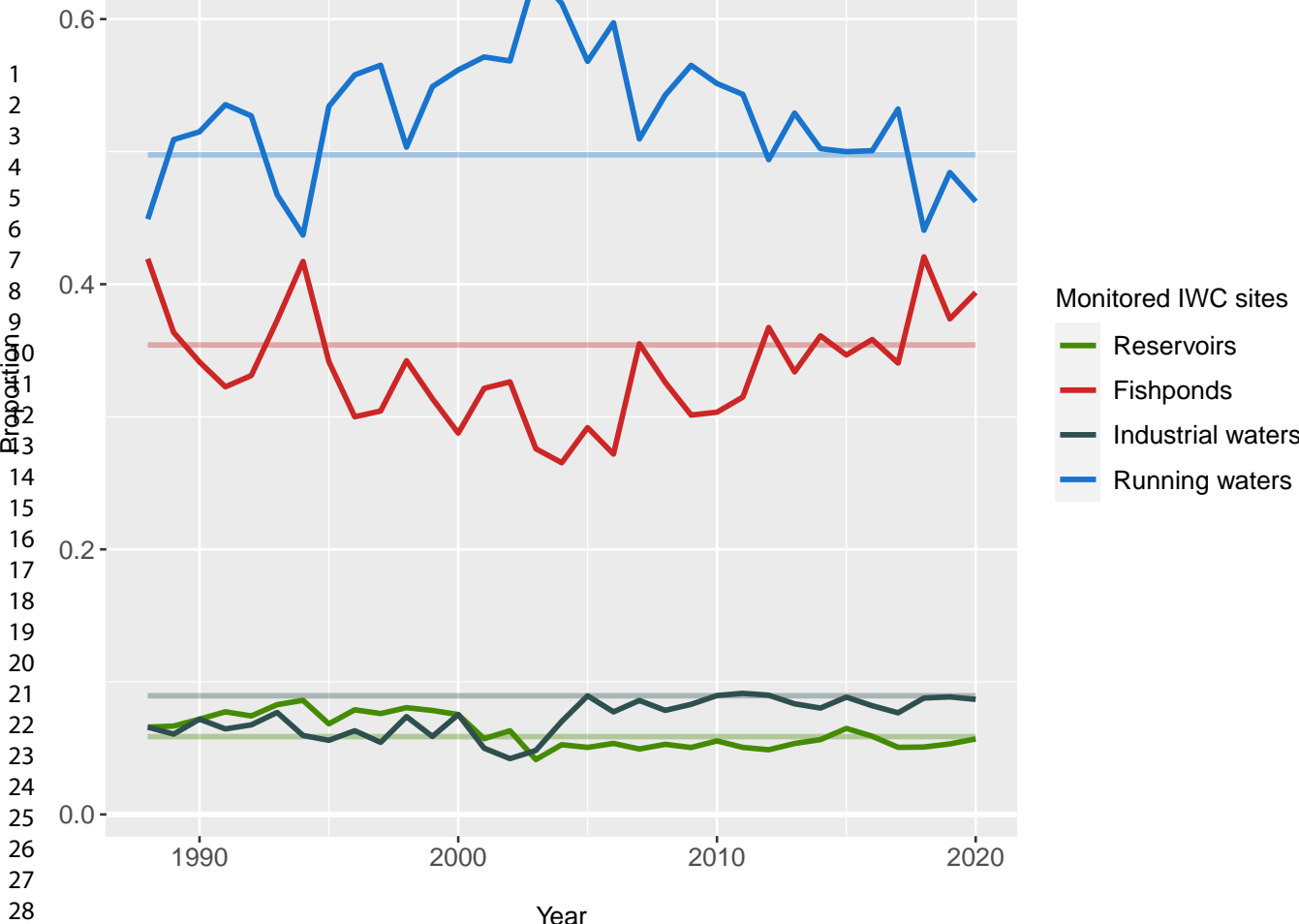
901 Notes: (i) The model specification contains the interactions of *wetland type* with all other
 902 covariates. To enhance readability, coefficients are presented in four columns, each related to
 903 one wetland type; moreover, the coefficients have been transformed to show the covariate
 904 effects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

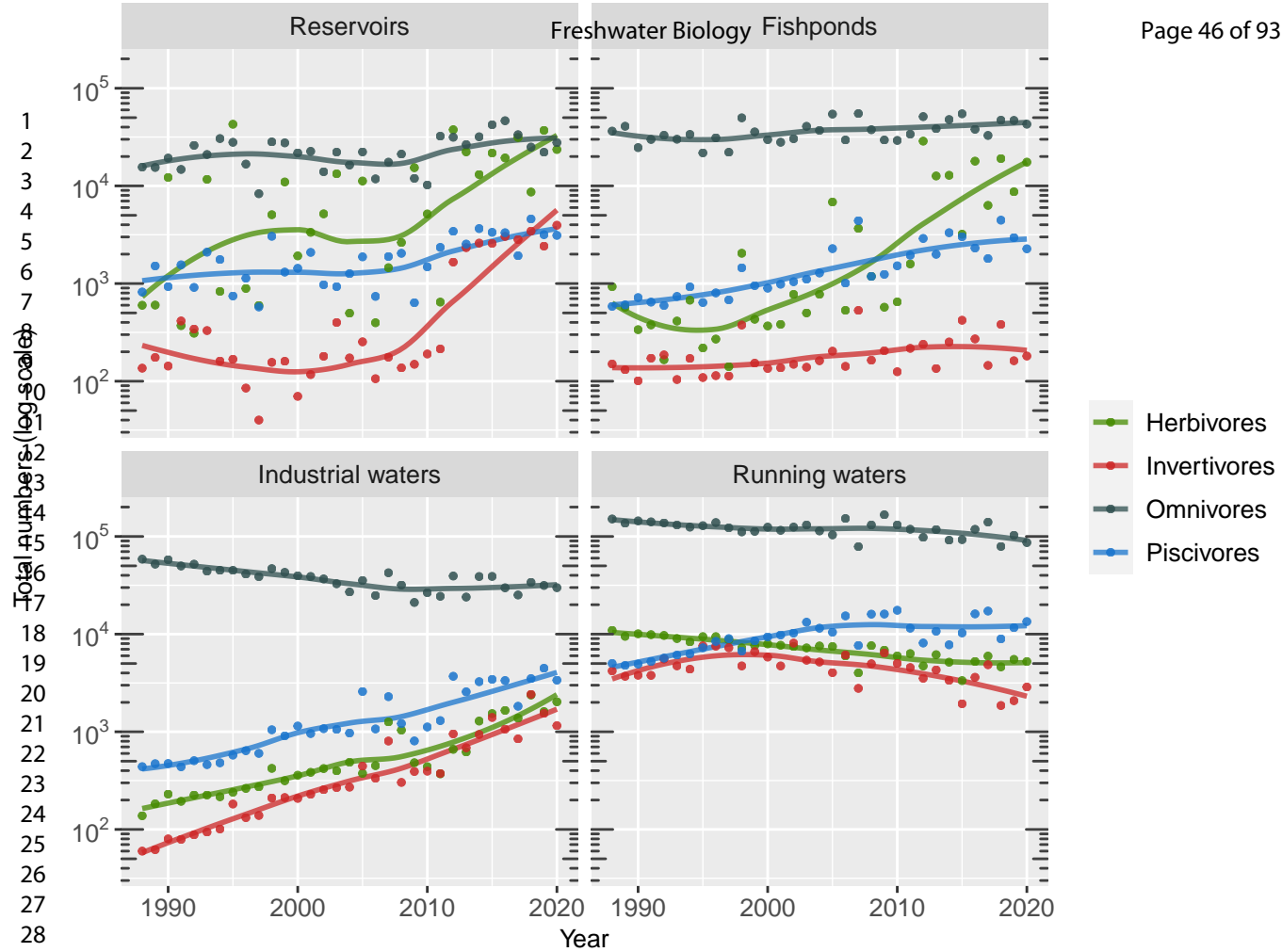


- resevoirs
- fishponds
- ◆ industrial waters
- ▲ running waters



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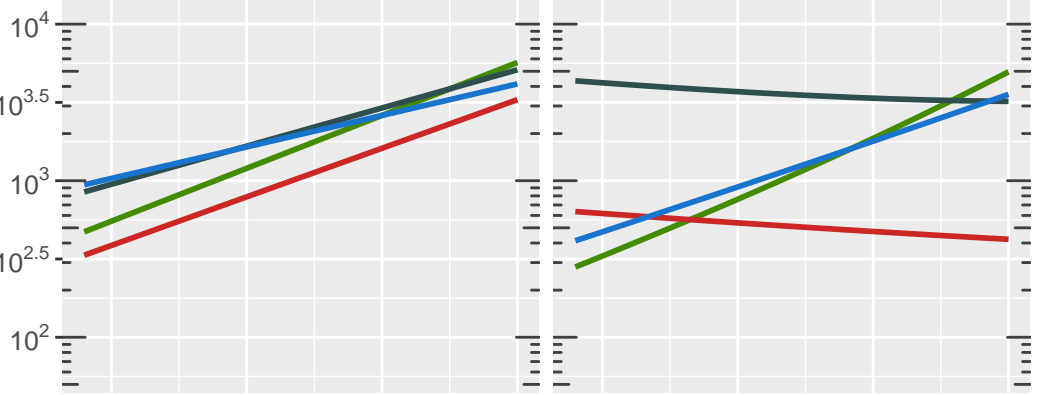
Reservoirs

Freshwater Biology

Fishponds

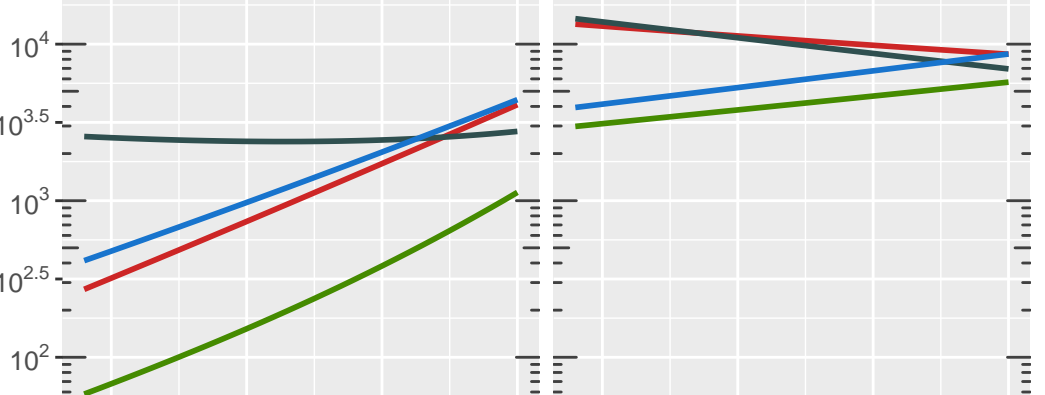
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Model-predicted total numbers (log scale)



Industrial waters

Running waters

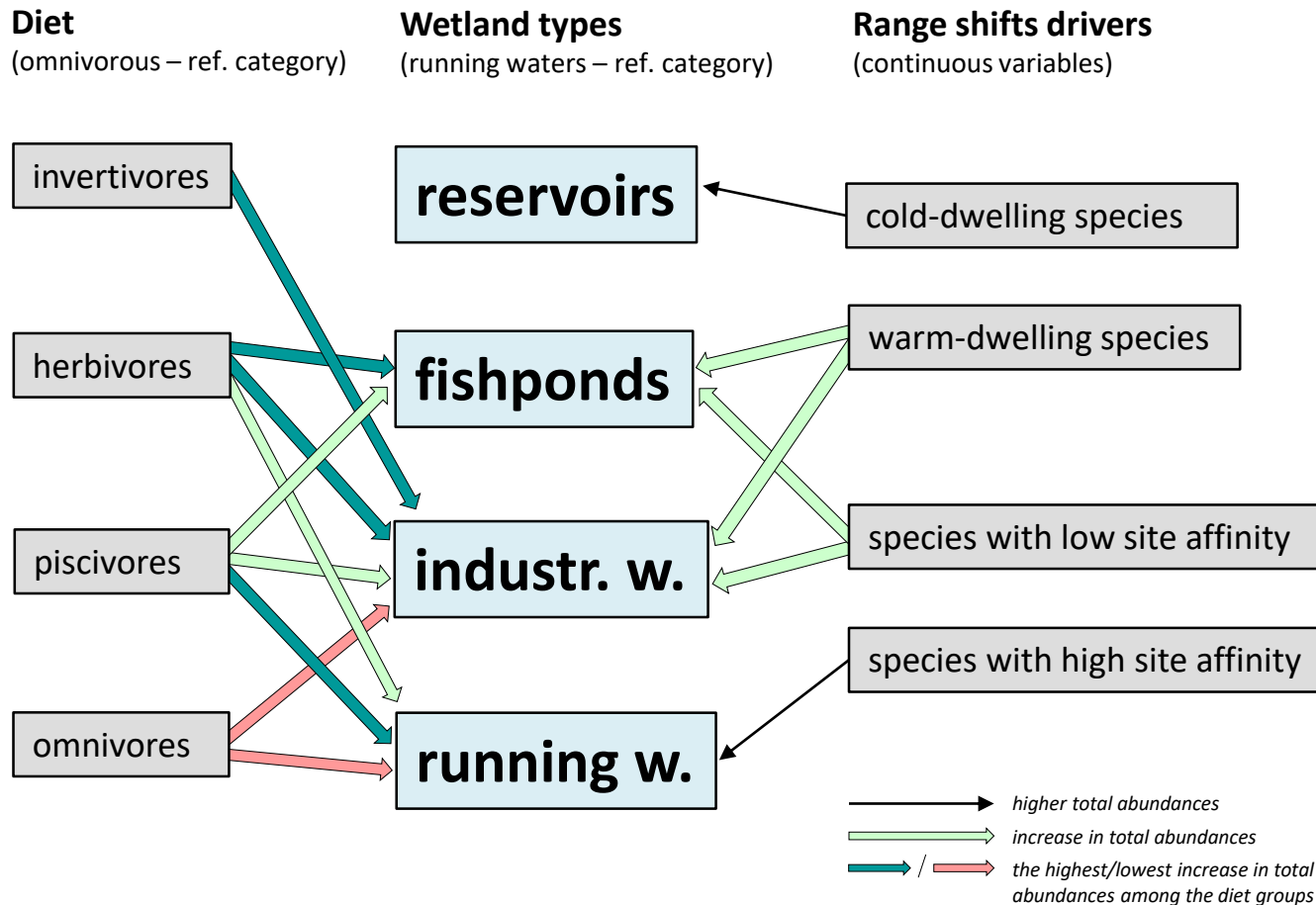


- Herbivores
- Invertivores
- Omnivores
- Piscivores

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)



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**

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10 1 Changes in wetland habitat use by waterbirds wintering in Czechia are related to diet and
11 2 distribution changes

13 3

14 4 Zuzana Musilová^{1*}, Petr Musil¹, Jan Zouhar^{1, 2}, Adéla Šenkýřová¹, Diego Pavón-Jordán³ &
15 5 Petri Nummi⁴

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31 17

32 18 Keywords: wetland type; range-shift drivers; waterbirds; long-term monitoring; artificial
33 19 wetlands

20 Abstract

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

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

32 3. ~~Trends in waterbird abundance positively correlated with s~~Species' diet ~~significantly~~
 33 ~~correlated with their trends in numbers~~ on fishponds, industrial and running waters. ~~Among~~
 34 ~~the diet groups, i~~nvertivores showed the largest increase in ~~abundancesnumbers among the~~
 35 ~~diet groups o~~n industrial waters, closely followed by herbivores. Herbivores showed the
 36 largest increase in ~~abundancesnumbers~~ in fishponds, and piscivores did so in running waters.
 37 ~~Regarding range-shift drivers, s~~Species with higher site ~~affinityconservatism~~ showed higher
 38 ~~abundancesnumbers~~ on running waters, while ~~cold-dwelling species with low STI (i.e.~~
 39 ~~wintering on average in sites with lower temperature)~~ were more abundant on reservoirs. ~~The~~
 40 ~~abundance~~number of both warm-dwelling and ~~less-conservative~~ species ~~with low site affinity~~
 41 increased on fishponds and industrial waters.

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

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

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

55 The extent of wetland habitats of natural origin has decreased worldwide, especially during
56 the last century (Davidson, 2014; Kingsford, Basset & Jackson, 2016; O'Hare *et al.*, 2018). In
57 Europe, for example, two thirds of all natural wetlands have disappeared in the past century
58 (Čížková *et al.*, 2013). Although the loss of natural inland wetlands has been partially offset
59 by the creation of man-made inland freshwater wetlands such as fishponds, reservoirs, and
60 industrial waters (including gravel lakes, sandpit lakes, flooded areas after mining, and settling
61 ponds), these differ in their physical and ecological characteristics (Tucker & Evans, 1997).
62 The importance of inland freshwater wetlands is increasing because climate warming is
63 shifting the zero-degree isotherm (i.e. average aerial temperature of 0 °C in January) (Pavón-
64 Jordán *et al.*, 2015, 2019; Musilová, Musil, Zouhar & Adam, 2018a). Some species are rapidly
65 responding to this phenomenon by altering their migratory behaviour (Sauter *et al.*, 2010;
66 Gunnarsson, Waldenström & Fransson, 2012; Podhrazský *et al.*, 2017; Adam *et al.*, 2015) to
67 adjust to the new environmental conditions, consequently reducing the high mortality risk and
68 energetic cost of a long migration (Newton, 2007) to minimise energy expenditure for
69 thermoregulation during winter (Ridgill & Fox, 1990; Musil *et al.*, 2008; Dalby *et al.*, 2013a).
70 This is especially evident in central European inland wetlands (both natural and of man-made
71 origin), which have become increasingly important for wintering waterbirds in recent decades
72 (Fox *et al.*, 2010; Musil, Musilová, Fuchs & Poláková, 2011; Beekman *et al.*, 2019), due to
73 the redistribution of the abundance of many species (Ridgill & Fox 1990; Rainio *et al.*, 2006;
74 Podhrazský *et al.*, 2017; Pavón-Jordán *et al.*, 2019) and range shifts (Lehikoinen *et al.*, 2013)

75 ~~probably linked to the above-mentioned behavioural changes in response to climate change.~~
 76 ~~These wetlands attract about four million waterbirds every winter (Wetlands International,~~
 77 ~~2018; see also <http://iwc-wetlands.org>). Moreover, wintering waterbird numbers have~~
 78 ~~increased in this region in the past decades (Keller, 2011; Musil, Musilová, Fuchs & Poláková,~~
 79 ~~2011; Wetlands International, 2018). Hence, recent changes in central European winter~~
 80 ~~weather creates favourable conditions that likely provide adequate foraging and safety~~
 81 ~~opportunities throughout the wintering period (Švažas *et al.*, 2001; Nilsson, 2008).~~
 82 Acquiring ~~information~~ regarding habitat use of different species (including and the temporal
 83 changes) ~~taking place in the habitat use~~ is crucial for proposing effective conservation
 84 measures (Pullin, 2002; Angert *et al.*, 2011; Dawson *et al.*, 2011; Davis *et al.*, 2014). Such
 85 information is especially ~~The relevant~~ in the context of ongoing of these issue knowledge of
 86 habitat use increases, especially now when species are undergoing climate-driven changes in
 87 species distributions changes (Maclean *et al.*, 2008; Chen *et al.*, 2011; Podhrázký *et al.*, 2017;
 88 Pavón-Jordán *et al.*, 2019).

89 The non-breeding distribution and habitat use of many waterbirds have changed considerably
 90 during recent decades, with new important wintering areas being established in northern and
 91 eastern Europe (Lehikoinen *et al.*, 2013; Nuijten *et al.*, 2020). ~~It is assumed that t~~This
 92 development phenomenon has been is linked to climate-driven range changes and
 93 redistribution of abundances (Maclean *et al.*, 2008; Thomas *et al.*, 2012; Pavón-Jordán *et al.*,
 94 2015; Musilová, Musil, Zouhar & Adam, 2018a; Pavón-Jordán *et al.*, 2019).

95 In addition to using newly available northern coastal areas around the Baltic Sea (Lehikoinen
 96 et al., 2013), many wintering waterbirds are progressively using inland waters in east and
 97 central Europe to a greater extent when compared to the 1990s (Musilová, Musil, Zouhar &
 98 Adam, 2018a; see also Guillemain & Hearn, 2017; Pavón-Jordán *et al.*, 2020). Climate

99 warming is shifting the zero-degree isotherm (i.e. average aerial temperature of 0 °C in
 100 January) and thus increasing also the availability of free-ice ~~The increased use of importance~~
 101 of inland freshwater wetlands is now feasible ~~increasing because in this region climate~~
 102 warming is shifting the zero-degree isotherm (i.e. average aerial temperature of 0 °C in

Commented [ZM9]: AG7: these ideas are very similar to those in the paragraph below, where they are easier to follow. I suggest you merge these paragraphs

Commented [MP10R10]: We have changed the introduction to avoid redundant parts.

Commented [ZM11]: AG6: compared to what? Coastal wetlands in other countries?

Commented [MP12R12]: The text was removed.

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103 ~~January~~ (Pavón-Jordán *et al.*, 2015, 2019, Musilová, Musil, Zouhar & Adam, 2018a). Some
104 species are rapidly responding to this phenomenon and increasingly using the newly available
105 wetlands in central and east Europe by altering their migratory behaviour (Sauter *et al.*, 2010;
106 Gunnarsson, Waldenström & Fransson, 2012; Adam *et al.*, 2015, Podhrazský *et al.*, 2017;
107 Adam *et al.*, 2015). This has several advantages - for example lowering to adjust to the new
108 environmental conditions, consequently reducing the high mortality risk and energetic cost of
109 a long migration (Newton, 2007) as well as to reducing minimise energy expenditure for
110 thermoregulation during winter in regions that were formerly hostile during winter (Ridgill &
111 Fox, 1990; Musil *et al.*, 2008; Dalby *et al.*, 2013a).
112 ~~even~~ Although the most important wintering requirements of food resources and safety from
113 predation are relatively well known (Snow & Perrins, 1998; Guillemain *et al.*, 2000;
114 Guillemain *et al.*, 2002; Schummer, Kaminski, Raedeke & Graber, 2010), long-term studies
115 revealing ~~In spite of the rapidity of these distribution changes, Ddetailed long-term studies~~
116 revealing the drivers of inland wetland use by waterbirds in light of their recent distribution
117 change during the non-breeding season are absent in the literature, especially in the context of
118 climate-driven changes in distributions remain scarce even though the most important
119 wintering requirements of food resources and safety from predation are relatively well known
120 (Snow & Perrins, 1998; Guillemain *et al.*, 2000; Guillemain *et al.*, 2002; Schummer,
121 Kaminski, Raedeke & Graber, 2010).
122 Food supply and availability of ice-free, open water in the wintering grounds are likely the
123 most important limiting factors (Newton, 1998; Newton, 2013; Lewis *et al.*, 2019) shaping
124 waterbirds wintering distribution (Dalby *et al.*, 2013; Guillemain *et al.*, 2015), followed by p-
125 Predation and air temperature (thermoregulation) are also be important factors affecting
126 waterbird distribution (Ridgill & Fox, 1990; Maclean *et al.*, 2008; Adam *et al.*, 2015).
127 HoweverHence, temperature alone does not simply explain the distribution pattern of
128 wintering waterbirds (Dalby *et al.*, 2013a). The competition for food likely increases during
129 winter, when individuals from low density breeding sites in the vast boreal and tundra areas in
130 Fennoscandia and Russia congregate in their common wintering grounds further down the

Commented [ZM13]: AG8: merge this paragraph with the above one. This one is better explained.

Commented [ZM14R14]: We have changed the introduction to avoid redundant parts.

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

134 ~~In our study,~~ we evaluate species-specific changes in the use of ~~four~~ different wetland types,
 135 ~~including man-made wetlands.~~ We hypothesize that the ~~habitat use distribution~~ of species
 136 among the investigated wetland types is driven by the species diet and that wetland types differ
 137 in their food supply (Kloskowski *et al.*, 2009; Kameníková & Rajchard, 2013; Čížková *et al.*,
 138 2019³; Lewis *et al.*, 2019). We expect a different speed of change in the use of fishponds by
 139 ~~individual-the different~~ diet groups, ~~because this particular type of wetlandey which isare~~
 140 characterised by high density of ~~stocked fishes stock.~~ Hence, with increasing fish density, ~~TIn~~
 141 ~~fishponds,hus,~~ we expect ~~a shift of invertivores from fishponds to other wetland types habitats~~
 142 ~~due to higher-level-of~~ competition for invertebrates with ~~a high density of fish stock (esp.~~
 143 ~~Common Carp *Cyprinus Carpio*).~~ On the other hand, fishponds constitute a food-rich habitat
 144 ~~and on the contrary higher food availability~~ for piscivorous species (Musil, 2006; Nummi,
 145 Väänänen, Holopainen & Pöysä, 2016).

146 We also defined two species-specific determinants to outline the distribution of species ~~in~~
 147 ~~regard to~~regarding ~~man-made~~the ~~four~~ wetland types (later named range shift drivers): (a) a
 148 species' site ~~affinity~~conservatism (the tendency to occupy the same sites in consecutive years)
 149 and (b) the species temperature index (STI) as a measure of the species thermal affinity (warm-
 150 dwelling or cold-dwelling species; ~~see description below. See also~~ Devictor *et al.*, 2008; Jiguet
 151 *et al.*, 2007)). ~~Based on these two species-specific traits and current climate warming (Hurrell~~
 152 ~~& Deser, 201009), w~~We predicted that the changes in use of different wetland types differ
 153 ~~according to range shift drivers, i.e. an-increasing wintering abundancesnumbers probability~~
 154 ~~of wintering in recently ice-free standing waters ofin~~ species with low site affinity (i.e. species
 155 ~~that show low site fidelity and thus show greater potential to change wintering sites) andas~~
 156 ~~well as warm-dwelling- species with high Species Temperature Index (STI; i.e. with high~~
 157 ~~average winter temperature across its wintering distribution) as the winter weather conditions~~
 158 ~~become more favourable for them to expand towards these previously unsuitable regions; see~~

Commented [ZM15]: AG9: these last two paragraphs need improvements to the objectives and hypotheses

Commented [ZM16R16]: The paragraphs were amended.

Commented [ZM17]: AG10: but you don't study competition directly, so explain what you expect to see. A shift from ponds into other habitats...

Commented [MP18R18]: The sentence was amended.

159 e.g. Gaget *et al.* 2021. ~~species~~ species with more probable range shifts and/or distribution
 160 changes (i.e. low-conservative and warm-dwelling species) as a consequence of climate
 161 warming (Hurrell & 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?

Commented [ZM20R20]: The sentence was amended.

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 164 Methods

165 Study region

166 The study region covers the Czech Republic that lies in central Europe. In total, 1,169
 167 monitored sites were classified according to the four wetland types considered: 68 reservoirs,
 168 443 fishponds, 108 industrial waters and 550 running waters (Fig. 1). ~~Running waters include~~
 169 ~~rivers and streams; they were defined as river sections with well-defined boundaries, such~~
 170 ~~as bridges, weirs or dams (see Chytil *et al.*, 1999, for the list of wetland habitats in the Czech~~
 171 ~~Republic).~~

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

180

181 Waterbird monitoring data

182 Site-specific count data of waterbird ~~abundances~~numbers (in total 492,297 observations) were
 183 obtained from the results of the International Waterbird Census (IWC) in the Czech Republic
 184 between 1988 and 2020. IWC is a worldwide citizen-science census with a standardized
 185 methodology (see further details in Delany, 2005; Delany, 2010) managed by the national
 186 coordinator in each country and globally coordinated by Wetlands International

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10 187 (www.wetlands.org). Censuses are carried out in mid-January each winter because it is
11 188 generally the coldest period of winter when the effect of food resources on waterbird
12 189 distribution is considered most apparent due to limited site availability.

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15 190 ~~The counts of w~~aterbird ~~numbers counts~~ ~~were~~are performed on a site during a day according
16 191 to a complete and predefined list of species on predetermined dates and sites with the aim to
17 192 maximize synchrony in the following years (Gilissen *et al.*, 2002). Census participants also
18 193 recorded zero counts of individual species as well as zero counts of all species on a site. About
19 194 350 experienced volunteer birdwatchers contributed annually to the monitoring in Czechia.
20 195 The most important element of IWC methodology is standardization: it requires a single count
21 196 at each site each winter, optimally conducted by the same person in consecutive winters in
22 197 order to make the comparisons between years straightforward and valid. Each site (up to a few
23 198 km² of standing water or a few km of a course of running water) established on the list of sites
24 199 ~~is~~was defined by boundaries (~~such as bridges, weirs or dam on rivers and streams~~) known by
25 200 the census participants. Observers used a telescope or binoculars from the shoreline to look
26 201 for flocks and/or individuals of waterbirds, usually moving from one observation site to
27 202 another by foot. Running waters ~~were~~are monitored using line transects along the shore. The
28 203 number of census participants per site (one, two or a group) and the duration of survey ~~ar~~were
29 204 designated according to bird abundance on each site, species and size of the water surface area,
30 205 and weather (Bibby, Burgess & Hill, 2007; Sutherland, Pullin, Dolman & Knight, 2004). The
31 206 counts at dawn ~~ar~~were recommended for geese. Observations taken under extreme weather
32 207 conditions (fog, rain, snow fall, strong wind) categorised as “strong effect” by the observer
33 208 and incomplete observations were excluded from the dataset prior to the analysis.

34 209 A repeated scanning of the flocks and shoreline observations ~~ar~~were used to increase the
35 210 detectability of counted species. Census records ~~ar~~were submitted to the national coordinator,
36 211 who compiles the submitted records and checks their validity using the participants’ feedback
37 212 if necessary. The quality of the IWC data has been verified in recently published studies (e.g.
38 213 Fox *et al.*, 2010; Lehikoinen *et al.*, 2013; Amano *et al.*, 2018; Musilová, Musil, Zouhar &

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214 Adam, 2018a; Musilová *et al.*, 2018b; Pavón-Jordán *et al.*, 2019; Gaget *et al.*, 2020; Pavón-
215 Jordán *et al.*, 2020). Monitoring methodology did not change over the study period.
216 The IWC targets all waterbirds, a group ecologically dependent on wetlands (Delany, 2010),
217 i.e. ~~grebes, cormorants, herons,~~ swans, geese, ducks, ~~grebes, cormorants, herons,~~ rallids,
218 waders and gulls. However, in this study, we only include 25 the most common wintering
219 waterbird species, namely those exceeding 50 individuals in Czechia annually (see also Musil
220 *et al.*, 2011; Musilová *et al.*, 2014; see Table 1 for an overview of the species). We followed
221 Gill & Donsker (2018) for the species taxonomy.
222
223 Wetland types
224 The wetland types included in this study differ with regard to their origin, age and management
225 practices (Chytil *et al.*, 1999). *Fishponds* represent shallow water bodies with a small stream
226 or canal for water inflow. As commercial subjects aimed at stocking and production of fish
227 (mostly Carp *Cyprinus carpio*), fishponds were formed in the Middle Ages (mostly in the 16th
228 century), have artificially managed water levels, chemistry and nutrient input. *Reservoirs* have
229 been built more recently (after 1900) and represent deep waterbodies with inflow from larger
230 rivers (compared to fishponds). The fish stock in reservoirs are not managed for the purpose
231 of commercial fisheries but rather managed by angling associations (recreation). The most
232 recent wetland type are *industrial waters*, which were created by flooding of former mining,
233 sand-pit or gravel-pit areas, or are sedimentary pools built in industrial areas since 1960s
234 (Hrdinka, 2007). Among all standing water wetland types described above, there is a gradient
235 of decreasing probability of complete ice-cover in winter with increasing depth: from
236 fishponds (the shallowest) to industrial waters and finally to reservoirs (the deepest). High
237 density ~~Fish stocks are most intensively managed in fishponds,~~ followed by reservoirs and
238 the least managed in industrial waters (Oerthli *et al.*, 2005; Musil, 2006, UNEP, 2017).
239 The trophic state of the wetland types ranges from oligotrophic waters (a low nutrient content),
240 through mesotrophic and eutrophic waters to hypereutrophic waters, which present
241 an extremely high nutrient content (Carlson, 1977). Among the four monitored wetland types,

Commented [ZM21]: AG12: but what is important is density or biomass, so talk about that

Commented [MP22R22]: The sentence was amended.

242 running waters contain the lowest content of nutrients, and fishponds are mostly eutrophic,
 243 sometimes hypertrophic (Chytil *et al.*, 1999; Musil, 2006; Seiche *et al.*, 2012; Čížková *et al.*,
 244 2019³). The distribution of the monitored sites is shown in Fig. 1.

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246 Species-specific variables

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

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

254 (ii) *Species temperature index (STI)*: The STI (see Devictor *et al.*, 2008; Jiguet *et al.*, 2007
 255 [for details of STI calculation](#)) reflects the long-term average January temperature (1950-
 256 2000) experienced by individuals of any given species across the species' entire wintering
 257 distribution. Species' distribution maps were downloaded from BirdLife International &
 258 HBW (2017) and all temperature data from the regions included in each species'
 259 wintering range (above) were downloaded from www.worldclim.org. [For each species,](#)
 260 [all grid cells \(5x5 degrees\) with temperature data within a species' wintering range](#)
 261 [\(BirdLife International & HBW 2017\) were downloaded and averaged.](#)

262 (iii) For each species, we calculated a measure of year-to-year variation in geographical
 263 distribution of the species across the study ~~region~~ (called *site affinity/conservatism*
 264 ~~hereafter~~). ~~Considering the nature of this variable~~ Thus, the species' fidelity to the
 265 ~~wintering sites fidelity of individuals constitutes the basis serves as a main driver of the~~
 266 ~~covariate site affinity, which. The measure~~ is bounded between 0 and 1, with the actual
 267 range of values being 0.14–0.82 in our data set. Values close to 1 indicate that the same
 268 sites are occupied in successive years, and with the same intensity; values close to zero
 269 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 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.

270 ~~time. [These values are calculation is based on Earth mover's distance; (see (Kranstauber,~~
 271 ~~Smolla & Safi, 2017 [see Zouhar, Musil, Musilová, in prep.) for further details].~~
 272 The Pairwise correlation of continuous species-specific variables ~~were all below 0.30~~ is 0.06,
 273 implying there is little collinearity (Hair, Anderson, Tatham & Black, 1995; Rogerson, 2001).
 274 ~~Hence all variables were included in our regression analysis (see e.g. Lehtikoinen *et al.*, 2016).~~
 275 The values of species-specific variables are listed in Table 1.
 276
 277 Statistical analysis
 278 Our analyses proceeded in two stages, differing in the level of detail at which the ~~monitoring~~
 279 ~~count~~ data were aggregated. In the first stage, we studied how ~~the~~ trends in ~~abundances~~ number
 280 of different species vary across wetland types. We first used a log-linear Poisson regression
 281 analysis to impute any missing waterbird count data from the long-term data series (in 1988–
 282 2020) using TRends and Indices for Monitoring data software (TRIM; Statistic Netherlands
 283 version 3.52, Pannekoek & Van Strien, 2005). Regression parameters were estimated using
 284 generalized estimating equations (GEE). Missing data were usually the result of incomplete
 285 coverage due to limited availability of observers in some ~~seasons~~ years. The proportion of
 286 missing counts varied between 33% and 65% in the whole dataset, which is regarded as
 287 tolerable (Soldaat *et al.*, 2017). ~~Consequently, we obtained the trend in numbers of adult~~
 288 ~~individuals for each investigated species for each wetland type.~~
 289 In this first stage, after imputing any missing data, we estimated the species-specific ~~long-term~~
 290 trends in ~~abundances~~ numbers (i.e. the change in ~~abundance~~ indices from one year to the next)
 291 ~~at each of the four wetland types~~ and assessed differences in these trends between the ~~four~~
 292 wetland types based on the rate of change: a strong increase or decrease ($\geq 5\%$ per year); a
 293 moderate increase or decrease ($< 5\%$ per year); a stable (trend was not significant and CIs were
 294 sufficiently narrow) or an uncertain trend (see also Fouque *et al.*, 2009; Musil *et al.*, 2011;
 295 Musilová *et al.*, 2018b). Then, a Wald test was used to assess the significance of differences
 296 in the ~~trends rate of changes in numbers in the~~ four wetland types. ~~We also used the imputed~~
 297 ~~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.

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10 298 type and site as covariates in the linear trend models (see also Pavón-Jordán *et al.*, 2015;
11 299 Musilová *et al.*, 2018b).

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13 300 In the second stage, we studied the effect of species-specific variables on population trends at
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15 301 different wetland types. As in the first step in this species-level analysis (above), we also used
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17 302 TRIM to fill the gaps in the data due to incomplete monitoring coverage. For each species, we
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19 303 obtained the TRIM-imputed ~~total abundance~~time totals ~~or yearly total abundance~~ (later termed
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21 304 ~~total numbers~~) by year and wetland type, producing a dataset of 3,267 observations (25
22
23 305 species, 33 years, 4 wetland types). Velvet Scoter (*Melanitta fusca*) was not recorded on
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25 306 fishponds and, therefore, excluded from the analyses.

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27 307 Next, we explained these total ~~abundances~~numbers estimated with TRIM and their trends with
28
29 308 species-specific variables in a regression approach. As the time ~~abundances~~ totals (i.e. ~~total~~
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31 309 ~~number of individuals~~) exhibited substantial overdispersion, we used negative binomial
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33 310 regression rather than the canonical Poisson distribution. The fact that observations for a
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35 311 species are repeated across years and wetland types led us to include species as a random effect
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37 312 in the model, meaning we fitted a Generalized Linear Mixed Model (GLMM). Moreover, to
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39 313 allow for (i) heteroskedasticity both between and within species, and (ii) arbitrary correlation
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41 314 within a species' values, we used a cluster-robust estimator of the standard errors in statistical
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43 315 inference, clustered at the species level (Cameron & Miller, 2015). To facilitate coefficient
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45 316 interpretation, all continuous variables were *z*-standardized (i.e. centred around the mean and
46
47 317 divided by the standard deviation) prior to running the regressions.

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49 318 For simplicity, our model specification assumes linear time trends in ~~total~~
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51 319 ~~abundances~~numbers; we do nevertheless expect these trends to vary systematically with
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53 320 species-specific characteristics and across wetland types. Therefore, we included interactions
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55 321 of year and wetland types with all species-specific variables in our model. All regression
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57 322 models were estimated in Stata 16 (StataCorp, College Station, TX).

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325 Results

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10 326 492,297 observations from 25 species in 1,169 wetlands between 1988 and 2020 were included
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12 327 in this study. The mean annual abundance for four diet groups was the following: herbivores
13 328 (23,466.7 ± 2,897.9 SE), omnivores (219,234.0 ± 3,264.4 SE), invertivores
14 329 (6,295.2 ± 240.2 SE) and piscivores (15,136.5 ± 933.2 SE). The first stage of our analysis
15
16 330 revealed significant differences in abundance trends between the four wetland types in 22 out
17
18 331 of the 25 investigated species (Table 2). Prevailing decreasing (10 species) or stable trends
19
20 332 (six species) were found in running waters while significant increasing trends in the abundance
21 333 of 15 species were found in standing waters (reservoirs, fishponds and industrial waters). The
22 334 significant differences (according to results of Wald test) in species trends among analysed
23 335 wetland types were found in five of six herbivore species, in six of eight omnivore species, in
24 336 all five invertivore species and in all six piscivore species. Increasing trend in abundances was
25
26 337 found in all herbivores on reservoirs and in almost all species in industrial waters (Table 2).
27
28 338 The results from our GLMM showed that species exhibiting higher site affinity conservatism
29 339 (i.e. low year-to-year variation in geographical distribution of the species across the study
30
31 340 region) recorded the highest total abundances numbers on running waters (Table 3). Similarly,
32 341 cold-dwelling species (identified by a lower value of average temperature across its wintering
33 342 range – STI species temperature index) were more abundant in reservoirs (Table 3).
34
35 343 The effects of the interaction terms between species-specific variables and year showed the
36 344 extent at which the trends in abundances numbers on different wetland types varied with
37 345 species-specific variables. For instance, the coefficient on year in the reservoirs column ($\beta =$
38 346 0.056) implied that the predicted yearly increase in total abundances numbers in an
39 347 omnivorous species (i.e. the reference diet group) with average values of site
40 348 affinity conservatism and STI is about 5.6 per cent; the coefficient on herbivorous \times year ($\beta =$
41 349 0.022) indicated that for a herbivorous species with average values of site
42 350 affinity conservatism and STI, the annual increase is was larger by ca. 2.2 per cent, i.e. about 8
43 351 per cent in total. The species' diet significantly affected the species trends on fishponds,
44 352 industrial and running waters. On fishponds, herbivorous species showed the largest (positive)
45 353 trend in total abundances numbers (over 11 per cent per year at average values of site affinity

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10 354 ~~conservatism~~ and STI), followed closely by piscivores. On industrial waters, omnivores
11 355 increased at the slowest pace by ca. 7–9 % slower than the other three diet groups. On running
12 356 waters, piscivores increased at the fastest rate during the 1990s and early 2000s, followed
13 357 closely by herbivores (Figures 3 and 4). Warm-dwelling and ~~less-conservative~~ species with
14 358 ~~low site affinity~~ showed the largest trend on fishponds and industrial waters.
15 359 The differences in trends and ~~abundances numbers~~ across diet groups and wetland types are
16 360 visualized in Figures 3 and 4. Figure 3 presents the underlying data on total
17 361 ~~abundances numbers~~, along with trend curves obtained via scatterplot smoothing using
18 362 LOESS. Figure 4 visualizes the trends predicted by the regression for different diet groups at
19 363 different wetland types. The apparent discrepancies between Figure 3 and 4 are caused by the
20 364 fact that in the regression that underlie Figure 4 (i) we estimate a (log-) linear for simplicity
21 365 (while some trends in Figure 3 show a substantial degree of nonlinearity) and (ii) the
22 366 predictions ~~are were~~ obtained at fixed values of STI and site ~~affinity conservatism~~, which
23 367 otherwise vary between different diet groups. Figure 5 summarizes the findings in a graphical
24 368 format.

371 Discussion

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

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381 Changes in habitat use in different diet groups

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10 382 Generally, food supply is of high importance for waterbirds (Guillemain *et al.*, 2015;
11 383 Holopainen *et al.*, 2015) due to its subsequent effect on breeding success, adult survival and
12 384 also overall flyway population dynamics (Newton, 1998; Newton, 2013; Jørgensen *et al.*,
13 385 2016). Use of feeding habitat is a hierarchical process, influencing the species geographical
14 386 distribution and the choice of a particular wetland (Green, 1998). Here, we demonstrated long-
15 387 term changes in wetland type use among diet groups in fishponds, industrial and running
16 388 waters, but not in reservoirs. Increased use of industrial waters was ~~demonstrated~~ found in
17 389 invertivoreous species, which predominantly used running waters in the beginning of the study
18 390 period and progressively switch to industrial waters. Invertebrate biomass, which provides the
19 391 majority of the food of invertivores, tend to be highest in early successional wetlands (Nummi
20 392 & Holopainen, 2014; Petrie *et al.*, 2016), such are industrial waters. Furthermore,
21 393 heterogeneity in the physical characteristics of foraging areas can affect foraging behaviour
22 394 (Fernández & Lank, 2008) and therefore affect the species habitat use. Consistent with this,
23 395 diving ducks represent most of the invertivoreous species; they feed at greater depths during
24 396 the non-breeding period (Hughes & Green in Kear, 2005) and industrial waters likely provide
25 397 favourable depths for their foraging behaviour. Lower foraging costs (Wood *et al.*, 2013a) in
26 398 industrial waters compared to higher water velocities in running waters can make foraging
27 399 more profitable for invertivores. The same effect could cause increased use of industrial waters
28 400 in herbivores (almost in the same degree as in invertivores).

29 401 ~~Assumed~~ The a priori assumption of a low increase in abundances numbers of invertivores in
30 402 fishponds was confirmed ~~in fishponds~~. ~~In~~ invertebrates are fundamental to, ~~an important~~
31 403 ~~element of~~ both terrestrial and aquatic food webs, and drastic decreases ~~have been~~ was shown
32 404 in terrestrial insects on a global level (Dirzo *et al.*, 2014; Wagner *et al.*, 2021). Long-term
33 405 studies on aquatic invertebrates are currently scarce (Gozlan *et al.*, 2019), but some indicate
34 406 changes in aquatic invertebrate structure (Fried-Petersen *et al.*, 2020; Pilotto *et al.*, 2020; van
35 407 der Lee, Aray-Ajoy, Futter & Angeler, 2021) associated with increasing levels of
36 408 eutrophication and brownification as one of the most important driver of these changes
37 409 (Jackson, Loewen, Vinebrooke & Chimimba, 2016; Lind *et al.*, 2018; Arzel *et al.*, 2020).

410 Fishponds are commercial ~~habitat~~subjects with artificially managed nutrient input that
 411 increase the level of eutrophication (Roy *et al.*, 2020) and are aimed at stocking and breeding
 412 fish (mostly Carp). The artificial nutrient input have ~~been~~ resulted in hypertrophy of fishponds,
 413 especially after the World War II (Pechar, 2000; Seiche *et al.*, 2012) and therefore ~~these ponds~~
 414 exceed the nutrient level of other wetland types in the study ~~region~~area. It ~~is noteworthy~~has
 415 ~~been shown~~ that high stocks of Carp in fishponds ~~create an environment with extremely high~~
 416 ~~competition cause the competition~~ for invertebrate food with invertivorous waterbird species
 417 ~~in~~during the breeding season (Musil, 2006). ~~In this study, we show that, whereas~~ this effect is
 418 also ~~noticeable significant in this study~~ during the wintering season by a lower increase in the
 419 use of fish-ponds by invertivores.
 420 Indeed, herbivores ~~stood out~~revealed as the most increasing diet group in fishponds, likely
 421 ~~keeping~~standing outside the Carp-waterbird food competition. The ~~alternative~~ importance of
 422 artificial fishponds ~~as alternative sites~~ for wintering herbivorous and omnivorous ducks was
 423 shown also in Doñana ~~National Park~~, Spain (Kloskowski *et al.*, 2009). However, some species
 424 of the herbivorous group (geese, Mute Swan and Eurasian Wigeon) are not strictly feeding
 425 inside of wetlands such as invertivores and piscivores and may feed both aquatically and
 426 terrestrially (Jacobsen & Ugelvik, 1994; Fox *et al.*, 2005; Wood *et al.*, 2013b). Therefore, the
 427 changes in wetland type use are less ~~strongly~~accurate related to wetland food supply in this
 428 group. Especially, ~~due to the characteristics of the census protocol (dawn counts), variation in~~
 429 geese ~~abundances~~numbers are ~~more~~ likely ~~to be~~ affected by this daily dynamic ~~this issue due~~
 430 ~~to dawn counts on~~between the roosting and feeding sites ~~the roost sites~~. In the study ~~region~~area,
 431 ~~geese have traditionally congregated in high numbers during winter and use the traditional~~
 432 ~~wintering grounds of high aggregations of geese are~~ reservoirs as a roosting sites and nearby
 433 fields as a dominant feeding sites, especially in south-Moravian lowland (Czech IWC data—;
 434 <http://www.waterbirdmonitoring.cz/vysledky/iwc20/>). Conversely, other herbivorous species
 435 are counted during the daylight activities in the wetlands and thus do not include individuals
 436 that ~~leave~~have left the wetlands (~~roosting sites~~) to forage in the fields. In addition, some
 437 waterbirds may often be feeding at different places during the night, such as omnivorous

Commented [ZM31]: AG17: the ponds are not in the National Park

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10 438 Mallards in the Netherlands (Kleyheeg *et al.*, 2017) and granivorous dabbling ducks feeding
11 439 on rice fields in the Mediterranean (Guillemain *et al.*, 2010; Brogi, Pernollet, Gauthier-Clerc
12 440 & Guillemain, 2015; Parejo *et al.*, 2019). Nevertheless, this nocturnal behaviour is likely
13 441 difficult to quantify (Tourenq *et al.*, 2001) and any obvious suitable nocturnal feeding wetlands
14 442 are not known from the study ~~area~~region.

15 443 On the species level, prevailing decreasing or stable trends in ~~abundances~~numbers were found
16 444 in running waters, which represent the traditional wintering grounds in the study ~~region~~area
17 445 (Adam *et al.*, 2015; Musilová, Musil, Zouhar & Romportl, 2015; Musilová, Musil, Zouhar &
18 446 Adam, 2018a). It is worth noting that running waters fulfil one of the most important habitat
19 447 requirements for wintering waterbirds: to avoid unfavourable winter harshness and destructive
20 448 winter extremes in the zero-degree-isotherm area (Musilová, Musil, Zouhar & Romportl,
21 449 2015; Musilová, Musil, Zouhar & Adam, 2018a). In recent decades, milder winter conditions
22 450 in Central Europe (IPCC, 2014) likely provide an ~~increased~~ availability of new wintering
23 451 areas, i.e. standing waters with reduced ice cover. ~~Conversely~~Still, running waters still remain
24 452 as suitable wintering sites, as revealed in this study, especially for piscivores and herbivorous.
25 453 Recent climate and land use changes affect the fish assemblages, diversity and distribution
26 454 (Comte *et al.*, 2013) as well as diversity and distribution of invertebrates (Haase *et al.*, 2019)
27 455 with predicted up and downstream direction of shifts in the fish species in rivers (Radinger *et*
28 456 *al.*, 2017), hence the use of rivers by piscivores is likely in accordance with these changes in
29 457 fish distribution.

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43 459 Wetland type use in species changing distribution

44 460 Generally, there is a trade-off between the cost and benefit of the wintering site use (Ridgill &
45 461 Fox, 1990; Adam *et al.*, 2015; Musilová, Musil, Zouhar & Romportl, 2015). Importantly, there
46 462 is a gradient among the four investigated wetland types in the level of the winter harshness
47 463 risk, i.e. the sensitivity to cold weather and freezing (running waters considered the most stable
48 464 compared to standing waters, see above), in the level of habitat change risk (fishponds
49 465 considered the most artificially affected), in the level of succession in freshwater communities

466 (industrial waters considered as an early successional stages), trophic status (the highest
467 nutrient content in fishponds); see the methods for details.

468 The nature of these differences reflected the use of wetland types in species with more or less

469 probable range shifts and/or distribution changes. ~~High-conservative-s~~Species with high site

470 affinity (i.e. species with ~~lower~~ year-to-year variation in geographical distribution across the

471 study ~~are~~region) revealed higher use of running waters. Higher stability in cold and extreme

472 weather conditions, low level of habitat change risk caused by possible management ~~and high~~

473 ~~level of succession~~ of running waters are likely important for these conservative species with

474 lower probability of range changes. However, saturation of traditional wintering grounds was

475 suggested to occur in Czech Republic (Musilová, Musil, Zouhar & Romportl, 2015) that could

476 increase the competition for resources (Newton, 1998; Newton, 2013). In addition, higher

477 water velocities in running waters compared to standing waters increase the foraging costs

478 (Wood *et al.*, 2013a).

479 ~~Conversely~~Furthermore, our study indicates the high importance of man-made standing

480 wetlands (fishponds and industrial waters) ~~for species with more likely to undergo probable~~

481 ~~range shifts~~, i.e. species with low site affinity ~~low-conservative~~ and warm-dwelling (higher

482 average temperature across its wintering range – high STI –) species. Wintering waterbird

483 populations are clearly changing their distribution (Lehikoinen *et al.*, 2013; Pavón-Jordán *et*

484 *al.*, 2015; Musilová, Musil, Zouhar & Adam, 2018a; Pavón-Jordán *et al.*, 2019; Pavón-Jordán

485 *et al.*, 2020). These distribution changes could be associated with changes in ice cover, food

486 availability, habitat and hunting pressure (Dalby *et al.*, 2013; Newton, 2013; Guillemain *et al.*,

487 2015; Pavón-Jordán *et al.*, 2020; this study). ~~Low-conservative-s~~Species with low site affinity

488 increase the use of these newly available wetlands that are also considered less stable as

489 wintering sites (higher winter harshness and habitat change risk, higher trophy in fishponds

490 and lower succession in industrial waters). It seems that ~~low-conservative~~ species with low site

491 affinity grasp the benefits of milder climate in recent decades (Hurrell & Deser, 2009) and

492 responded by increasingly use these alternative wetlands. The tendency of ~~less-conservative~~

493 species with low site affinity to annually change the wintering sites implies they may be useful

Commented [ZM33]: AG18: I do not understand what you mean by succession here

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Commented [MP36R36]: The sentence was amended.

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11 494 ~~early-warning indicators as a pilot species to indicate~~of changing use of wintering sites (see
12 495 also Green & Elmberg, 2014).

13 496 The thermal affinity was determined as an important trait explaining the species distribution
14 497 and range changes leading by climate change (Gaget *et al.*, 2020; Devictor *et al.*, 2008). The
15 498 changes of nonbreeding distribution of waterbirds seems highly affected by climate warming
16 499 (Pavón-Jordán *et al.*, 2015; Gaget *et al.*, 2018). Our study reveals the use of reservoirs by cold-
17 500 dwelling species (mostly seaducks), while reservoirs represent deeper water bodies with
18 501 inflow from larger rivers and have the lowest probability of complete ice-cover in winter
19 502 among standing waters. In the light of climate warming, related northeastwards shifts of
20 503 species distributions (Lehikoinen *et al.*, 2013; Pavón-Jordán *et al.*, 2015; Gaget *et al.*, 2020;
21 504 Pavón-Jordán *et al.*, 2020), and consequent decline and even local extinction of cold-dwelling
22 505 species caused by distribution change (Devictor *et al.*, 2008; Tayleur *et al.*, 2016; Gaget *et al.*,
23 506 2020), ~~we~~ assume that reservoirs could serve as a refuges for cold-dwelling species in the near
24 507 future. ~~Larger stochasticity and frequency of extreme weather events are also predicted by~~
25 508 ~~most climate change scenarios and thus such as a deep and large wetlands with stable~~
26 509 ~~temperature conditions suitable for survival of benthic invertebrates will provide the~~
27 510 ~~resources required by these species.~~ However, the overall increase in ~~abundance~~numbers of
28 511 cold-dwelling species in the study ~~region~~area indicate that this issue could be much
29 512 ~~complicated~~complex, as temperature is not the only driver ~~hence the temperature do not simply~~
30 513 ~~explain the~~of species distribution ~~changes~~ (Dalby *et al.*, 2013). Conversely, warm-dwelling
31 514 species increase the use of both fishponds and industrial waters. The availability of these
32 515 shallower man-made wetlands may likely increase ~~in recent years~~ due to climate warming
33 516 (Hurrell & Deser, 2010). The ‘wintering strategy’ of warm-dwelling species is driven by the
34 517 geographic avoidance of the zero-degree isotherm to reduce winter harshness risk (Gaget *et*
35 518 *al.*, 2020), therefore warm-dwelling species likely do not reflect the difference in wetland types
36 519 in terms of winter harshness risk and increase the use of industrial waters and fishponds with
37 520 higher winter harshness risk. Increasing our knowledge of the habitat use of warm-dwelling
38 521 species ~~habitat use~~ is of high importance ~~due to its forecasted~~ since they are more likely to

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

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527 Conclusion

528 Our study highlight the general pattern that wintering waterbirds are expected to select sites
 529 with higher food availability (Fox *et al.*, 1995; Green, 1998; Green, Fox, Hughes & Hilton,
 530 1999; Guillemain, Fritz & Guillon *et al.* 2000; Chatterjee, Adhikari, Pal & Mukhopadhyay,
 531 2020), higher energy content (van Eerden, 1984) and lower foraging cost (Wood *et al.*, 2013a)
 532 to balance the costs and benefits of feeding site choice during wintering (Newton, 1998;
 533 Newton, 2013; Aharon-Rotman, Clark, Klaassen & Buttemer, 2016). [The effort to meet these](#)

534 [requirements resulted in a considerable change of the habitat use in the given species.](#)

535 ~~Based on the flyway-level waterbird data, dramatic changes in relative abundances are~~
 536 ~~expected (see e.g. Pavón-Jordán *et al.*, 2020) with temperature-dependent inter-annual and~~
 537 ~~long-term north-eastwards shift of the species distribution (Pavón-Jordán *et al.*, 2019).~~

538 ~~Understanding the role of habitat use in this~~ context of changing distributions of different
 539 species is of high importance for conservation (see e.g. Janke *et al.*, 2017), especially since the
 540 climate-driven range changes are already underway (e.g. Lehtikoinen *et al.*, 2013; Pavón-
 541 Jordán *et al.*, 2015; Musilová, Musil, Zouhar & Adam, 2018a; Pavón-Jordán *et al.*, 2019;
 542 Pavón-Jordán *et al.*, 2020) and may lead to the decrease of effectiveness of the conservation
 543 efforts (Musilová *et al.*, 2018b). Consistent with this view, increasing use of industrial waters
 544 and fishponds for warm-dwelling and ~~low-conservative~~ species [with low site affinity](#)
 545 ~~with~~[exhibiting](#) more probable range shifts and/or distribution changes, and conversely use of
 546 reservoirs by cold-dwelling species and running waters by ~~high-conservative~~ species [with high](#)
 547 [site affinity](#) indicates importance of individual wetland types as wintering grounds, which
 548 should be considered in future conservation planning and effective management. The
 549 development and implementation of measures to increase the suitability of existing modified

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10 550 habitats for wildlife appears essential to conserve biodiversity (Sinclair, Fryxell & Caughley,
11 551 2006; Navedo, 2017). The implementation should be based on the core knowledge of the
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13 552 species habitat use and distribution changes (Musilová *et al.*, 2018b). ~~C~~The climate-driven
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15 553 changes in ~~the~~ species distribution~~s~~ should not necessarily have the north/eastwards direction
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17 554 (see e.g. Lehikoinen *et al.*, 2013, 2016; Pavón-Jordán *et al.*, 2015; Pavón-Jordán *et al.*, 2020),
18 555 ~~but climate changes could also modify the use of habitats and their use within~~inside the
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20 556 species' current ranges.

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23 559 Acknowledgments

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26 560 We are indebted to all those who have volunteered in International Waterbird Census (IWC)
27
28 561 counts as well as to the census IWC co-ordinators in the Czech Republic (i.e. Bohuslav
29
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31
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36 565 entitled “The reduction of habitat fragmentation consequences in various types of landscape
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38 566 in the Czech Republic”, the project TH 04030185 of Technology Agency of the Czech
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40 567 Republic entitled “Identification of important wintering sites of waterbirds, with a focus on
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42 568 the presence of conflict species and in the context of site protection, habitat characteristics and
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44 569 climate change“ and the project No.20194209 of Internal Grant Agency of FES CULS entitled
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46 570 “Waterbirds as bioindicators of wetlands health: food specialisation determines the waterbird’
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48 571 response to climatic and environmental changes“.

Commented [ZM41]: AG22: but you have not presented any results on changes within each of the four habitats

Commented [MP42R42]: The sentence was amended.

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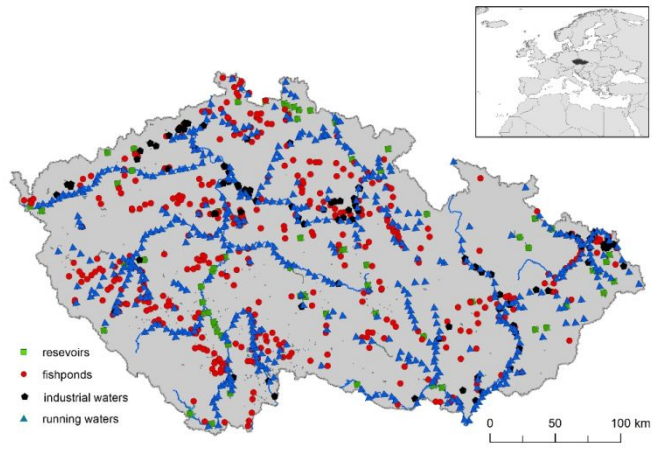
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42 942 Data availability statement:
43 943 The data that support the findings of this study are available from the corresponding author
44 944 upon reasonable request.
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50 946 Additional Information:
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52 947 The authors declare no competing interests.
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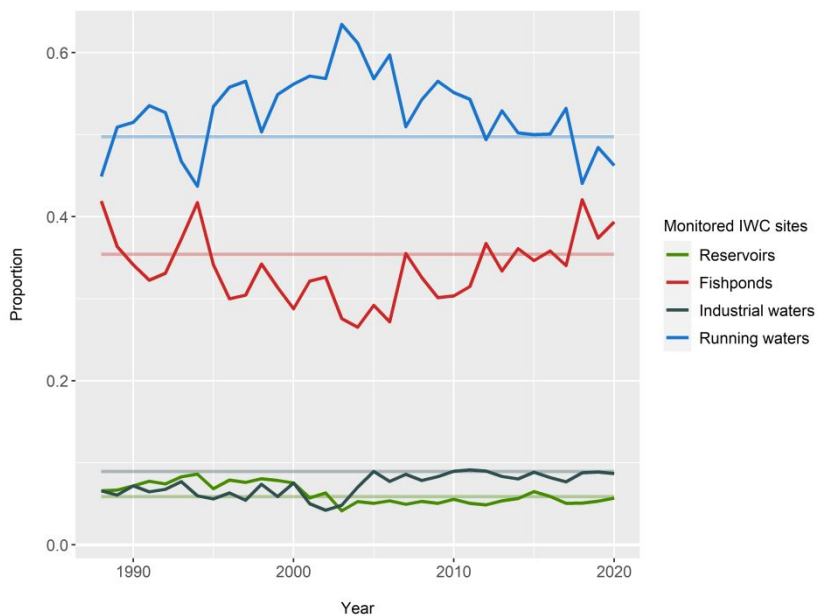
949 Figure 1. Distribution of monitored wetland sites in the Czech Republic between 1988 and
950 2020



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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.

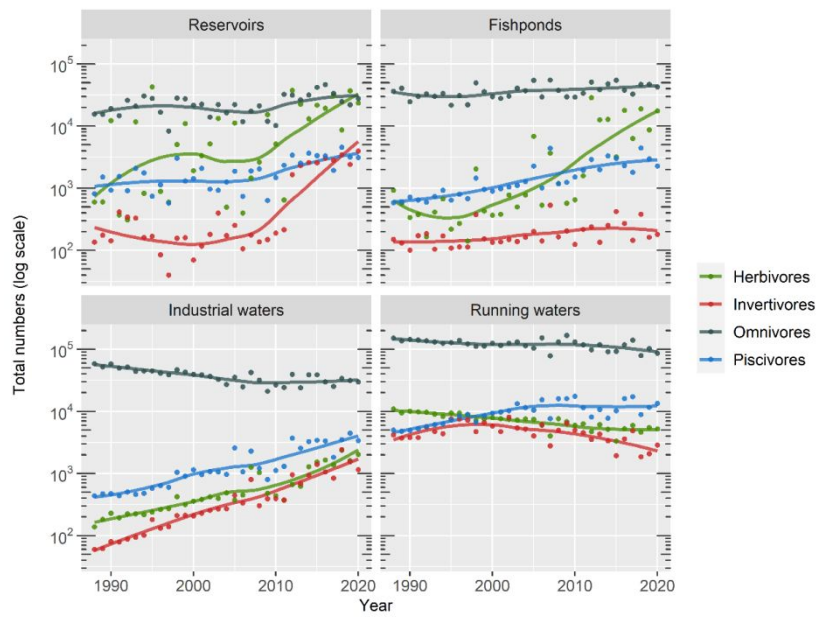


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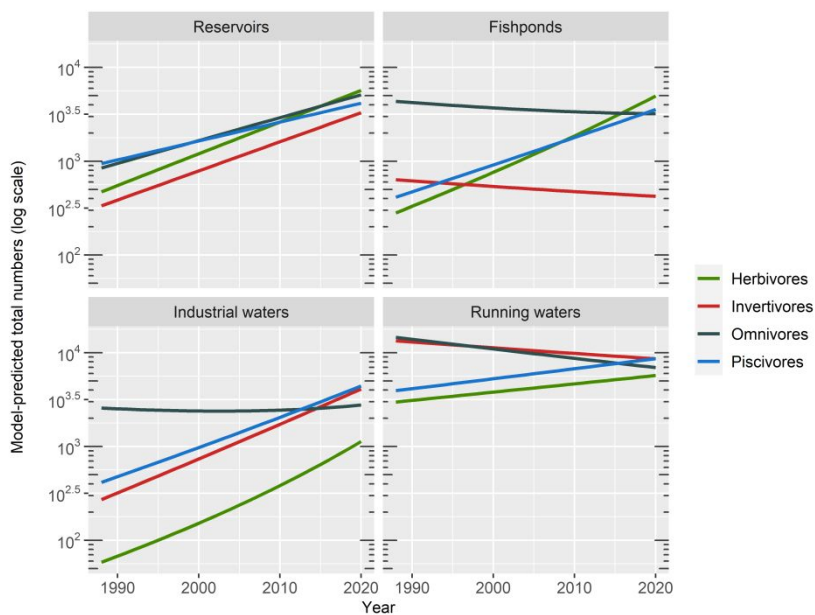
959 Figure 3. Yearly total abundances and their trends (obtained by LOESS smoothing) at
960 individual wetland types, by diet group.



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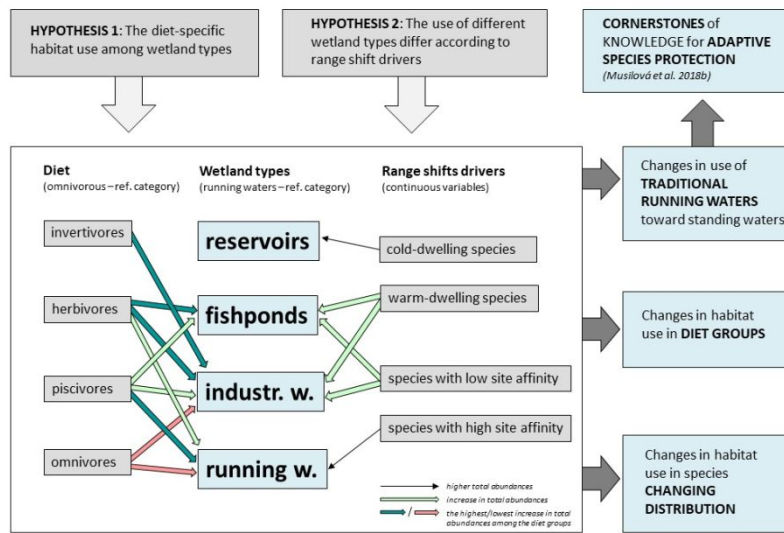
963 Figure 4. Predicted ~~time~~-totals abundances at individual wetland types and for different diet
 964 groups at mean values of STI and site ~~affinity~~conservatism (based on the regression presented
 965 in Table 3).



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



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970 Table 1. List of investigated species and its species-specific variables (diet, species
 971 temperature index and site [affinity-conservatism](#))

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

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

978 Table 2. Changes in [abundancesnumbers](#) 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 Bean 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***

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7 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***

8 979 *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,*
980 *SD – strong decrease, U – uncertain.*

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981 Table 3. Results of a random-effects negative binomial regression explaining total
 982 [abundancesnumbers](#).

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

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