

This is an electronic reprint of the original article.

This reprint *may differ* from the original in pagination and typographic detail.

Author(s): Hannu Pöysä

Title: Impacts of climate-driven changes in habitat phenology on dynamics of niche overlaps and spatial associations in a boreal waterbird community

Year: 2023

Version: Publisher's version

Copyright: The author(s) 2023

Rights: CC BY 4.0

Rights url: <https://creativecommons.org/licenses/by/4.0/>

Please cite the original version:

Hannu Pöysä (2023) Impacts of climate-driven changes in habitat phenology on dynamics of niche overlaps and spatial associations in a boreal waterbird community. *Oikos*. doi: 10.1111/oik.09696

All material supplied via *Jukuri* is protected by copyright and other intellectual property rights. Duplication or sale, in electronic or print form, of any part of the repository collections is prohibited. Making electronic or print copies of the material is permitted only for your own personal use or for educational purposes. For other purposes, this article may be used in accordance with the publisher's terms. There may be differences between this version and the publisher's version. You are advised to cite the publisher's version.

Research article

Impacts of climate-driven changes in habitat phenology on dynamics of niche overlaps and spatial associations in a boreal waterbird community

Hannu Pöysä  ^{1,2}

¹Dept of Environmental and Biological Sciences, Univ. of Eastern Finland, Joensuu, Finland

²Natural Resources Inst. Finland, Joensuu, Finland

Correspondence: Hannu Pöysä (Hannu.Poysa@luke.fi)

Oikos

2023: e09696

doi: [10.1111/oik.09696](https://doi.org/10.1111/oik.09696)

Subject Editor: Dries Bonte

Editor-in-Chief: Dries Bonte

Accepted 21 February 2023



A fundamental, yet little-explored, question is if climate change has affected niche relationships and spatial associations of native non-invasive species in established local communities, potentially affecting interspecific interactions and community organization. Here, long-term (1991–2020) changes in habitat niche overlaps (HNOs; measured in terms of three habitat categories describing the amount and development of shore vegetation and shore depth) and spatial associations (SAs; measured as co-occurrence on lakes) were studied in relation to climate-driven changes in habitat phenology in a community of eight migratory waterbird species breeding on 37 lakes in southeastern Finland. Overall timing of ice-out date (IOD) and within-season variation in the timing of ice-out (standard deviation of IOD, SDIOD) in lakes determine habitat (lake) availability for waterbirds during the settling phase. Previous work has documented that IOD has advanced and SDIOD increased during 1991–2020, with species responding differently to these changes in their habitat use. HNO and SA varied considerably in the 28 species pairs of eight species during the study period. The effect of IOD and SDIOD on that variation was generally small, effect sizes differing from zero only in eight out of 112 cases. However, the direction and magnitude of the effects of IOD and SDIOD on HNO and SA varied considerably among the species pairs. Although not statistically significant, overall differences in the direction and magnitude of the effect sizes suggested that the impacts of IOD and SDIOD on HNO and SA were stronger in species pairs in which the species were more similar in terms of settling phenology, and stronger for early settling species than for late settling species. Observed changes in niche relationships probably reflect changes in interspecific interactions and affect the possibilities for heterospecific information use in habitat selection.

Keywords: climate change, habitat niche, ice breakup, interspecific relationships, settling phenology, species co-occurrence



www.oikosjournal.org

© 2023 The Author. Oikos published by John Wiley & Sons Ltd on behalf of Nordic Society Oikos.

This is an open access article under the terms of the Creative Commons Attribution License, which permits use, distribution and reproduction in any medium, provided the original work is properly cited.

Introduction

Understanding how climate change influences processes structuring ecological communities is a major challenge for ecologists. Without ignoring the importance of large-scale processes and historical events in determining species richness of ecological communities, the negative and positive interactions between species are important biological forces shaping the structure and organization of local communities (Diamond and Case 1986, Ricklefs and Schluter 1993, Tokeshi 1999, Stachowicz 2001, Crowley and Cox 2011). Recent work has found that biotic mechanisms, associated with altered species interactions, are more important drivers of the relationship between populations and climate than abiotic ones, emphasizing the importance of understanding species interactions within ecological communities to predict the impacts of climate change (Ockendon et al. 2014). In animal communities at the same trophic level, heterospecific attraction, in which individuals choose habitat patches by the presence of established individuals of a heterospecific species (Mönkkönen et al. 1990, 1999, Elmberg et al. 1997), is one example of interactions that may involve both positive and negative effects. Attraction to heterospecifics involves heterospecific information use, and it is predicted to be strongest when benefits from aggregating with potential competitors exceed effects of competition (Mönkkönen et al. 1999, Parejo 2016, Parejo and Avilés 2016). In such systems, climate change may induce informational mismatches by altering the phenology, distribution and abundance of some species but not of others, with consequences to interspecific interactions and community organization (Parejo 2016).

In general, similarity between species in the use of space and time (niche overlap) increases the potential for both negative and positive interactions by affecting the frequency and duration of interaction between heterospecific individuals (Seppänen et al. 2007, Parejo and Avilés 2016). The niche concept has been central in ecology for a century in describing species distributional patterns (Soberón 2007, Colwell and Rangell 2009, Wiens et al. 2009), and its importance has even increased as species' climatic niches have been the focus of ecological research owing to ongoing climate change (Wiens et al. 2009, La Sorte and Jetz 2012, Quintero and Wiens 2013, Jezkova and Wiens 2016). Indeed, considerable research has been devoted to finding out how species have responded to latitudinal and altitudinal shifts in temperature regimes, for example by moving their geographic distributions (Parmesan and Yohe 2003, Devictor et al. 2012, La Sorte and Jetz 2012, Comte et al. 2013, Lenoir et al. 2020) in order to track their climatic niches (Tingley et al. 2009, La Sorte and Jetz 2012). For example, wintering distributions of many waterbirds in Europe have changed in response to climate warming (Lehikoinen et al. 2013, Nuijten et al. 2020). Such large-scale impacts on species' distributions may result in changes in interspecific interactions as climate-tracking species colonize new regions and face communities with novel compositions (Gilman et al. 2010, Ockendon et al. 2014, Nagelkerken and Munday 2016, Bell et al. 2021). However,

analyses focusing on changes in species regional distributions and community changes alone cannot reveal changes in species interactions, as these take place between individuals in local communities. This being the case, it is surprising how little attention has been paid to the possibility that climate change may also affect species spatial distributions at local scale, realized via impacts on habitat selection and use. Species may respond differently to climate change-driven alterations in phenology-related characteristics of habitats, resulting in changes in habitat niche overlap (HNO) and co-occurrence.

Indeed, a fundamental and as yet little-explored question is whether climate change has affected species HNOs and associations in established local communities, ultimately affecting interactions and community organization (Parejo 2016). Migratory boreal waterbirds provide a useful focal system for assessing such impacts of climate change. First, the timing of ice-out (ice-out date, IOD) in lakes throughout the Northern Hemisphere has advanced considerably owing to climate warming (Hewitt et al. 2018, Patterson and Swindles 2015, Magee et al. 2016, Sharma et al. 2016, Lopez et al. 2019, Hallerbäck et al. 2022). For example, IOD has advanced about 0.9 day per decade during 1913–2014 in southern Sweden (Hallerbäck et al. 2022) and about 3.3 day per decade during 1991–2020 in south-eastern Finland (Pöysä 2022). The timing of ice-out affects key hydrological and ecological processes in freshwater ecosystems (Weyhenmeyer 2001, Winder and Schindler 2004, Peeters et al. 2007, Thackeray et al. 2013, Preston et al. 2016, Caldwell et al. 2020), extending to impacts on settling phenology and dynamics of migratory waterbirds (Pöysä 2019, 2022). The timing of ice-out and its advancement can vary substantially among lakes, even within the same catchment area (i.e. at the spatial scale relevant to habitat selecting birds), resulting in spatial and temporal variation in habitat availability for settling waterbirds (Pöysä and Paasivaara 2021, Pöysä 2022). Second, while migratory boreal waterbirds, being fully dependent on open water for feeding and other activities such as breeding, generally track year-to-year variation in IOD, species differ in migration and settling schedules (Pöysä 2019). Moreover, some species have shifted their habitat use in response to changes in IOD, while others have not (Pöysä and Paasivaara 2021). In other words, the lake-level presence/absence of some species during the settling period has changed due to changes in IOD, and so the possibility of accessing useful information from heterospecifics (Parejo 2016, below) may have changed differently depending on the timing of migration and settling. Third, the occurrence and mechanisms of interspecific competition in waterbird communities have been studied extensively, and competition has been found to be important in affecting resource use and coexistence in some circumstances (reviewed by Nudds 1992; Pöysä et al. 1994, Nudds et al. 1994, Elmberg et al. 1997, Nummi and Väänänen 2001, Guillemain et al. 2002, Osnas and Ankney 2003). On the other hand, studies done at spatial scales extending from feeding patches to landscape level indicate that positive interspecific interactions may also be widespread in waterbird assemblages (Pöysä 1986, Silverman et al. 2001, Osnas and

Ankney 2003, Sebastián-González et al. 2010, Bidwell et al. 2014). For example, it has been found in dabbling ducks breeding in boreal lakes in Europe that lake occupancy by later arriving teals *Anas crecca* is positively associated with the presence of earlier arriving mallards *A. platyrhynchos*, indicating heterospecific attraction (Elmberg et al. 1997). Support for heterospecific attraction has also been found in a community of seven waterbird species breeding in artificial irrigation ponds in south-eastern Spain, including species pairs such as mallard and little grebe *Tachybaptus ruficollis*, and mallard and common shelduck *Tadorna tadorna* (Sebastián-González et al. 2010). Furthermore, Eurasian wigeon *Mareca penelope* abundance and the overall abundances of three foraging guilds (surface-feeding ducks, diving ducks and piscivorous ducks) have been found to be positively associated with whooper swan *Cygnus cygnus* occurrence at breeding lakes in Finland (Pöysä et al. 2018, Holopainen et al. 2022). Finally, while commensal feeding associations between swans and several duck species (commensals) have been reported from stopover sites during autumn migration (Källander 2005, Gyimesi et al. 2012), whooper swans have also been found to behave aggressively towards smaller waterbirds in wintering areas (Wood et al. 2020).

Similarity between species in the use of habitats, and in the use of space in general, importantly affects the potential for interspecific interactions, and climate change has differently affected habitat use of species in boreal waterbird communities. For these reasons I address the following main questions. 1) Has recent climate change caused changes in the overlap of species' habitat niches? 2) Has recent climate change caused alterations in species' spatial associations (SAs), measured as co-occurrence in individual habitat patches (lakes)? 3) Are possible climate change-caused changes in HNOs and SAs among species associated with the similarity between the species in settling phenology?

Material and methods

Study area and species

The study area in south-eastern Finland (61°35'N, 29°40'E; see Supporting information for map) is about 59 km² and dominated by pine *Pinus sylvestris* or mixed (pine, birch *Betula* spp. and spruce *Picea abies*) forests interspersed with lakes of varying size and luxuriant, emergent vegetation. The 37 study lakes (mean size 3.5 ha, range 0.05–24.0 ha) are covered by ice during winter (approximately from late November to late April), have a relatively stable water level in summer and are only used by waterbirds for breeding. Hence, waterbirds breeding in the study area are migratory, and the habitat selection process is repeated each spring.

Sixteen species were recorded breeding in the study area during the study period (1991–2020) but half of them only occasionally and in small numbers (Supporting information). In this study I focused on eight species: whooper swan, Eurasian wigeon, common teal, mallard, tufted duck *Aythya*

fuligula, common goldeneye *Bucephala clangula*, common goosander *Mergus merganser* and horned grebe *Podiceps auritus*. These eight species have been recorded breeding (at least one pair) in the study area each year in 1991–2020, except for the whooper swan. This was recorded in 1995 for the first time, reflecting the increase in the breeding numbers of the species in northern Europe in recent decades (Pöysä and Sorjonen 2000, Holopainen et al. 2022). Hence, time series length was $n=30$ years in all cases, except that when the whooper swan was involved it was $n=26$ years. The sum of the pair numbers of these eight species together makes 97.6% of the total pair number in the community. Generally, these eight species are also the most abundant species in other European boreal waterbird communities (Supporting information), implying that the community studied here well represents the European boreal areas. Relative settling order of the species at the study lakes (below) corresponds well with differences among the species in the overall timing of spring migration in Finland (Supporting information).

Waterbird and IOD data

Annual (1991–2020) lake-specific waterbird data are from Pöysä and Paasivaara (2021), with two additional years (2019 and 2020) and three additional species (whooper swan, common goldeneye and common goosander) (methodological details in Pöysä 2019, Pöysä and Paasivaara 2021). In brief, a standard waterbird point count (Koskimies and Väisänen 1991, Koskimies and Pöysä 1989) was made on each lake four times in April–May at an interval of approximately seven days (mean survey interval = 7.0 day, SE = 0.1) each year from 1991 to 2020. In the point count, a lake is surveyed for waterbirds from one or more fixed vantage points so that all the shoreline and open water areas are visible and carefully observed. All lakes were monitored within a few days (mean range 2.5 day, SE = 0.1) on each of the four surveys. The first survey in each year coincided with an early stage of ice breakup in the study area (i.e. some lakes had some open water, while other lakes were still fully ice covered), while all the lakes were free of ice during the last (fourth) survey (Supporting information in Pöysä 2019). Waterbird observations from each survey and lake were interpreted as 'pair numbers' using the species-specific criteria of Koskimies and Väisänen (1991); summarized in Supporting information. The annual number of breeding pairs for each species and lake was estimated as the mean of the pair numbers from the survey when the lake was free of ice and the survey before or after the ice-free survey, whichever had a higher pair number. That is, in each year and for each species and lake, data from two consecutive surveys (adjusted to year-specific IOD) were used to estimate the annual number of breeding pairs (breeding population size, BPOP). Relative settling order for each species was calculated as mean of the annual first observations, i.e. on which of the four annual waterbird surveys the species was first observed, possible annual values ranging from 1 to 4.

Annual IOD data are from Pöysä (2022). During each of the four waterbird surveys in April–May, the progress of the

breakup of ice cover on each lake was marked on a field map and later scored as follows (open water score, Pöysä, 1996): 0=lake fully ice-covered; 1)=small openings along shoreline, central parts fully ice-covered; 2)=half of the shoreline open, central parts fully ice-covered; 3)=more than half of the shoreline open, central parts partially (< 50%) open; 4)=shoreline fully open, small scattered ice rafts or build-ups; and 5)=lake fully open. An annual IOD for each lake was estimated as the mean of the dates of two consecutive surveys when the open water scores were 4 and 5; if the lake was already free of ice (score 5) during the first visit, the IOD was estimated as the date of the first survey -3.5 days (i.e. the mean difference in days between two consecutive surveys divided by 2). The annual mean IOD was calculated as the mean of the lake-specific IOD values. In addition to the annual mean IODs, standard deviation around the mean (SDIOD) was calculated for each year to measure the within-season variation in the availability of habitat (Pöysä 2022). While both IOD and SDIOD show a trend across time, they reflect different aspects of climate change impacts on habitat phenology: IOD measures overall timing of habitat availability in the study area each year (i.e. the date when lakes on average were free of ice), whereas SDIOD measures within-season variation in habitat availability as the 37 study lakes differ in annual IODs (Pöysä 2022). Factors affecting variation among the study lakes in mean IOD, and its standard deviation (SDIOD), have been reported in Pöysä (2022). Note that these two phenological habitat availability measures should not be confused with the availability of habitat in the three habitat structure categories explained in the next section.

Habitat structure data

I used the lake-specific habitat structure index in Pöysä (2001) to assign the lakes into three habitat structure categories. The index is based on the abundance of emergent (helophyte) and floating-leaved vegetation and shore water depth (details of vegetation classification and field procedures are described in Nummi and Pöysä 1993, Elmberg et al. 1993). In brief, the structure of emergent vegetation along the shoreline of each lake was described using six variables for the type of the vegetation: 1) forest and bog, 2) *Phragmites* on dry land, 3) *Carex* on dry land, 4) *Phragmites*, 5) *Carex* and 6) *Equisetum/Typha*. Shores belonging to the first three types did not have clear zones of emergent vegetation extending to the water, whereas types 4–6 did. Four variables were used to describe the width: 1) 0–1 m, 2) 1–5 m, 3) 5–10 m, and 4) > 10 m and the height: 1) 0–25 cm, 2) 25–50 cm, 3) 50–100 cm and 4) > 100 cm of the vegetation. Sections of each vegetation type, width and height category were marked on a field map and the percentage of each of the 14 vegetation categories of the shoreline in each lake was later measured from the maps. The cover of floating vegetation was estimated using four classes: 0) 0%, 1) 1–5%, 2) 5–15% and 3) > 15%. Water depth was measured at the distance of 0.5 m from the shoreline, the number of measurement

sites per lake varying from 5 to 10 depending on lake size. The mean of these measurements was used to classify the shore water depth of each lake as one of the three classes: 1) 0–50 cm, 2) 50–100 cm or 3) > 100 cm. I used principal component analysis (PCA) (Pimental 1979) to derive a single gradient of habitat structure along which the lakes were ordered. The PCA was performed upon the correlation matrix among the 16 variables; that is, the percentages of each of the 14 vegetation categories, the cover of floating vegetation (scores 1–4 representing the four cover classes) and shore water depth (scores 1–3 representing the three depth classes). Each of the 37 lakes had one value for each of the 16 variables. The first principal component axis represented a gradient from deep-shore lakes with low and narrow belts of sparse, emergent vegetation and little floating-leaved vegetation (high negative values on 1st PCA axis) to shallow-shore lakes with tall, wide and heterogeneous emergent vegetation and abundant floating-leaved vegetation (high positive values on 1st PCA axis), the mean of the 37 lake-specific values being zero (range from -3.117 to 4.218). Specifically, lakes with a high positive score typically had large stands of common reed, water horsetail *Equisetum fluviatile*, broadleaf cattail *Typha latifolia* or sedges *Carex* spp., whereas lakes with a strongly negative score were characterized by shores with barren moraine and forest or narrow belts of poor bog or open fen. Finally, based on the lake-specific values on the 1st PCA axis, I divided the first component into three sections of equal length to get three habitat categories that were used to calculate niche metrics. Habitat category I included lakes from the positive end of the 1st PCA axis ($n=8$, 1st PCA values from 1.773 to 4.218), category II included lakes from the middle ($n=10$, 1st PCA values from -0.672 to 1.773) and category III included lakes from the negative end of the 1st PCA ($n=19$, 1st PCA values from -3.117 to -0.672). Accordingly, the amount and development of the shore vegetation decreased, and shore depth increased from habitat category I to III (see Supporting information for examples of lakes in each category). Because the same 37 lakes, assigned to the three habitat categories, constituted the database for all study years, availability in each habitat category remained constant across time, and was measured as the sum of the sizes of lakes in each category divided by the total sum of sizes of all lakes. This habitat classification has been used successfully in studies addressing dynamics of habitat distribution of breeding waterbirds in another study area in southern Finland (Nummi and Pöysä 1993, Suhonen et al. 2011). The amount and development of the shore vegetation, as described by the 1st PCA axis, is a biologically relevant habitat characteristic from the viewpoint of waterbirds breeding in boreal lakes (Pöysä and Paasivaara 2021). Moreover, when studying changes in vegetation structure and habitat classification of 52 lakes in southern Finland between 1989 and 2009, Suhonen et al. (2011) found that, while the score value of some the lakes on the 1st PCA axis changed from 1989 to 2009, the classification of the lakes did not change with respect to the three habitat categories (i.e. a given lake belonged to the same habitat category in 1989 and in 2009).

Niche metrics and statistical analyses

The annual HNO between two species was calculated as proportional similarity in the use of the three habitat structure categories (Colwell and Futuyma 1971):

$$HNO = 1 - 0.5 \times \sum_i |p_i - q_i| = \sum_i \min(p_i, q_i),$$

where p_i is the proportion of habitat category i out of all habitat categories used by the breeding pairs of a species p in a given year and q_i is the corresponding proportion for species q . HNO takes its maximum value of 1.0 when the proportional distributions of the species p and q among the habitat categories are the same, and its minimum value of 0 when the two species share no habitat categories (Colwell and Futuyma 1970). Annual habitat niche breadth (HNB) for each species was measured as the similarity between the frequency distribution of the three habitat categories used by breeding pairs of the species in a given year and the frequency distribution of the three habitat categories available (see Habitat structure data for calculating the availability of habitat in the three categories), using the same equation as for HNO (Feinsinger et al. 1981). In the case of HNB, p_i is the proportion of habitat category i out of all habitat categories used by the breeding pairs of a species, and q_i is the proportion of i habitat category among the three habitat categories available. Values for HNB range from 1.0 for the broadest possible habitat niche (a species uses habitat categories in proportion to their availability) to $[\min q_i]$ for the narrowest possible habitat niche (a species is specialized exclusively on the rarest habitat category) (Feinsinger et al. 1981).

HNO between two species does not measure actual spatial co-occurrence of the species, because individuals of two species having a high HNO may breed on different lakes that belong to the same habitat category. Therefore, I also measured annual SA between two species, based on the occurrence patterns of the species in a given year in a two-by-two contingency table setting (a = number of lakes with both species [p and q] present, b = number of lakes with species p present and species q absent, c = number of lakes with species p absent and species q present, d = number of lakes with both species absent), also known as Cramer's phi (Zar 1996):

$$SA = \frac{ad - bc}{\sqrt{(a+b)(a+c)(b+d)(c+d)}}$$

Values of SA range from 1 (complete positive association between the two species) to -1 (complete negative association between the two species).

The idea of this study was to analyse impacts of climate-driven changes in IOD and SDIOD on changes in HNOs and SAs. Preliminary analyses based on zero-order bivariate correlations suggested relatively strong relationships between HNO and SA and the climatic variables IOD and SDIOD in several species pairs (Supporting information). However, because the study was based on time series data, directional

change across time (trend) in both the response variable and the explanatory variables may cause spurious correlations (Lindström and Forchhammer 2010). Indeed, both HNO and SA showed a trend during 1991–2020 in several species pairs (Supporting information), a corresponding trend being documented for IOD and SDIOD in an earlier study (Pöysä 2022). The common trend can be controlled for by including 'year' as an additional explanatory variable in the model (Freckleton 2002, Iler et al. 2017). Similarly, because habitat distribution of breeding individuals is typically density dependent, affecting HNB of species (Fretwell and Lucas 1969, O'Connor 1985), the BPOPs and HNBs of species 1 and 2 potentially affect the level of HNO between the species (increasing species-specific HNBs can lead to higher HNO) and the level of SA between the species (increasing species-specific BPOPs can lead to higher SA). Hence, to control for the potentially confounding effect of these variables on the relationships in focus, for HNOs I fitted general linear models in which Year, HNB of species 1 and HNB of species 2 were included as additional explanatory variables; and for SA I fitted general linear models in which Year, BPOP of species 1 and BPOP of species 2 were included as additional explanatory variables. All models were fitted using non-transformed original data to facilitate the comparison of effect sizes across models (below). I checked the assumption of normality of residuals in the general linear models with plots of residuals versus predicted values (Zuur et al. 2010); serious violations indicating heteroscedasticity were not observed. I used Cook's d (Cook 1977) to identify influential observations, and one apparently influential observation (Cook's $d > 1$) was found in six models (out of 56 models in all): Ccy-Mpe: HNO (Cook's $d = 1.333$); Ccy-Mme: HNO (1.730); Ccy-Pau: HNO (1.329); Mpe-Mme: HNO (2.180); Apl-Afu: HNO (1.123); and Mme-Pau: HNO (1.003). I checked the influence of these observations on the results by comparing outputs from models with and without the observation in question. It turned out that differences between the model outputs mainly concerned the additional explanatory variables Year, HNBs and BPOPs, while the climate-related phenological variables in focus (IOD and SDIOD) were less affected (Supporting information). Most important, the six influential observations were from four different years (1995, 1 case; 2000, 2 cases; 2007, 2 cases; and 2016, 1 case), meaning that there was not an exceptional year in the time-series data of the climate-related explanatory variables (the full time series of IOD and SDIOD are shown in Pöysä 2022: Fig. 1, 2, respectively). Therefore, because the six observations are genuine observations in the ecological time-series data, I decided not to remove them for the final analyses (Zuur et al. 2010); the cases in which the influential observations may have affected results are considered in the Results section. I checked for multicollinearity for all models using tolerance values of the general linear model outputs. A tolerance value ≥ 0.334 is the equivalent of a variance inflation factor (VIF) < 3 (VIF = $1/\text{tolerance}$) which is a generally used criterion for acceptable multicollinearity (Zuur et al. 2010). Multicollinearity turned out to be negligible, except in a

few cases, mainly attributable to the variable Year (note that all VIFs for the explanatory variables in focus were < 2.61 (tolerance ≥ 0.385); Supporting information). Removing Year from the model in those cases removed multicollinearity (VIFs < 3 for all the remaining variables in the re-run models), except in one case: Ccy-Afu: SA; when the variable with the second lowest tolerance (BPOP1) was also excluded from the model for Ccy-Afu: SA, all the remaining variables had $VIF < 3$. Because the exclusion of Year (and BPOP1 in the case Ccy-Afu: SA) had only negligible effect on the main results (i.e. effect sizes of IOD and SDIOD; effect sizes explained below), and because it is important to keep the set of explanatory variables identical in models when comparing effect sizes (Nakagawa and Cuthill 2007, Aloe and Thompson 2013, Aloe 2014), I used for interpretation in all cases the models in which also Year and BPOP1, as appropriate, were included.

I used the t tests of the regression coefficients of the explanatory variables in the general linear models to calculate partial correlations (partial effect sizes) and the associated 95% confidence intervals for each explanatory variable according to the procedure described in Alone and Thompson (2013: Eq. 2, 3). The partial correlation provides a scale-free index of the magnitude and direction of the relationship between variables of interest, and it has been used as an index to assess the importance of explanatory variables (Murray and Conner 2009) and as an effect size statistic in meta-analyses (Nakagawa and Cuthill 2007, Schielzeth 2010, Aloe and Thompson 2013, Alone 2014); hereafter, the term ‘effect size’ is used to indicate ‘partial effect size’.

I used the effect sizes of IOD and SDIOD from the general linear models in additional analyses to study if the magnitude and direction of the impact of IOD and SDIOD on the among-year variation in HNOs and SAs was related to differences between the species in settling phenology. This was done at species pair level and at species level, using Pearson correlation. In the species pair-level analysis, the seven different species pairs for each of the eight focal species constituted the sample units in the analyses ($n=7$ species pairs in all cases). The analysis was run separately for each focal species, and separately for the effects of IOD and SDIOD on HNO and SA, and for both raw effect sizes and absolute ($|r|$) effect sizes. Difference in the relative settling order between the species in each pair ($|$ relative settling order of species 1 minus relative settling order of species 2 $|$) was used in these analyses. Because the number of correlation tests in the species pair-level analysis was high (64 correlations) and, hence, the risk of committing type I error was high, I calculated also p -values adjusted for multiple testing using two procedures: the Bonferroni correction (aimed to control the risk of rejecting a null hypothesis when it is true; ‘one-step Bonferroni’ in García 2004) and Benjamini and Hochberg’s (1995) control of false discovery rate (FDR, aimed to control the proportion of false positives among the rejected null hypotheses; ‘step-up FDR’ in García 2004, where differences between the methods are also discussed). The one-step Bonferroni corrected critical p -value is derived by dividing the original pre-defined

critical p -value (e.g. $p=0.05$) with the number of tests (k); i.e. p/k . In the step-up FDR procedure, the n p -values are first ranked from smallest to largest, the smallest p -value having a rank of $i=1$, the second smallest a rank of $i=2, \dots$, and the largest a rank of $i=k$. Each of the original $p_{(i)}$ is compared sequentially with $i/k \times 0.05$, starting with $p_{(k)}$. The largest original p -value that has $p < i/k \times 0.05$ is significant, and all the p -values smaller than it are also significant. The adjusted p -values will be given in the results for correlations deemed to be significant at $p=0.05$. In the species-level analysis, means of the corresponding effect sizes and absolute effect sizes were calculated for each species using the seven species pair-specific values, and the means were used as the sample units in the analyses ($n=8$ species in all cases). The means were correlated with the relative settling order of the species.

All models and statistical tests were run in SYSTAT 13.

Results

The abbreviations of species names and response and explanatory variables used in the text, tables and figures are listed in Table 1.

HNOs and SAs

HNOs and SAs varied considerably across years in individual species pairs, the three most varying (in terms of range) HNOs being found in Ccy-Afu (range 0.000–1), Afu-Mme (range 0.000–0.977) and Ccy-Mme (range 0.000–0.889), while the three most varying SAs were found in Ccy-Pau (range -0.121 – 0.753), Mpe-Afu (range -0.219 – 0.614) and Ccy-Afu (range -0.131 – 0.687) (Table 2). On the other hand, HNO was relatively high and varied little across years in some species pairs such as Apl-Bcl (mean 0.890, range 0.710–0.989), Mpe-Apl (mean 0.840, range 0.610–0.995) and Mpe-Bcl (mean 0.830, range 0.612–0.961), while some species pairs showed both relatively high and little varying

Table 1. Abbreviations of species names and variables used in the analyses.

Species	Abbreviation
Whooper swan <i>Cygnus cygnus</i>	Ccy
Eurasian wigeon <i>Mareca penelope</i>	Mpe
Common teal <i>Anas crecca</i>	Acr
Mallard <i>Anas platyrhynchos</i>	Apl
Tufted duck <i>Aythya fuligula</i>	Afu
Common goldeneye <i>Bucephala clangula</i>	Bcl
Common goosander <i>Mergus merganser</i>	Mme
Horned grebe <i>Podiceps auritus</i>	Pau
Response variables	
Habitat niche overlap	HNO
Spatial association	SA
Explanatory variables	
Ice-out date	IOD
Standard deviation of ice-out date	SDIOD
Breeding population size	BPOP
Habitat niche breadth	HNB

Table 2. Habitat niche overlaps (HNOs; above the diagonal) and spatial associations (SA; below the diagonal) for individual species pairs (mean, SD and range for 1991–2020). Possible values of HNO vary from 0 (the two species share none of the three habitat categories) to 1.0 (the proportional distributions of the two species among the three habitat categories are the same), and those of SA vary from -1 (complete negative association between the two species) to 1 (complete positive association between the two species). Numbers within the brackets in the above diagonal part indicate species pair codes used in Fig. 1. See Table 1 for species' abbreviations.

	Ccy	Mpe	Acr	Apl	Afu	Bcl	Mme	Pau
Ccy	Mean	0.647 (1)	0.568 (2)	0.603 (3)	0.543 (4)	0.633 (5)	0.475 (6)	0.542 (7)
	SD	0.182	0.212	0.167	0.273	0.121	0.227	0.180
	Range	0.333–1	0.211–0.980	0.281–0.971	0.000–1	0.426–0.885	0.000–0.889	0.200–0.805
Mpe	Mean	0.332	0.799 (8)	0.840 (9)	0.662 (10)	0.830 (11)	0.720 (12)	0.746 (13)
	SD	0.166	0.112	0.081	0.169	0.090	0.152	0.147
	Range	-0.088–0.687	0.513–0.945	0.610–0.995	0.091–0.872	0.612–0.961	0.250–0.960	0.348–0.950
Acr	Mean	0.176	0.227	0.803 (14)	0.684 (15)	0.829 (16)	0.714 (17)	0.748 (18)
	SD	0.161	0.170	0.098	0.193	0.099	0.135	0.121
	Range	-0.223–0.429	-0.063–0.529	0.587–0.962	0.262–0.971	0.588–0.967	0.467–0.944	0.514–0.988
Apl	Mean	0.251	0.310	0.264	0.645 (19)	0.890 (20)	0.724 (21)	0.801 (22)
	SD	0.105	0.161	0.164	0.168	0.067	0.124	0.113
	Range	0.023–0.438	0.014–0.596	-0.071–0.623	0.156–0.838	0.710–0.989	0.389–0.951	0.459–0.979
Afu	Mean	0.222	0.244	0.176	0.221	0.678 (23)	0.601 (24)	0.605 (25)
	SD	0.243	0.196	0.191	0.139	0.194	0.266	0.226
	Range	-0.131–0.687	-0.219–0.614	-0.289–0.479	-0.154–0.441	0.260–0.938	0.000–0.977	0.111–0.939
Bcl	Mean	0.256	0.244	0.184	0.279	0.188	0.737 (26)	0.811 (27)
	SD	0.094	0.114	0.154	0.145	0.117	0.137	0.116
	Range	0.108–0.484	0.041–0.481	-0.122–0.430	-0.009–0.572	-0.047–0.404	0.395–0.951	0.470–0.988
Mme	Mean	0.217	0.242	0.136	0.096	0.202	0.682 (28)	0.682 (28)
	SD	0.191	0.169	0.150	0.223	0.150	0.144	0.144
	Range	-0.103–0.687	-0.197–0.618	-0.307–0.406	-0.128–0.469	-0.183–0.561	0.182–0.903	0.182–0.903
Pau	Mean	0.147	0.079	0.004	0.090	0.250	0.121	0.121
	SD	0.241	0.151	0.208	0.235	0.094	0.168	0.168
	Range	-0.121–0.753	-0.226–0.329	-0.340–0.453	-0.226–0.453	0.075–0.385	-0.194–0.439	-0.194–0.439

positive SA: Mpe-Apl (mean 0.310, range 0.014–0.596), Bcl-Pau (mean 0.250, range 0.075–0.385) and Mpe-Bcl (mean 0.244, range 0.041–0.481).

Impacts of climate-related variables on HNOs and SAs

The magnitude and direction of the effects of IOD and SDIOD on HNO and SA varied among the 28 species pairs, only eight of the 112 effect sizes differing from zero (i.e. the 95% confidence interval did not include zero), in some of them only marginally so (Fig. 1, Supporting information). Considering these eight species pairs, in Ccy-Acr, HNO between the species increased with earlier IOD (effect size -0.454) while the opposite was true in Mpe-Mme (effect size 0.355). In Mpe-Apl (effect size 0.380), Acr-Bcl (effect size 0.428) and Afu-Bcl (effect size 0.385), HNO between the species increased with increasing SDIOD; that is, with increasing within-season variation between the lakes in IOD. In Mpe-Afu (effect size -0.449) SA between the species increased with earlier IOD, whereas in Acr-Apl (effect size 0.352) and Apl-Mme (effect size 0.364), SA decreased with earlier IOD.

Considering effect sizes from the six models in which suspected influential observations were found (Material and methods, Supporting information), only one of the eight

species-pair cases considered above belonged to the suspected cases: Mpe-Mme: HNO. In this case, the effect size of IOD on HNO did not differ from zero when the model was re-run without the influential observation (Supporting information). On the other hand, there were two other cases in which the effect size of SDIOD on HNO differed from zero in the model from which the influential observation was removed, but not in the model in which it was included: Ccy-Mpe (without the suspected observation, effect size 0.395 versus with the suspected observation, effect size 0.297) and Apl-Afu (without the suspected observation, effect size 0.484 versus with the suspected observation, effect size 0.345) (Supporting information). Nevertheless, because there is no biological justification to remove observations from the time series data (Material and methods), the results and conclusions are based on the effect sizes from the models in which all the observations were included.

Overall, the effects of IOD and SDIOD on the among-year variation in HNOs and SAs were small. In the case of HNO, the mean absolute effect size (i.e. direction of the effect ignored) of IOD (0.167) and SDIOD (0.195) was smaller than that of Year (0.222) and the HNBs of the constituting species (0.477 and 0.516), whereas in the case of SA the mean absolute effect size of all the explanatory variables was of about the same magnitude (all means ≤ 0.217 , Table 3).

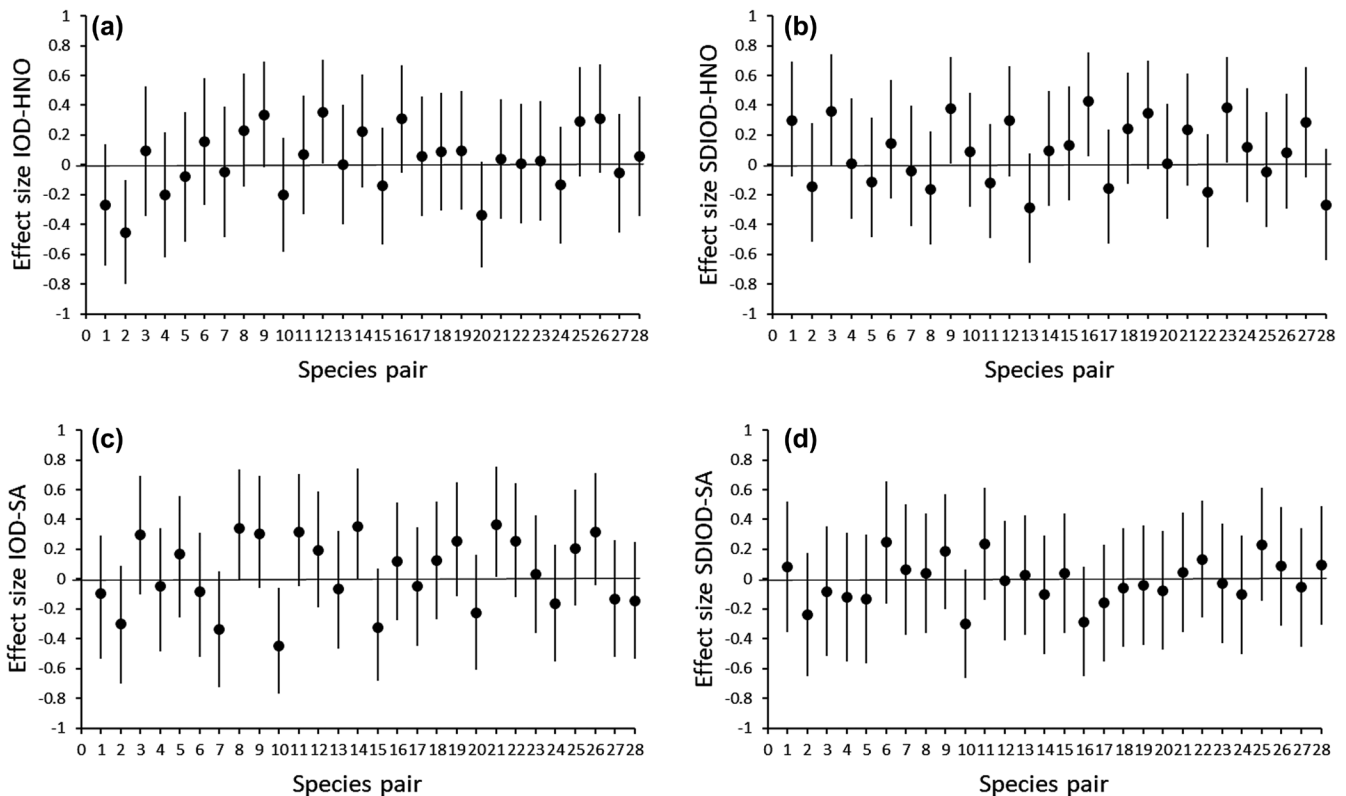


Figure 1. Effect sizes ($r \pm 95\%$ confidence intervals) of ice-out date (IOD) on habitat niche overlap (HNO) (a), standard deviation of IOD (SDIOD) on HNO (b), IOD on spatial association (SA) (c) and SDIOD on SA (d) in 28 different species pairs (see Table 2 for the species pairs associated with the numerical codes). Horizontal lines crossing the y axes at 0 give the reference for the 95% confidence intervals, i.e. whether the effect size differs from zero. The effect sizes are partial effect sizes (partial correlations) from general linear models, in which the effect of additional explanatory variables was controlled for (see Supporting information for all effect sizes and additional test statistics).

Table 3. Summary of the effect sizes of explanatory variables from general linear models to explain among-year variation in habitat niche overlap (HNO) and spatial association (SA) in 28 species pairs. Note that the order of species 1 and 2 within the pairs is arbitrary. See Supporting information for detailed statistics. BPOP, breeding population size; HNB, habitat niche breadth; IOD, ice-out date; SDIOD, standard deviation of IOD.

Response variable in the model	Explanatory variable	Effect size (n=28)			Absolute effect size (n=28)		
		Mean	SD	Range	Mean	SD	Range
HNO	IOD	0.029	0.209	-0.454–0.355	0.167	0.125	0.001–0.454
	SDIOD	0.086	0.216	-0.288–0.428	0.195	0.122	0.007–0.428
	Year	-0.013	0.266	-0.565–0.484	0.222	0.140	0.007–0.565
	HNB1	0.460	0.299	-0.121–0.949	0.477	0.269	0.015–0.949
	HNB2	0.476	0.331	-0.330–0.924	0.516	0.261	0.021–0.924
SA	IOD	0.044	0.246	-0.449–0.364	0.217	0.166	0.036–0.449
	SDIOD	-0.010	0.147	-0.299–0.247	0.118	0.085	0.012–0.299
	Year	-0.076	0.179	-0.402–0.294	0.148	0.124	0.009–0.402
	BPOP1	0.129	0.221	-0.268–0.620	0.201	0.156	0.003–0.620
	BPOP2	0.014	0.236	-0.678–0.393	0.175	0.155	0.007–0.678

Impacts of climate-related variables and species settling phenology

Each of the eight species occurred in seven different species pairs, and the species in those pairs differed to a varying degree from each other in terms of settling phenology (Supporting information). The difference in settling phenology between the two species in a pair was generally not strongly associated with the variation in the strength and direction of the effects of IOD and SDIOD on HNO and SA between the two species, nor with the variation in the magnitude of the absolute effect size (Table 4). Even though the association was statistically significant only in three out of 64 cases (none of the correlations being significant after adjusting the p-values for multiple testing; Table 4), negative correlations (ignoring statistical significance) seemed to prevail (23 negative versus 9 positive correlations for both effect size and absolute

effect size), suggesting that the effect of IOD and SDIOD on HNO and SA in the species pairs tended to be stronger the more similar the species were in settling phenology. Similarly, when the species-specific means of the effect sizes and absolute effect sizes were related to the settling order of the species (i.e. a species-level analysis), no strong relationships emerged (Fig. 2); still, the correlation was negative in seven out of eight cases (Fig. 2), suggesting that the effect of IOD and SDIOD on HNO and SA tended to be stronger for early settling species than for late settling species, although none of the individual correlations was statistically significant.

Discussion

Global climate warming has advanced the timing of ice-out in lakes across the Northern Hemisphere. This, in turn, has

Table 4. Pearson correlations between the between-species difference in settling phenology and the effect size of ice-out date (IOD) and standard deviation of IOD (SDIOD) on habitat niche overlap (HNO) and spatial association (SA) in the same species pairs. Correlations are calculated separately for each focal species, each species occurring in seven different species pairs. Correlations deemed significant at the original $p < 0.05$ ($n=7$ in all cases) level are in bold; however, none of the correlations is significant after adjusting the p-values for multiple testing. One-step Bonferroni correction, critical $p=0.00078$ (instead of 0.05) in all cases; step-up FDR, critical p-values (instead of 0.05) for the three originally significant correlations are: $p=0.00078$ for $p=0.014$; $p=0.00156$ for $p=0.032$; $p=0.00234$ for $p=0.035$. See Material and methods for further explanation of the adjusted p-values, and Table 1 for species' abbreviations.

Focal species		Effect size				Absolute effect size			
		IOD:HNO	SDIOD:HNO	IOD:SA	SDIOD:SA	IOD:HNO	SDIOD:HNO	IOD:SA	SDIOD:SA
Ccy	r	-0.124	-0.146	-0.261	-0.046	-0.231	-0.587	-0.211	-0.516
	p	0.791	0.755	0.572	0.923	0.618	0.166	0.649	0.236
Mpe	r	-0.437	-0.071	-0.715	-0.686	-0.224	-0.532	-0.605	0.788
	p	0.327	0.881	0.071	0.089	0.630	0.219	0.150	0.035
Acr	r	-0.090	0.313	-0.262	0.719	-0.458	-0.103	0.183	-0.688
	p	0.847	0.494	0.570	0.068	0.302	0.825	0.694	0.088
Apl	r	0.210	-0.013	0.216	0.342	-0.396	0.410	-0.427	0.014
	p	0.652	0.978	0.641	0.452	0.379	0.361	0.340	0.976
Afu	r	-0.498	0.694	-0.079	-0.411	-0.855	0.559	-0.312	-0.798
	p	0.256	0.084	0.866	0.359	0.014	0.192	0.495	0.032
Bcl	r	-0.040	0.495	-0.190	0.195	-0.753	0.569	-0.590	-0.470
	p	0.932	0.259	0.683	0.675	0.051	0.182	0.163	0.287
Mme	r	-0.551	-0.182	-0.527	-0.292	-0.103	0.114	-0.081	-0.267
	p	0.200	0.697	0.224	0.525	0.827	0.808	0.863	0.563
Pau	r	-0.687	0.344	-0.225	-0.499	-0.607	0.303	0.237	-0.415
	p	0.088	0.450	0.628	0.254	0.149	0.509	0.608	0.354

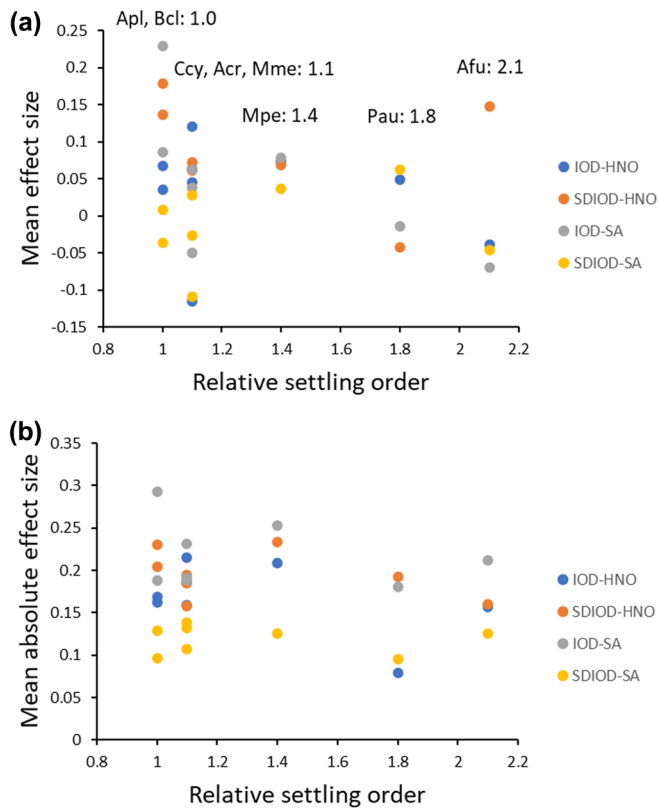


Figure 2. Species-specific mean effect size (a) and mean absolute effect size (b) of ice-out date (IOD) and standard deviation of IOD (SDIOD) on habitat niche overlap (HNO) and spatial association (SA) in relation to species relative settling order. Mean effect sizes and mean absolute effect sizes were calculated for each species using the seven species pairs in which the species was a member, and this was done for each of the four effect size types (effect of IOD on HNO, effect of SDIOD on HNO, effect of IOD on SA, effect of SDIOD on SA) for both effect size and absolute effect size. Species' relative settling orders are given in the upper part of panel (a), corresponding to the position of the data points on the x-axis (note overlapping data points for Apl and Bcl and for Ccy, Acr and Mme, see Table 1 for species' abbreviations). Pearson correlation coefficients: mean effect size IOD-HNO versus settling order, $r = -0.212$, mean effect size SDIOD-HNO versus settling order, $r = -0.235$, mean effect size IOD-SA versus settling order, $r = -0.615$, mean effect size SDIOD-SA versus settling order, $r = 0.187$, mean absolute effect size IOD-HNO versus settling order, $r = -0.483$, mean absolute effect size SDIOD-HNO versus settling order, $r = -0.359$, mean absolute effect size IOD-SA versus settling order, $r = -0.213$, mean absolute effect size SDIOD-SA versus settling order, $r = -0.121$ ($n = 8$ and $p > 0.05$ in all cases).

affected the temporal and spatial dynamics of habitat availability for migratory waterbirds during the settling phase (Pöysä 2022), with potential impacts on niche relationships and co-occurrence of species in local communities. This study revealed that HNO and SA in species pairs of migratory waterbirds varied considerably during the 1991–2020 study period. However, the effects of the overall timing of IOD in the study lakes and its within-season variation (SDIOD) on the dynamics of HNOs and SAs were generally

small. The study also revealed considerable variation among the species pairs in the direction and magnitude of the effect of IOD and SDIOD on HNO and SA. This variation was not strongly related to differences between the species in relative settling phenology. Nevertheless, overall differences among the species pairs and species in the direction and magnitude of the effect sizes suggested that the impact of IOD and SDIOD on HNO and SA was stronger in species pairs in which the species differed less in terms of settling phenology, and stronger for early settling species than for late settling species.

While earlier ice-out in lakes is a well-documented phenomenon caused by climate change in the Northern Hemisphere (Hewitt et al. 2018, Patterson and Swindles 2015, Magee et al. 2016, Sharma et al. 2016, Lopez et al. 2019, Hallerbäck et al. 2022), the rate of the advancement of IOD in this study area during the last three decades has been one of the fastest reported so far (Pöysä 2022). In addition, some of the waterbird species have responded to this change by shifting their local habitat distribution (Pöysä and Paasivaara 2021). Against this background, the generally low effect sizes of IOD and SDIOD may be considered surprising, suggesting a weak role for climate-driven shifts in habitat phenology in affecting changes in HNO and SA between the species in the community. However, effect sizes judged small in a statistical sense may be biologically important (Garamszegi 2006, Garamszegi et al. 2012). Furthermore, because both positive and negative interactions may occur in waterbird assemblages (Introduction), it is possible that weak impacts of IOD and SDIOD reflect a balance in the response of the species in terms of changes in HNO and SA (Parejo 2016, Parejo and Avilés 2016). Also, species pairs may differ in the prevalence of positive versus negative interactions, possibly explaining why the direction of the impacts of IOD and SDIOD on HNO and SA varied among the species pairs.

In eight species pairs the effect of IOD or SDIOD on HNO or SA was relatively strong (range of absolute effect sizes 0.352–0.454) compared to standards suggested by Cohen (1988) for low ($r = 0.10$), medium ($r = 0.30$) and large ($r = 0.50$) effect sizes, although partial effect sizes (this study) and effect sizes based on bivariate correlations are not directly comparable (Aloe 2014). The effect sizes in the eight species pairs are also clearly higher than the mean effect size calculated by Møller and Jennions (2002) for ecological and evolutionary studies in general (absolute mean $r = 0.190$). Moreover, considering that the effect of several confounding variables – including intraspecific drivers such as population density and HNB – was controlled for in the analyses, the effect sizes reported for IOD and SDIOD can be considered genuine (but note that in one of the eight species pairs (Mpe-Mme) the effect size of IOD on HNO may be considered uncertain due to an influential observation). It should be emphasized, however, that the variation in HNO and SA does not necessarily mean that the interaction between the species in these species pairs has changed. This is because similarity in resource use (reflected by HNO) as such may not tell about the strength of the interaction (see Wiens 1977,

Schoener 1983, Abrams 1998 for interspecific competition), nor may pure presence–absence data (the basis for SA) be sufficient to reveal ecological interactions (Blanchet et al. 2020). Nevertheless, climate-driven changes or trends in resource use overlaps and SAs can provide critical information on potential changes in interspecific relationships and interaction networks, particularly if we have prior knowledge of how the species interact (Keil et al. 2021). Indeed, this study focused on climate-driven long-term changes in HNOs and SAs in individual species pairs, and we have a reasonably good knowledge of species interrelationships in various waterbird assemblages. It has been demonstrated with field experiments that food can be a limiting factor for breeding ducks in typical boreal lakes (Sjöberg et al. 2000, Gunnarsson et al. 2004), also affecting habitat selection of breeding pairs (Pöysä et al. 2000). Hence, interspecific competition for food as a driver of habitat distribution of breeding pairs is at least possible in this study system. Considering positive interspecific interactions, a decrease in HNO and SA means fewer possibilities for heterospecific information use, possibly inducing an informational mismatch (sensu Parejo 2016), whereas an increase in HNO and SA would mean the opposite. Indeed, heterospecific attraction has been documented in waterbird assemblages (Elmberg et al. 1997, Sebastián-González et al. 2010), implying that heterospecific information use is at least possible in this study system. At any rate, the relatively strong effect sizes of IOD and SDIOD on HNO and SA in the eight species pairs suggest that the ecological conditions that mediate the patterns in HNO and SA have altered owing to climate change. Further research is needed to clarify how these changes relate to possible changes in interspecific interactions, and if individuals are balancing between negative and positive interactions in their responses to climate-induced changes in habitat phenology.

The direction and magnitude of the impacts of IOD and SDIOD on HNOs and SAs were generally not related to the similarity between the species in settling phenology, although some suggestive trends emerged. Hence, factors other than the difference in settling phenology are also mediating the impacts of climate change on changes in HNO and SA between the species. Negative interspecific interactions among waterbirds typically are attributed to competition for food resources (Nudds and Bowlby 1984, Pöysä et al. 1994, Nummi and Väänänen 2001, Gurd 2008), whereas positive interactions generally are thought to enhance foraging efficiency or reduce predation risk (Mönkkönen et al. 1990, 1999, Parejo et al. 2005, see Elmberg et al. 1997, Sebastián-González et al. 2010 for waterbirds). It is possible that climate-driven changes in HNOs and SAs depend on how similar the species are in terms of feeding and nesting ecology. Considering the eight species pairs with the strongest effect sizes of IOD and SDIOD, in three species pairs the species belong to the same feeding guild (in Mpe-Apl and Acr-Apl the species are surface-feeding dabbling ducks, and in Afu-Bcl the species are benthic-feeding diving ducks; Pöysä 1983) while in two pairs the species belong to the same nest-site guild (Mpe-Apl and Acr-Apl; all these three species

are ground-nesting, the nest being typically located in shore meadows, fields or forests; Väänänen et al. 2016, Pöysä et al. 2019a). It is worth noting that Mpe, Acr and Apl are similar in terms of both feeding ecology and nest location. On the other hand, the species in the other four pairs with high effect sizes (Ccy-Acr, Mpe-Mme, Acr-Bcl and Apl-Mme) differ in terms of both feeding ecology and nest location. Finally, the horned grebe (Pau) was the only species that was not a member of any of the eight species pairs that showed relatively strong impacts of IOD or SDIOD on HNO or SA. While the horned grebe is the second-latest settler in this community, and late-settling species seem to be relatively little affected by IOD and SDIOD in their relationships with other species, it also differs from the other species in terms of feeding ecology, being the only insectivorous pursuit feeder (Cramp and Simmons 1977).

There are also other global or smaller-scale drivers than climate change that have affected boreal lake ecosystems, potentially masking impacts of climate-induced changes in habitat phenology on habitat selection of waterbirds and, hence, changes in HNOs and SAs in local communities. For example, eutrophication and brownification are processes that affect water quality and functioning of aquatic food webs (Creed et al. 2018, Kritzberg et al. 2020, Woolway et al. 2020, Shuvo et al. 2021), and their impacts on waterbird habitat use have been discussed in Pöysä and Paasivaara (2021). Particularly alarming is the finding that the abundance of aquatic invertebrates that are a critical resource for breeding ducks and ducklings has decreased, probably due to lake water brownification (Arzel et al. 2020). Because lakes even within the same catchment area may differ in vulnerability to eutrophication and brownification (Arvola et al. 2010, Heino et al. 2021, Pöysä 2022), causing differences between lakes in how much their quality as waterbird breeding habitat has deteriorated, these processes may have affected habitat distribution of waterbirds in local communities (Pöysä and Paasivaara 2021). Still another change in the ecological conditions of boreal lakes as breeding habitat for waterbirds is the increase of two alien predators, the American mink *Neovison vison* and the raccoon dog *Nyctereutes procyonoides*. They are important predators of waterbird nests, but it is unclear if their increase has affected habitat distribution of breeding birds in local communities, although generally nest predation risk has probably increased more at wetlands and lakes in agricultural areas than at lakes in forested areas (Holopainen et al. 2020, 2021, Pöysä and Linkola 2021).

On a more general level, this study addressed recent calls by Wisz et al. (2013) and others for studies that are based on data gathered at fine spatial and temporal resolutions to give insight into how the nature of local biotic interactions has changed and, ultimately, how such changes affect broad-scale distributions of species. While this study does not specifically demonstrate ‘how’ local biotic interactions have changed, it takes the first step to answer the question by providing a detailed analysis of how climate-induced changes in habitat phenology have affected interspecific relationships in habitat use and SAs in boreal waterbird communities. The temporal

scale of this study can be considered exceptionally long for studies addressing ecological niche dynamics in local communities. Moreover, as the focus here was in the dynamics of HNOs and SAs among co-existing species, the spatial scale arguably is fine-grained, being the scale at which habitat selection and interactions between individuals typically take place. On the other hand, replication of such long-term and fine-grained data on niche dynamics geographically in one study is an insurmountable challenge. Therefore, it is highly recommended that corresponding data on waterbird and other communities are gathered in other parts of the Northern Hemisphere to confirm the findings of this study and to address the additional questions raised here. This is particularly important for waterbird communities in European boreal areas, because several waterbird species breeding in these areas are declining, including the Eurasian wigeon, common teal, tufted duck and horned grebe studied here (Pöysä et al. 2013, Lehikoinen et al. 2016, Elmberg et al. 2020, Pöysä and Linkola 2021, Piha et al. 2022). We do not know, however, if habitat niches or other ecological niches of the species have changed, if the role of interspecific interactions in affecting niche relationships in local communities has changed, and what is the role of climate change-driven impacts and of other anthropogenic environmental stressors in these changes. Ultimately, we need more information to understand how these changes are related to biodiversity change in boreal waterbird communities (Pöysä et al. 2019b, Pöysä and Linkola 2021) and beyond. So far, climate change-related questions addressing interspecific relationships among native non-invasive species have been neglected when considering factors critical to the conservation of European waterbird populations and communities (Guillemain et al. 2013) and boreal freshwater biodiversity in general (Heino et al. 2009, Reid et al. 2019, Yeung et al. 2019, Lind et al. 2022). In the light of the findings of this study, impacts of climate change on interspecific interactions in local communities deserve more attention to enhance our understanding of mechanisms of population declines and biodiversity change.

Conclusions

This study revealed considerable variation among species pairs in the direction and magnitude of the impacts of IOD and SDIOD on HNO and SA. While the impacts of the climate change-related variables on HNO and SA were generally weak, some species pairs showed relatively strong responses and some preliminary patterns emerged, offering avenues for further research. In particular, the role of differences between species in settling phenology, and possible changes in species relative settling order, in affecting the vulnerability of species to impacts of climate-driven changes in interactions should be studied more. The role of similarity between species in feeding and nesting ecology – and other ecological traits – in affecting the vulnerability to such impacts also deserves further research. Given that earlier studies have demonstrated heterospecific attraction in some species pairs, while

the current results indicate that SA between the same species (notably Acr-Apl) has decreased due to climate change, it would be interesting to study in more detail how climate change has affected heterospecific attraction in boreal waterbird communities. Related to heterospecific attraction and social information use in general, the occurrence of climate change-induced informational mismatches (sensu Parejo 2016) is an intriguing research topic worth exploring further. Such research should examine the general deterioration of information acquisition in natural systems due to anthropogenic environmental changes (Szymkowiak and Schmidt 2021). Overall, the impacts of climate change on niche relationships among native non-invasive species deserve more attention to enhance our understanding of mechanisms of biodiversity change in local communities.

Acknowledgements – I would like to thank three anonymous reviewers for constructive comments that improved the manuscript.

Data availability statement

Data are available from the Dryad Digital Repository: <https://doi.org/10.5061/dryad.sj3tx968s> (Pöysä 2023).

Supporting information

The Supporting information associated with this article is available with the online version.

References

- Abrams, P. A. 1998. High competition with low similarity and low competition with high similarity: exploitative and apparent competition in consumer-resource systems. – *Am. Nat.* 152: 114–128.
- Aloe, A. M. 2014. An empirical investigation of partial effect sizes in meta-analysis of correlational data. – *J. Gen. Psychol.* 141: 47–64.
- Aloe, A. M. and Thompson, C. G. 2013. The synthesis of partial effect sizes. – *J. Soc. Social Work Res.* 4: 390–405.
- Arvola, L., Rask, M., Ruuhijärvi, J., Tulonen, T., Vuorenmaa, J., Ruoho-Airola, T. and Tulonen, J. 2010. Long-term patterns in pH and colour in small acidic boreal lakes of varying hydrological and landscape settings. – *Biogeochemistry* 101: 269–279.
- Arzel, C., Nummi, P., Arvola, L., Rask, M., Olin, M., Pöysä, H., Davranche, A., Holopainen, S., Viitala, R., Einola, E. and Manninen-Johansen, S. 2020. Invertebrates are declining in boreal aquatic habitat: the effect of brownification? – *Sci. Tot. Environ.* 724: 138199.
- Bell, D. A., Kovach, R. P., Muhlfeld, C. C., Al-Chokhachy, R., Cline, T. J., Whited, D. C., Schmetterling, D. A., Lukacs, P. M. and Whiteley, A. R. 2021. Climate change and expanding invasive species drive widespread declines of native trout in the northern Rocky Mountains, USA. – *Sci. Adv.* 7: eabj5471.
- Benjamini, Y. and Hochberg, Y. 1995. Controlling for false discovery rate: a practical and powerful approach to multiple testing. – *J. R. Stat. Soc. B* 57: 289–300.
- Bidwell, M. T., Green, A. J. and Clark, R. G. 2014. Random placement models predict species–area relationships in duck communities despite species aggregation. – *Oikos* 123: 1499–1508.

- Blanchet, F. G., Cazelles, K. and Gravel, D. 2020. Co-occurrence is not evidence of ecological interactions. – *Ecol. Lett.* 23: 1050–1063.
- Caldwell, T. J., Chandra, S., Feher, K., Simmons, J. B. and Hogan, Z. 2020. Ecosystem response to earlier ice break-up date: climate driven changes to water temperature, lake-habitat-specific production, and trout habitat and resource use. – *Global Change Biol.* 26: 5475–5491.
- Cohen, J. 1988. *Statistical power analysis for the behavioral sciences*, 2nd edn. – Lawrence Erlbaum Associates Publisher.
- Colwell, R. K. and Futuyma, D. J. 1971. On the measurement of niche breadth and overlap. – *Ecology* 52: 567–576.
- Colwell, R. K. and Rangel, T. F. 2009. Hutchinson's duality: the once and future niche. – *Proc. Natl Acad. Sci. USA* 106: 19651–19658.
- Comte, L., Buisson, L., Daufresne, M. and Grenouillet, G. 2013. Climate-induced changes in the distribution of freshwater fish: observed and predicted trends. – *Freshwater Biol.* 58: 625–639.
- Cook, R. D. 1977. Detection of influential observation in linear regression. – *Technometrics* 19: 15–18.
- Crampton, S. and Simmons, K. E. L. (eds) 1977. *The birds of the western palearctic*, vol. 1. – Clarendon Press.
- Creed, I. F. 2018. Global change-driven effects on dissolved organic matter composition: implications for food webs of northern lakes. – *Global Change Biol.* 24: 3692–3714.
- Crowley, P. H. and Cox, J. J. 2011. Intraguild mutualism. – *Trends Ecol. Evol.* 26: 627–633.
- Devictor, V. et al. 2012. Differences in the climatic debts of birds and butterflies at a continental scale. – *Nat. Clim. Change* 2: 121–124.
- Diamond, J. M. and Case, T. J. (eds) 1986. *Community ecology*. – Harper and Row.
- Elmberg, J., Nummi, P., Pöysä, H. and Sjöberg, K. 1993. Factors affecting species number and density of dabbling duck guilds in North Europe. – *Ecography* 16: 251–260.
- Elmberg, J., Pöysä, H., Sjöberg, K. and Nummi, P. 1997. Interspecific interactions and coexistence in dabbling ducks: observations and an experiment. – *Oecologia* 111: 129–136.
- Elmberg, J., Arzel, C., Gunnarsson, G., Holopainen, S., Nummi, P., Pöysä, H. and Sjöberg, K. 2020. Population change in breeding boreal waterbirds in a 25-year perspective: what characterises winners and losers? – *Freshwater Biol.* 65: 167–177.
- Feinsinger, P., Spears, E. E. and Poole, R. W. 1981. A simple measure of niche breadth. – *Ecology* 62: 27–32.
- Freckleton, R. P. 2002. On the misuse of residuals in ecology: regression of residuals vs. multiple regression. – *J. Anim. Ecol.* 71: 542–545.
- Fretwell, S. D. and Lucas, Jr, H. L. 1969. On territorial behavior and other factors influencing habitat distribution in birds. I. Theoretical development. – *Acta Biotheor.* 19: 16–36.
- Garamszegi, L. Z. 2006. Comparing effect sizes across variables: generalization without the need for Bonferroni correction. – *Behav. Ecol.* 17: 682–687.
- Garamszegi, L. Z., Markó, G. and Herczeg, G. 2012. A meta-analysis of correlated behaviours with implications for behavioural syndromes: mean effect size, publication bias, phylogenetic effects and the role of mediator variables. – *Evol. Ecol.* 26: 1213–1235.
- García, L. V. 2004. Escaping the Bonferroni iron claw in ecological studies. – *Oikos* 105: 657–663.
- Gilman, S. E., Urban, M. C., Tewksbury, J., Gilchrist, G. W. and Holt, R. D. 2010. A framework for community interactions under climate change. – *Trends Ecol. Evol.* 25: 325–331.
- Guillemain, M., Fritz, H., Guillon, N. and Simon, G. 2002. Ecomorphology and coexistence in dabbling ducks: the role of lamellar density and body length in winter. – *Oikos* 98: 547–551.
- Guillemain, M., Pöysä, H., Fox, A. D., Arzel, C., Dessborn, L., Ekroos, J., Gunnarsson, G., Holm, T. E., Christensen, T. K., Lehikoinen, A., Mitchell, C., Rintala, J. and Møller, A. P. 2013. Effects of climate change on European ducks: what do we know and what do we need to know? – *Wildl. Biol.* 19: 404–419.
- Gunnarsson, G., Elmberg, J., Sjöberg, K., Pöysä, H. and Nummi, P. 2004. Why are there so many empty lakes? Food limits survival of mallard ducklings. – *Can. J. Zool.* 82: 1698–1703.
- Gurd, D. B. 2008. Mechanistic analysis of interspecific competition using foraging trade-offs: implications for duck assemblages. – *Ecology* 89: 495–505.
- Gyimesi, A., van Lith, B. and Nolet, B. A. 2012. Commensal foraging with Bewick's swans *Cygnus bewickii* doubles instantaneous intake rate of common pochards *Aythya ferina*. – *Ardea* 100: 55–62.
- Hallerbäck, S., Huning, L. S., Love, C., Persson, M., Stensen, K., Gustafsson, D. and AghaKouchak, A. 2022. Climate warming shortens ice durations and alters freeze and break-up patterns in Swedish water bodies. – *Cryosphere* 16: 2493–2503.
- Heino, J., Alahuhta, J., Bini, L. M., Cai, Y., Heiskanen, A. S., Hellsten, S., Kortelainen, P., Kotamäki, N., Tolonen, K. T., Vihervaara, P., Vilmi, A. and Angeler, D. G. 2021. Lakes in the era of global change: moving beyond single-lake thinking in maintaining biodiversity and ecosystem services. – *Biol. Rev.* 96: 89–106.
- Heino, J., Virkkala, R. and Toivonen, H. 2009. Climate change and freshwater biodiversity: detected patterns, future trends and adaptations in northern regions. – *Biol. Rev.* 84: 39–54.
- Hewitt, B. A., Lopez, L. S., Gaibisels, K. M., Murdoch, A., Higgins, S. N., Magnuson, J. J., Paterson, A. M., Rusak, J. A., Yao, H. and Sharma, S. 2018. Historical trends, drivers and future projections of ice phenology in small north temperate lakes in the Laurentian Great Lakes Region. – *Water* 10: 70.
- Holopainen, S., Väänänen, V.-M. and Fox, A. D. 2020. Landscape and habitat affect frequency of artificial duck nest predation by native species, but not by an alien predator. – *Basic Appl. Ecol.* 48: 52–60.
- Holopainen, S., Väänänen, V.-M., Vehkaoja, M. and Fox, A. D. 2021. Do alien predators pose a particular risk to duck nests in northern Europe? Results from an artificial nest experiment. – *Biol. Inv.* 23: 3795–3807.
- Holopainen, S., Čehovská, M., Jaatinen, K., Laaksonen, T., Lindén, A., Nummi, P., Piha, M., Pöysä, H., Toivanen, T., Väänänen, V.-M. and Lehikoinen, A. 2022. A rapid increase of large-sized waterfowl does not explain the population declines of small-sized waterbird at their breeding sites. – *Global Ecol. Conserv.* 36: e02144.
- Iler, A. M., Inouye, D. W., Schmidt, N. M. and Høye, T. T. 2017. Detrending phenological time series improves climate–phenology analyses and reveals evidence of plasticity. – *Ecology* 98: 647–655.
- Jezkova, T. and Wiens, J. J. 2016. Rates of change in climatic niches in plant and animal populations are much slower than projected climate change. – *Proc. R. Soc. B* 283: 20162104.
- Källander, H. 2005. Commensal association of waterfowl with feeding swans. – *Waterbirds* 28: 326–330.
- Keil, P., Wiegand, T., Tóth, A. B., McGlenn, D. J. and Chase, J. M. 2021. Measurement and analysis of interspecific spatial associations as a facet of biodiversity. – *Ecol. Monogr.* 91: e01452.

- Koskimies, P. and Pöysä, H. 1989. Waterfowl censusing in environmental monitoring: a comparison between point and round counts. – *Ann. Zool. Fenn.* 26: 201–206.
- Koskimies, P. and Väisänen, R. A. (eds) 1991. Monitoring bird populations. A manual of methods applied in Finland. – Zoological Museum, Finnish Museum of Natural History.
- Kritzberg, E. S., Hasselquist, E. M., Škerlep, M., Löfgren, S., Olsson, O., Stadmark, J., Valina, S., Hansson, L.-A. and Laudon, H. 2020. Browning of freshwaters: consequences to ecosystem services, underlying drivers, and potential mitigation measures. – *Ambio* 49: 375–390.
- La Sorte, F. A. and Jetz, W. 2012. Tracking of climatic niche boundaries under recent climate change. – *J. Anim. Ecol.* 81: 914–925.
- Lehikoinen, A., Jaatinen, K., Vähätalo, A., Clausen, P., Crowe, O., Deceuninck, B., Hearn, R., Holt, C. A., Hornman, M., Keller, V., Nilsson, L., Langendoen, T., Tománková, I., Wahl, J. and Fox, A. D. 2013. Rapid climate driven shifts in wintering distributions of three common waterbird species. – *Global Change Biol.* 19: 2071–2081.
- Lehikoinen, A., Rintala, J., Lammi, E. and Pöysä, H. 2016. Habitat-specific population trajectories in boreal waterbirds: alarming trends and bioindicators for wetlands. – *Anim. Conserv.* 19: 88–95.
- Lenoir, J., Bertrand, R., Comte, L., Bourgeaud, L., Hattab, T., Murielle, J. and Grenouillet, G. 2020. Species better track climate warming in the oceans than on land. – *Nat. Ecol. Evol.* 4: 1044–1059.
- Lind, L., Eckstein, R. L. and Relyea, R. A. 2022. Direct and indirect effects of climate change on distribution and community composition of macrophytes in lentic systems. – *Biol. Rev.* 97: 1677–1690.
- Lindström, J. and Forchhammer, M. C. 2010. Time-series analyses. – In: Møller, A. P., Fiedler, W. and Berthold, P. (eds), *Effects of climate change on birds*. Oxford Univ. Press, pp. 57–66.
- Lopez, L. S., Hewitt, B. A. and Sharma, S. 2019. Reaching a breaking point: how is climate change influencing the timing of ice breakup in lakes across the northern hemisphere? – *Limnol. Oceanogr.* 64: 2621–2631.
- Magee, M. R., Wu, C. H., Robertson, D. M., Lathrop, R. C. and Hamilton, D. P. 2016. Trends and abrupt changes in 104 years of ice cover and water temperature in a dimictic lake in response to air temperature, wind speed and water clarity drivers. – *Hydrol. Earth Syst. Sci.* 20: 1681–1702.
- Møller, A. P. and Jennions, M. D. 2002. How much variance can be explained by ecologists and evolutionary biologists. – *Oecologia* 132: 492–500.
- Mönkkönen, M., Helle, P. and Soppela, K. 1990. Numerical and behavioral responses of migrant passerines to experimental manipulation of resident tits (*Parus* spp.) – Heterospecific attraction in northern breeding bird communities. – *Oecologia* 85: 218–225.
- Mönkkönen, M., Härdling, R., Forsman, J. T. and Tuomi, J. 1999. Evolution of heterospecific attraction: using other species as cues in habitat selection. – *Evol. Ecol.* 13: 91–104.
- Murray, K. and Conner, M. M. 2009. Methods to quantify variable importance: implications for the analysis of noisy ecological data. – *Ecology* 90: 348–355.
- Nagelkerken, I. and Munday, P. L. 2016. Animal behaviour shapes the ecological effects of ocean acidification and warming: moving from individual to community-level responses. – *Global Change Biol.* 22: 974–989.
- Nakagawa, S. and Cuthill, I. C. 2007. Effect size, confidence interval and statistical significance: a practical guide for biologists. – *Biol. Rev.* 82: 591–605.
- Nudds, T. D. 1992. Patterns in breeding waterfowl communities. – In: Batt, B. D. J., Afton, A. D., Anderson, M. G., Ankney, C. D., Johnson, D. H., Kadlec, J. A. and Krapu, G. L. (eds), *The ecology and management of breeding waterfowl*. Univ. Minnesota Press, pp. 540–567.
- Nudds, T. D. and Bowlby, J. N. 1984. Predator–prey size relationships among North American dabbling ducks. – *Can. J. Zool.* 62: 2002–2008.
- Nudds, T. D., Sjöberg, K. and Lundberg, P. 1994. Ecomorphological relationships of Palearctic dabbling ducks on Baltic coastal wetlands and a comparison with the Nearctic. – *Oikos* 69: 295–303.
- Nuijten, R. J. M., Wood, K. A., Haitjema, T., Rees, E. C. and Nolet, B. A. 2020. Concurrent shifts in wintering distribution and phenology in migratory swans: individual and generational effects. – *Global Change Biol.* 26: 4263–4275.
- Nummi, P. and Pöysä, H. 1993. Habitat associations of ducks during different phases of the breeding season. – *Ecography* 16: 309–328.
- Nummi, P. and Väinänen, V.-M. 2001. High overlap in diets of sympatric dabbling ducks – an effect of food abundance? – *Ann. Zool. Fenn.* 38: 123–130.
- Ockendon, N., Baker, D. J., Karr, J. A., White, E. C., Almond, R. E. A., Amano, T., Bertram, E., Bradbury, R. B., Bradley, C. I. E., Butchart, S. H., Doswald, N., Foden, W., Gill, D. J. C., Green, R. E., Sutherland, W. J., Tanner, E. V. J. and Pearce-Higgins, J. W. 2014. Mechanisms underpinning climatic impacts on natural populations: altered species interactions are more important than direct effects. – *Global Change Biol.* 20: 2221–2229.
- O'Connor, R. J. 1985. Behavioural regulation of bird populations: a review of habitat use in relation to migration and residency. – In: Sibly, R. M. and Smith, R. H. (eds), *Behavioural ecology: ecological consequences of adaptive behaviour*. Blackwell Scientific, pp. 105–142.
- Osnas, E. E. and Ankney, C. D. 2003. Null models of North American prairie duck communities: local habitat conditions and temporal scale influence community patterns. – *Evol. Ecol. Res.* 5: 913–932.
- Parejo, D. 2016. Informational mismatches: a neglected threat of climate change to interspecific interactions. – *Front. Ecol. Evol.* 4: 31.
- Parejo, D. and Avilés, J. M. 2016. Social information use by competitors: resolving the enigma of species coexistence in animals? – *Ecosphere* 7: e01295.
- Parejo, D., Danchin, E. and Avilés, J. M. 2005. The heterospecific habitat copying hypothesis: can competitors indicate habitat quality? – *Behav. Ecol.* 16: 96–105.
- Parmesan, C. and Yohe, G. 2003. A globally coherent fingerprint of climate change impacts across natural systems. – *Nature* 421: 37–42.
- Patterson, R. T. and Swindles, G. T. 2015. Influence of ocean-atmospheric oscillations on lake ice phenology in eastern North America. – *Clim. Dyn.* 45: 2293–2308.
- Peeters, F., Straile, D., Lorke, A. and Livingstone, D. M. 2007. Earlier onset of spring phytoplankton bloom in lakes of temperate zone in a warmer climate. – *Global Change Biol.* 13: 1898–1909.
- Piha, M., Lindén, A., Lehikoinen, A. and Rajala, T. 2022. Vesilintuseurannan tulokset 2022. – Luonnonvara- ja biotalouden tutkimus 66/2022. – Luonnonvarakeskus.
- Pimental, R. A. 1979. Morphometrics. The multivariate analysis of biological data. – Kendall/Hunt Publishing Company.
- Preston, D. L., Caine, N., McKnight, D. M., Williams, M. W., Hell, K., Miller, M. P., Hart, S. J. and Johnson, P. T. J. 2016.

- Climate regulates alpine lake ice cover phenology and aquatic ecosystem structure. – *Geophys. Res. Lett.* 43: 5353–5360.
- Pöysä, H. 1983. Resource utilization pattern and guild structure in a waterfowl community. – *Oikos* 40: 295–307.
- Pöysä, H. 1986. Foraging niche shifts in multispecies dabbling duck (*Anas* spp.) feeding groups: harmful and beneficial interactions between species. – *Ornis Scand.* 17: 333–346.
- Pöysä, H. 1996. Population estimates and the timing of waterfowl censuses. – *Ornis Fenn.* 73: 60–68.
- Pöysä, H. 2001. Dynamics of habitat distribution in breeding mallards: assessing the applicability of current habitat selection models. – *Oikos* 94: 365–373.
- Pöysä, H. 2019. Tracking ice phenology by migratory waterbirds: settling phenology and breeding success of species with divergent population trends. – *J. Avian Biol.* 2019: e02327.
- Pöysä, H. 2022. Local variation in the timing and advancement of lake ice breakup and impacts on settling dynamics in a migratory waterbird. – *Sci. Tot. Environ.* 811: 151397.
- Pöysä, H. 2023. Data from: Impacts of climate-driven changes in habitat phenology on dynamics of niche overlaps and spatial associations in a boreal waterbird community. – Dryad Digital Repository, <https://doi.org/10.5061/dryad.sj3tx968s>.
- Pöysä, H. and Linkola, P. 2021. Extending temporal baseline increases understanding of biodiversity change in European boreal waterbird communities. – *Biol. Conserv.* 257: 109139.
- Pöysä, H. and Paasivaara, A. 2021. Shifts in fine-scale distribution and breeding success of boreal waterbirds along gradients in ice-out timing and habitat structure. – *Freshwater Biol.* 66: 2038–2050.
- Pöysä, H. and Sorjonen, J. 2000. Recolonization of breeding waterfowl communities by the whooper swan: vacant niches available. – *Ecography* 23: 342–348.
- Pöysä, H., ElMBERG, J., Nummi, P. and SjöBERG, K. 1994. Species composition of dabbling duck assemblages: ecomorphological patterns compared with null models. – *Oecologia* 98: 193–200.
- Pöysä, H., ElMBERG, J., Nummi, P. and SjöBERG, K. 2000. Nesting mallards (*Anas platyrhynchos*) forecast brood-stage food limitation when selecting habitat: experimental evidence. – *Oecologia* 122: 582–586.
- Pöysä, H., Rintala, J., Lehtikoinen, A. and Väisänen, R. A. 2013. The importance of hunting pressure, habitat preference and life history for population trends of breeding waterbirds in Finland. – *Eur. J. Wildl. Res.* 59: 245–256.
- Pöysä, H., ElMBERG, J., Gunnarsson, G., Holopainen, S., Nummi, P. and SjöBERG, K. 2018. Recovering Whooper Swans do not cause a decline in Eurasian Wigeon via their grazing impact on habitat. – *J. Ornithol.* 159: 447–455.
- Pöysä, H., Lammi, E., Pöysä, S. and Väänänen, V.-M. 2019a. Collapse of a protector species drives secondary endangerment in waterbird communities. – *Biol. Conserv.* 230: 75–81.
- Pöysä, H., Holopainen, S., ElMBERG, J., Gunnarsson, G., Nummi, P. and SjöBERG, K. 2019b. Changes in species richness and composition of boreal waterbird communities: a comparison between two time periods 25 years apart. – *Sci. Rep.* 9: 1725.
- Reid, A. J., Carlson, A. K., Creed, I. F., Eliason, E. J., Gell, P. A., Johnson, P. T. J., Kidd, K. A., MacCormack, T. J., Olden, J. D., Ormerod, S. J., Smol, J. P., Taylor, W. W., Tockner, K., Vermaire, J. C., Dudgeon, D. and Cooke, S. J. 2019. Emerging threats and persistent conservation challenges for freshwater biodiversity. – *Biol. Rev.* 94: 849–873.
- Ricklefs, R. E. and Schuter, D. (eds). 1993. Species diversity in ecological communities: historical and geographical perspectives. – Univ. of Chicago Press.
- Quintero, I. and Wiens, J. J. 2013. What determines the climatic niche width of species? The role of spatial and temporal climatic variation in three vertebrate clades. – *Global Ecol. Biogeogr.* 22: 422–432.
- Schielzeth, H. 2010. Simple means to improve the interpretability of regression coefficients. – *Met. Ecol. Evol.* 1: 103–113.
- Schoener, T. W. 1983. Field experiments on interspecific competition. – *Am. Nat.* 122: 240–285.
- Sebastián-González, E., Sánchez-Zabata, J. A., Botella, F. and Ovaskainen, O. 2010. Testing the heterospecific attraction hypothesis with time-series data on species co-occurrence. – *Proc. R. Soc. B* 277: 2983–2990.
- Seppänen, J.-T., Forsman, J. T., Mönkkönen, M. and Thomas, R. L. 2007. Social information use is a process across time, space, and ecology, reaching heterospecifics. – *Ecology* 88: 1622–1633.
- Sharma, S., Magnuson, J. J., Batt, R. D., Winslow, L. A., Korhonen, J. and Aono, Y. 2016. Direct observations of ice seasonality reveal changes in climate over the past 320–570 years. – *Sci. Rep.* 6: 25061.
- Shuvo, A., O'Reilly, C. M., Blagrove, K., Ewins, C., Filazzola, A., Gray, D., Mahdiyan, O., Moslenko, L., Quinlan, R. and Sharma, S. 2021. Total phosphorus and climate are equally important predictors of water quality in lakes. – *Aquat. Sci.* 83: 16.
- Silverman, E. D. 2001. Testing a simple stochastic model for the dynamics of waterfowl aggregations. – *Oecologia* 128: 608–617.
- SjöBERG, K., Pöysä, H., ElMBERG, J. and Nummi, P. 2000. Response of mallard ducklings to variation in habitat quality: an experiment of food limitation. – *Ecology* 81: 329–335.
- Soberón, J. 2007. Grinnelian and Eltonian niches and geographic distributions of species. – *Ecol. Lett.* 10: 1–9.
- Stachowicz, J. J. 2001. Mutualism, facilitation, and the structure of ecological communities. – *Biosci.* 51: 235–246.
- Suhonen, S., Nummi, P. and Pöysä, H. 2011. Long term stability of boreal lake habitats and use by breeding ducks. – *Boreal Environ. Res.* 16: 71–80.
- Szymkowiak, J. and Schmidt, K. A. 2021. Deterioration of nature's information webs in the Anthropocene. – *Oikos* 2022: 1–11.
- Thackeray, S. J., Henrys, P. A., Feuchtmayr, H., Jones, I. D., Maberly, S. C. and Winfield, I. J. 2013. Food web de-synchronization in England's largest lake: an assessment based on multiple phenological metrics. – *Global Change Biol.* 19: 3568–3580.
- Tingley, M. W., Monahan, W. B., Beissinger, S. R. and Cet, M. 2009. Birds track their Grinnelian niche through a century of climate change. – *Proc. Natl Acad. Sci. USA* 106: 19637–19643.
- Tokeshi, M. 1999. Species coexistence: ecological and evolutionary perspectives. – Blackwell Science.
- Weyhenmeyer, G. A. 2001. Warmer winters: are planktonic algal populations in Sweden's largest lakes affected? – *Ambio* 30: 565–571.
- Wiens, J. A. 1977. On competition and variable environments. – *Am. Sci.* 65: 590–607.
- Wiens, J. A., Stralberga, D., Jongsomjita, D., Howella, C. A. and Snyderb, M. A. 2009. Niches, models, and climate change: assessing the assumptions and uncertainties. – *Proc. Natl Acad. Sci. USA* 106: 19729–19736.
- Winder, M. and Schindler, D. E. 2004. Climatic effects on the phenology of lake processes. – *Global Change Biol.* 10: 1844–1856.
- Wisz, M. S. et al. 2013. The role of biotic interactions in shaping distributions and realised assemblages of species: implications for species distribution modelling. – *Biol. Rev.* 88: 15–30.
- Wood, K. A., Ham, P., Scales, J., Wyeth, E. and Rose, P. E. 2020. Aggressive behavioural interactions between swans (*Cygnus*

- spp.) and other waterbirds during winter: a webcam-based study. – *Avian Res.* 11: 1–16.
- Woolway, R. I., Kraemer, B. M., Lenters, J. D., Merchant, C. J., O'Reilly, C. M. and Sharma, S. 2020. Global lake responses to climate change. – *Nat. Rev. Earth Environ.* 1: 388–403.
- Väänänen, V.-M., Pöysä, H. and Runko, P. 2016. Nest and brood stage association between ducks and small colonial gulls in boreal wetlands. – *Ornis Fenn.* 93: 47–54.
- Yeung, A. C. Y., Paltsev, A., Daigle, A., Duinker, P. N. and Creed, I. F. 2019. Atmospheric change as a driver of change in the Canadian boreal zone. – *Environ. Rev.* 27: 346–376.
- Zar, J. H. 1996. *Biostatistical analysis*, 3rd edn. – Prentice Hall.
- Zuur, A. F., Ieno, E. N., Elphick, C. S. 2010. *A protocol for data exploration to avoid common statistical problems*. – *Met. Ecol. Evol.* 1: 3–14.