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Local variation in the timing and advancement of lake ice breakup and impacts on settling dynamics in a migratory waterbird

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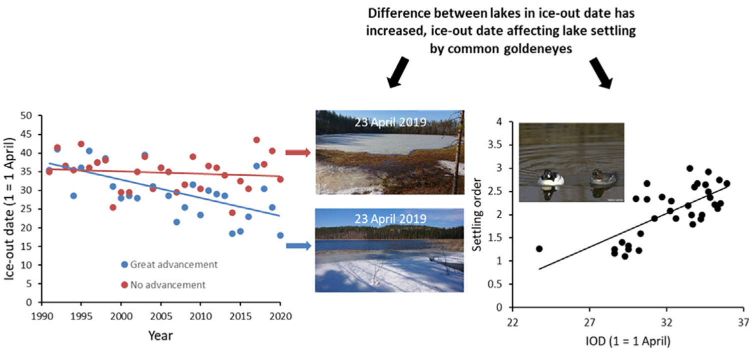
HIGHLIGHTS

- Variation in the advancement of ice-out date (IOD) in 37 boreal lakes was studied.
- The rate of the advancement of IOD varied from 1.5 to 16.1 days in 1991–2020.
- IOD advanced more in large lakes than in small lakes.
- Within-season difference between lakes in IOD increased from 1991 to 2020.
- Variation in IOD governed lake settling dynamics by breeding common goldeneyes.

GRAPHICAL ABSTRACT


Difference between lakes in ice-out date has increased, ice-out date affecting lake settling by common goldeneyes

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ABSTRACT

Timing of ice-out is important to fundamental hydrological and ecological processes in freshwater ecosystems at high northern latitudes. While earlier ice-out in lakes during the last century is a well-documented phenomenon across the Northern Hemisphere, local variation in the rate of advancement of ice-out has received little attention. Here, records of ice-out date in 1991–2020 from 37 small lakes in a boreal catchment area in southeastern Finland were used to study variation in the timing of ice-out and its advancement. In addition, data of settling phenology of migratory common goldeneyes (*Bucephala clangula*) at the study lakes were used to examine how between-year and within-season variation in the timing of ice-out affects lake settlement of the species. Overall, ice-out date (IOD, the timing of ice break-up in the spring) advanced 9.8 days during the 30-year study period, April temperature being more important than winter temperature (severity) in determining the IOD. Rate of the advancement of IOD in individual lakes varied from 1.5 to 16.1 days, having advanced more in relatively larger lakes. Lakes at higher elevations had later mean IOD than lakes at lower elevations. Within-season differences among the lakes in IOD increased from 1991 to 2020, this variation being mainly driven by temperature during the ice melting period. Lakes with late mean IOD were settled later in a season by breeding common goldeneyes than lakes with early IOD. The faster the ice melting progressed within a season, the faster common goldeneyes settled the breeding lakes. The results demonstrate how global warming differently affects IOD in boreal lakes even within the same catchment area. More research in the landscape context is needed to enhance our understanding of changes in IOD in boreal lakes and how differently advancing IOD affects local dynamics of species dependent on open water.

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1. Introduction

The timing and duration of the ice season plays an important role in affecting fundamental biogeochemical processes in northern freshwater lakes, extending to various ecosystem services provided by the ice-covered water bodies to humans such as winter ice roads and ice fishing (Prowse and Brown, 2010; Hampton et al., 2017; Knoll et al., 2019; Sharma et al., 2020). While the timing of both autumn ice-in and spring ice-out have changed due to climate change and affect the duration of the ice season (e.g. Wynne et al., 1996; Benson et al., 2012), timing of ice-out is of particular importance to key hydrological and ecological processes in freshwater ecosystems, such as thermal stratification (Winder and Schindler, 2004; Preston et al., 2016), the start of spring and summer production (Weyhenmeyer, 2001; Peeters et al., 2007; Prowse et al., 2011), the occurrence peak of primary consumers (Berger et al., 2014; Thackeray et al., 2013), the synchrony between primary and secondary consumers (Thackeray et al., 2013) and the availability of suitable oxythermal habitat for cold-water organisms (Guzzo and Blanchfield, 2017; Caldwell et al., 2020). Recent climate warming has caused dramatic changes in the timing of ice-out (Magnuson et al., 2000; Hewitt et al., 2018; Magee et al., 2016; Patterson and Swindles, 2015; Sharma et al., 2016; Warne et al., 2020). In general, because ice melting is tightly linked with spring temperatures, the timing of ice-out in the spring serves a valuable climate change indicator and helps understand how these changes affect aquatic ecosystems, and more generally, regulate earth surface processes and create feedbacks with local and regional climate through strongly increasing evaporation and heat exchange with the overlying air masses (Magnuson et al., 2000; Rouse et al., 2005; Adrian et al., 2009; MacKay et al., 2009; Prowse et al., 2011; Lopez et al., 2019).

Earlier ice-out in lakes during the last century is a well-documented phenomenon across the Northern Hemisphere (Hewitt et al., 2018; Magee et al., 2016; Patterson and Swindles, 2015; Sharma et al., 2016; Lopez et al., 2019). Furthermore, large-scale comparisons between lakes have revealed that the timing of ice-out varies between lakes, depending on regional differences in latitude/longitude, temperature, snow conditions and other large-scale environmental attributes, in addition to lake characteristics such as lake surface area and depth (e.g. Wynne et al., 1996; Weyhenmeyer et al., 2004, 2011; Williams et al., 2004; Jensen et al., 2007; Lopez et al., 2019). Some studies have also documented strong temporal coherence of ice-out dates between lakes at multiple spatial scales (e.g. Blenckner et al., 2004; Magnuson et al., 2004; Arp et al., 2013). However, local variation in the rate of long-term advancement of ice-out has been studied surprisingly little. For example, Beier et al. (2012) analyzed the timing of ice-out for five montane lakes in the Adirondack Mountains in the northeastern United States, at a local scale (maximum distance between any two lakes about 9 km) over a period of 33 years (1975–2007). These authors were primarily interested in common local climate drivers of the timing of ice-out, not in lake-specific characteristics per se; however, they reported that none of the five lakes showed a significant trend of earlier ice-out. Hodgkins (2013) in turn studied the importance of record length in estimating changes in the timing of ice-out for 28 lakes in New England, USA (maximum distance between any two lakes about 570 km). The magnitude of earlier ice-out trends over time appeared to depend on the length of the period considered. Neither of these studies specifically analyzed factors explaining differences among lakes in the rate of advancement of ice-out, a topic addressed in this study for the first time at local level. Considering the wide-ranging impacts of ice-free conditions in the spring on aquatic ecosystems and species (see above), it is important to increase our understanding of the variation in the timing of ice-out and its drivers, in the face of warming climate.

In addition to biogeochemical processes occurring within aquatic ecosystems, the timing of ice-out is critically important to ecological processes at the interface between aquatic and terrestrial systems, such as settlement and habitat use of migratory waterbirds in the spring (Gaston et al., 2005; Love et al., 2010; Pöysä, 2019). These species are fully dependent on open water for feeding and many other activities but many of them nest in terrestrial habitats. The timing of ice-out in boreal lakes is particularly important for early arriving species such as the common goldeneye (*Bucephala clangula*) a diving duck. Previous research, done at the landscape (study area) level, has found that annual settling phenology of common goldeneye tracks closely the overall timing of ice-out (Pöysä, 2019). Moreover, the timing of ice-out affects the timing of egg laying (Oja and Pöysä, 2007; Clark et al., 2014), which in turn affects individual breeding success so that early breeding females produce more recruits to the next generation than late breeding females (Milonoff et al., 1998; Clark et al., 2014). In addition to the dependence on open water, waterbirds are linked via food-web interactions with various hydrological processes that occur in lake ecosystems (see above). Advanced timing of ice-out may influence ecological conditions in boreal lakes, for example, via phenological mismatches (Durant et al., 2007), as discussed by Pöysä and Paasivaara (2021). Also, shorter ice season may enhance fish survival and increase fish abundance, resulting in higher fish predation on zooplankton and benthos (Gyllström et al., 2005; Jeppesen et al., 2010) and, hence, increased competition for aquatic invertebrates between fish and common goldeneye. Indeed, negative impacts of fish on common goldeneye density and lake use have been documented in several studies (see Nummi et al., 2016 for a review). Hence, the timing of ice-out is a crucial determinant of the settling and breeding phenology of the species, ultimately affecting fitness of individuals.

Here, I used records of ice-out date from 1991 to 2020 from 37 small lakes in a boreal catchment area in southeastern Finland to study drivers of local variation in the timing of ice-out, with special attention to differences among lakes in the rate of advancement of lake-specific ice-out over time. I first analyzed long-term trends and within-season variation (variation among lakes) in the timing of ice-out in relation to local spring temperature. Then I studied potential differences among the lakes in the rate of change in the timing of ice-out and if those differences can be explained by lake-specific characteristics such as lake area and elevation, i.e. factors that have been found to explain differences among lakes in the overall timing of ice-out (e.g. Williams et al., 2004) but have not been studied before at the local scale (see 2.1. Study area). Finally, I used common goldeneye settling phenology data for the study lakes in 1991–2020 to ask: 1) Do differences in ice-out date (IOD) among lakes affect the settling order of lakes by breeding pairs? 2) Do differences in the progress of ice melting among years affect the dynamics of lake settling by breeding pairs within a season?

2. Material and methods

2.1. Study area

The study area in southeastern Finland (61°34 N, 29°38 E; Fig. S1) is about 59 km^2 (maximum distance between any two lakes was 11.8 km.) and dominated by pine (*Pinus sylvestris* L.) or mixed (pine, birch *Betula* spp. and spruce (*Picea abies* L. Karst) forests interspersed with lakes of varying size and luxuriant emergent vegetation (see also Pöysä, 2001). The study area as a whole belongs to the Simpelejärvi catchment area, about 400 km^2 in size (ID 2007082004431; definition of the catchment area done with the web service tool provided by the Finnish Environment Institute; http://paikkatieto.ymparisto.fi/value; accessed 22 February 2021; access to the user guide (in Finnish) available by clicking the button 'Käyttöohje'; in brief, catchment area IDs and other information can be derived by zooming in on the map until the borders (marked in red) of the catchment areas become visible and by clicking an appropriate lake or river-bed within the catchment area). Within the main catchment area, the 37 study lakes are situating within two sub-catchments (IDs 2,007,082,002,977 and 2,007,082,004,458). The 37 study lakes (mean size 3.5 ha, range

0.05–24.0 ha) are covered by ice during winter and have a relatively stable water level in summer. For consistency, all of the 37 studied water bodies are considered lakes even though three of them (each 0.05 ha in size) are smaller than the size criteria used for a lake in some global surveys, e.g. 0.1 ha in Downing et al. (2006) and 0.2 ha in Verpoorter et al. (2014). The study area and lakes have been used in several earlier studies addressing, for example, impacts of habitat change and climate warming on settling phenology and habitat distribution of migratory waterbirds (e.g. Pöysä, 1996, 2001, 2019; Pöysä and Paasivaara, 2021), providing a solid basis and unique long-term data for the topics of this study, particularly in terms of lake-specific IODs (see below). All lakes with a continuous time-series of IODs from 1991 to 2020 were included for this study.

The spatial scale of this study has two important advantages. First, it can be assumed that large-scale climatic drivers of IOD, notably air temperature, typically associated with geographic position (latitude or longitude; e.g. Blenckner et al., 2004; Magnuson et al., 2004; Warne et al., 2020), or atmospheric circulation, such as North Atlantic Oscillation (Blenckner et al., 2004), can be ruled out when studying local factors that could explain differences among lakes in the timing of ice-out; large-scale variability in these global drivers should affect similarly all the lakes in this study area. This is important, because the effect of local drivers may be negated by large-scale drivers if study lakes are situated in different regions (e.g. Blenckner et al., 2004; Williams et al., 2004; Warne et al., 2020). Second, given that migratory common goldeneyes easily fly distances far longer than the spatial extent of the study area, it can be assumed that all the lakes are equally available to common goldeneye pairs arriving from spring migration, making it possible to focus on IOD in affecting settling decisions of breeding pairs.

2.2. IOD data

The progress of ice melting in the 37 lakes was recorded in situ, in connection with waterbird surveys done on each lake four times in April–May at an interval of approximately seven days (mean survey interval = 7.0 d, SE = 0.1) each year from 1991 to 2020 (see Pöysä, 2019 for details and Fig. S2 for photos illustrating differences among lakes in habitat structure and IOD in the spring). All lakes were monitored within a few days (mean range 2.5 d, SE = 0.1) on each of the four surveys. The first survey in each year coincided with an early stage of ice melting 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 (see below and Supplementary material Appendix 1 Fig. A1 in Pöysä, 2019). During each of the four waterbird surveys, the progress of ice melting on each lake was marked on a field map and later scored as follows (open water score; see 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 ice rafts or buildups here and there; 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 (this occurred in 81 lake-year cases out of 1110 (37 lakes × 30 yr) first visits, i.e. 7.3%), the IOD was estimated as the date of the first survey minus 3.5 days (i.e., the mean difference in days between two consecutive surveys divided by 2). The annual mean IOD (overall IOD, see below) did not correlate with the annual number of score 5 cases during the first visit ($r = -0.141$, df = 28, $p = 0.456$), meaning that the occurrence of score 5 cases did not bias estimates of annual mean IODs. All IODs are reported as days from April 1 for each year.

2.3. Temperature data and lake characteristics

Air temperature has been found to be the most important meteorological driver of lake IOD (Palecki and Barry, 1986; Vavrus et al., 1996; Livingstone, 1997; Weyhenmeyer et al., 2004; Benson et al., 2012; Sharma et al., 2013; Hewitt et al., 2018). Below-freezing temperatures in winter contribute to ice growth and thickness, which can affect the timing and duration of ice melting (e.g. Hewitt et al., 2018; Ariano and Brown, 2019). Spring temperature, in turn, is an important driver of the ice melting process (Vavrus et al., 1996; Livingstone, 1997; Weyhenmeyer et al., 2004); for example, the timing of ice-out in southern Finland has been found to be strongly correlated with April mean temperature (Palecki and Barry, 1986; Korhonen, 1996; Jylhä et al., 2014). In addition, the duration and prolongation of ice melting depends on diurnal temperature fluctuation around 0 °C (Ariano and Brown, 2019). I obtained daily mean temperature data for the period 1990–2020 from the 10 × 10 km gridded daily weather data set of the Finnish Meteorological Institute (Venäläinen et al., 2005); I used data from the nearest grid point (ID 863) situated about 7 km west of the study area. I used the Hellman index (Hellmann, 1918) as a measure of local winter severity; the index is calculated as the sum of mean daily temperatures that were below 0 °C between 1 November and 30 March (winter severity; more negative values mean more severe winter). I used daily mean temperatures and calculated mean April temperature (hereafter, April temperature) to study the dependence of the overall timing of ice-out (overall IOD, the annual mean ice-out date calculated using the 37 lake-specific IODs; see above) on spring temperature. Finally, for each year, I used the daily mean temperatures from a period extending 1 week before the annual overall IOD and 1 week after the annual overall IOD and calculated mean temperature for the main ice melting period (hereafter, melting period temperature); this information was used to study the effect of temperature on the degree of within-season variation among the lakes in IODs (i.e. variation among annual lake-specific IODs). It is important to note that, while the April temperature data are from the same fixed period for all years, the melting period temperature data are from different Julian dates in different years.

In lakes that have both inlet and outlet ditches, snow meltwaters running via ditches into the lake cause a flow of water, which may speed up the melting of ice (e.g. Ariano and Brown, 2019). Within a catchment basin, the occurrence of inlet and outlet ditches might be associated with topographic elevation so that low-elevation lakes more often have both ditch types, whereas high-elevation lakes do not. On the other hand, lake elevation may be important in terms of local climatic conditions and hence affect the timing of ice-out (e.g. Williams et al., 2004; Jensen et al., 2007). Surface area, elevation and the occurrence of inlet and outlet ditches were recorded for each lake using the open MapSite service provided by the National Land Survey of Finland as data source (https://www.maanmittauslaitos.fi; accessed 31 July 2020).

The study lakes differ in terms of the amount and structure of shore/littoral zone emergent vegetation, such as the common reed (*Phragmites australis*) and broadleaf cattail (*Typha latifolia*), the brown stems of which stand upright still in the spring. Wide and dense stands of such emergent vegetation potentially increase the absorption of solar radiation and, hence, could affect the onset of ice melt near the shoreline and accelerate the shore-to-centre ice melting process (e.g. Ariano and Brown, 2019). I used the lake-specific vegetation (habitat structure) index in Pöysä (2001) to characterize the shore/littoral zone emergent vegetation. The index is based on the abundance of emergent (helophyte) and floating-leaved vegetation and shore water depth; see Elmberg et al. (1993) and Nummi and Pöysä (1993) for details of vegetation classification and field procedures. In brief, the structure of emergent vegetation along the shore line of each lake was described using six categories for the type of the vegetation [1) forest and bog, 2) *Phragmites* on dry land, 3) *Carex* on dry land, 4) *Phragmites*, 5) *Carex*, 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] and four categories for both the width [1) 0–1 m, 2) 1–5 m, 3) 5–10 m, 4) >10 m] and height [1) 0–25 cm,

2) 25–50 cm, 3) 50–100 cm, 4) >100 cm] of the vegetation. The cover of floating vegetation was estimated using four categories: 0) 0%, 1) 1–5%, 2) 5–15%, 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 categories: 1) 0–50 cm, 2) 50–100 cm, 3) >100 cm. I used a principal component analysis (Pimental, 1979) to derive a single gradient of habitat structure, along which the lakes were ordered. 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 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. The 1st PCA axis was used as the lake vegetation index in the analyses.

2.4. Common goldeneye settling data

Common goldeneye observations from each survey and lake were used to assess lake settling by breeding pairs; an observation of adult male and female together or a single adult male indicates one breeding pair (Koskimies and Väisänen, 1991). A lake was considered settled in a survey if at least one breeding pair was recorded. Using this information from all surveys and years, I calculated for each lake an average lake settling order, i.e., a score indicating on which of the four surveys the lake was first settled. Only years in which a given lake was settled by common goldeneye pairs were included in the calculation; hence, possible settling order values ranged from 1.0 (a lake was settled already on the first survey in all the years included) to 4.0 (the lake was settled not until the fourth survey in all the years included). Three smallest lakes (each 0.05 ha in size) did not have common goldeneye pairs on any survey and year; therefore, they were excluded from further analyses that focused on lake-specific characteristics affecting lake settling order.

2.5. Statistical analyses

I used Sen's (1968) estimate of regression coefficient based on Kendall's rank correlation (i.e. Sen slope) to calculate trends (days/30 years) in IOD during 1991–2020 and Mann-Kendall test to assess statistical significance of the trends (two-tailed trend test). This was done separately for each of the 37 lakes (lake-specific IODs) and for composite data consisting of means of the 37 lake-specific annual IODs (overall IODs). Sen slope is a robust and frequently used non-parametric alternative to estimate and study trends in various environmental time series data (e.g. Libiseller and Grimvall, 2002; Gocic and Trajkovic, 2013), including the timing of IOD (e.g. Benson et al., 2012; Hewitt et al., 2018; Lopez et al., 2019). I used general linear models to study the importance of winter severity and April temperature in explaining among-year variation in overall IOD (response variable) and the importance of winter severity, April temperature and melting period temperature in explaining the within-season variation among lake-specific IODs, measured as the standard deviation of the overall IOD (response variable). Also, general linear models were used to study the importance of elevation, lake area, lake vegetation index and presence of ditches (binomial variable: 0 = no inlet and outlet ditches, 1 = both inlet and outlet diches) in explaining differences among the 37 lakes in lake-specific mean IODs (lake-specific means for 1991–2020) (response variable) and in the lake-specific trends of IOD (lake-specific changes (days) in IOD during 1991–2020) (response variable).

The role of the variation, both among lakes and among years, in IOD in affecting the dynamics of lake settling by common goldeneye pairs was studied from two viewpoints. First, focusing on the importance of the differences among lakes in IOD, I used general linear models to study the effect of the lake-specific mean IOD on lake settling order by common goldeneye pairs (response variable). In this analysis, I included lake area, lake vegetation index and occurrence of ditches as additional explanatory variables to control for their potential impact on lake selection by common goldeneye pairs. Lake area is potentially important as it may affect the probability of lake settling due to sampling effect (e.g. Hill et al., 1994; specifically, a larger lake can physically accommodate more birds). Previous work has shown that lake shore vegetation structure affects lake use of common goldeneye pairs (Nummi and Pöysä, 1993; Suhonen et al., 2011). The occurrence of outlet and inlet ditches, in turn, is potentially important for lake settling by common goldeneye pairs, because common goldeneye is an early arrival, and early spots of open water typically spring up at the mouth of ditches, potentially attracting common goldeneye pairs. Second, I wanted to know how differences among years in the progress of ice melting affect the dynamics of lake settling by common goldeneye pairs within a season. Overall changes in ice melting were greatest between the first and second survey, these being also the surveys during which the between-lake variation in the progress of ice melting was greatest (Supplementary material Table S1). I recorded the number of lakes settled in the first and second survey for each year and calculated the rate of change in the number of lakes settled from the first survey to the second as: $\log_{10}$ number of lakes settled in the second survey – $\log_{10}$ number of lakes settled in the first survey. Similarly, I used lake-specific open water scores from these surveys and calculated corresponding rate of change in ice melt (amount of open water) as: $\log_{10}$ open water score in the second survey – $\log_{10}$ open water score in the first survey. I used general linear models to study if differences among years in the rate of ice melting affect differences among years in the rate of change in lake settling by common goldeneye pairs (response variable).

All response variables, as specified above, were used as continuous variables in the general linear models. Continuous explanatory variables (lake elevation, lake area and lake vegetation index) were log-transformed; occurrence of ditches was included as a binomial covariate in the analyses. Pair-wise correlation between any two explanatory variables was <0.7 (Supplementary material Table S2), indicating no serious multicollinearity (Dormann et al., 2013). Multicollinearity among the explanatory variables was further checked by calculating variance inflation factors (VIFs) for each explanatory variable in different models; multicollinearity appeared not to be a problem as all VIFs were < 2.10 (Supplementary material Table S3; see Zuur et al., 2010). Hence, full models including all the explanatory variables, without interaction terms, were fitted and used as the basis for interpretation in all cases (Whittingham et al., 2006; Fieberg and Johnson, 2015). Even though the VIFs indicated absence of multicollinearity among the explanatory variables, I used an all-possible-models approach to make sure that spurious effects or masking effect of potential suppressor variables did not confound interpretations based on the full model (e.g. Mac Nally, 2000). Specifically, I fitted in each case all possible models (combinations of explanatory variables) to the data and used the regression coefficients of the models and hierarchical partitioning to assess the independent effect of each explanatory variable (e.g. Mac Nally, 2000; Murray and Conner, 2009; see the latter reference for the technique and equation to calculate independent effects). The assumption of normality of residuals in general linear models was checked with normal probability plots (e.g. Zuur et al., 2010). The linearity assumption was satisfied for all models (Supplementary material Fig. S3).

Finally, analyses based on time series data can produce spurious relationships if both the response variable and the explanatory variables change across time, i.e. show a trend (Lindström and Forchhammer, 2010; Iler et al., 2017). This appeared to be the case here with some of the response and explanatory variables (Supplementary material

Table S4). Hence, the potential confounding effect of year was controlled for by including year as a fixed effect in the models, where appropriate (Freckleton, 2002; see also Iler et al., 2017, p. 649).

All statistical analyses, including plotting of regressions, were performed in SYSTAT 13.

3. Results

3.1. Overall trends and within-season variation in IOD

Overall (i.e., mean) IOD showed an advancement of 9.8 days during 1991–2020 (Fig. 1; Sen's slope = −0.327, 95% CL, lower −0.549, upper −0.086; Z = −2.659, $p = 0.008$). Overall IOD advanced with increasing April temperature, winter severity having only marginal effect on IOD (Table 1).

Within-season variation between the lakes in IOD (i.e. standard deviation of annual overall IOD) was not constant but varied between years, showing an increasing trend during 1991–2020 (Fig. 2; Sen's slope = 0.059, 95% CL, lower 0.018, upper 0.097; Z = 2.605, $p = 0.009$). While winter severity, April temperature and melting period temperature all seemed to affect the within-season variation in IOD, the last-mentioned variable had the highest explanatory power (Table 1); specifically, low temperature during the melting period increased the within-season variation in IOD.

3.2. Among-lake variation in IOD

There was considerable variation among the lakes in mean IOD and in the rate of advancement of IOD, the former ranging from 24 April to 6 May and the latter from 1.5 days to 16.1 days during 1991–2020 (Supplementary material Table S5). Variation among the lakes in mean IOD was best explained by elevation, none of the other explanatory variables having much explanatory power (Table 2); lakes at higher elevations had later IOD than lakes at lower elevations (Fig. 3a). Variation among the lakes in the rate of advancement of IOD, in turn, was best explained by lake area: IOD had advanced more in large lakes than in small lakes (Table 2, Fig. 3b). Explanatory power of the other variables (lake elevation, vegetation index and the occurrence of ditches) was poor.

3.3. Lake settling by common goldeneye pairs in relation to variation in IOD

In general, while taking into account potential effects of lake area and vegetation index on lake settling by common goldeneye pairs, lake-specific mean IOD affected the variation among the lakes in average settling order (Table 3): lakes with earlier mean IOD were settled earlier within a season than lakes with later mean IOD (Fig. 4a). The occurrence of ditches was not important in explaining the order of lake settling by common goldeneye pairs (Table 3).

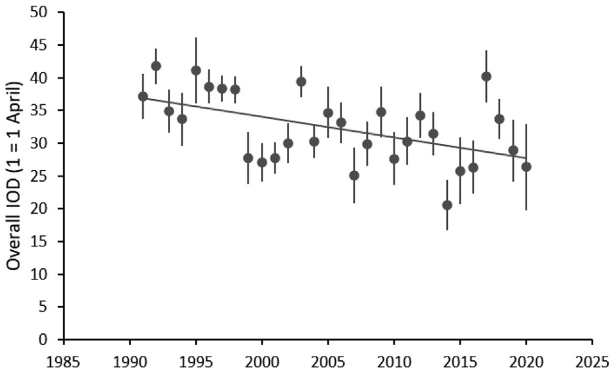

Fig. 1. Mean (±SD) annual ice-out date (Overall IOD) of 37 boreal lakes in southeastern Finland in 1991–2020. Trend line shows a regression through the raw mean IODs (see '3.1 Overall trends and within-season variation in IOD' for test statistics).

Table 1
Models to explain among-year variation in overall IOD and in the standard deviation of overall IOD. Explanatory variables are listed in decreasing order of importance based on the independent effect, with the most important variable in bold. Independent effect of each explanatory variable represents the average contribution of the variable to the variance in the response variable over all possible models (see '2.5 Statistical analyses' for further details).

Explanatory variable	β	SD	t	p	Independent effect	
					Value	Weight
Overall IOD						
April temperature	**−2.605**	**0.398**	**−6.547**	**0.000**	**0.543**	**0.756**
Year	−0.157	0.071	−2.222	0.035	0.152	0.212
Winter severity	−0.002	0.002	−1.191	0.244	0.023	0.032
Overall model: $r^2 = 0.719$, $F_{3,26} = 22.229$, $p < 0.001$						
Standard deviation of overall IOD						
Melting period temperature	**−0.286**	**0.060**	**−4.667**	**0.000**	**0.383**	**0.580**
Winter severity	0.001	0.000	2.358	0.027	0.115	0.174
Year	0.012	0.015	0.805	0.429	0.104	0.158
April temperature	0.140	0.080	1.750	0.092	0.058	0.088
Overall model: $r^2 = 0.660$, $F_{4,25} = 12.156$, $p < 0.001$						

Considering the within-season progress in lake settling by common goldeneye pairs, the number of lakes settled ranged from 2 to 19 (mean = 8.7) in the 1st survey, and from 8 to 21 (mean = 15.7) in the 2nd survey. The rate of increase in the number of lakes settled from the 1st to the 2nd survey was dependent on the rate of ice melting between the surveys ($\beta = 0.756$, SE = 0.132, $r^2 = 0.540$, $F_{1,28} = 32.847$, $p < 0.001$); the greater the increase in mean open water score from the 1st to the 2nd survey within a year, the greater the increase in the number of lakes settled by common goldeneye pairs from the 1st to the 2nd survey (Fig. 4b). Inclusion of year as a fixed effect in the model (see 2.5. Statistical analyses) did not change the result (rate of ice melting: $\beta = 0.746$, SE = 0.139, $t = 5.377$, $p < 0.001$; year: $\beta = 0.001$, SE = 0.003, $t = 0.298$, $p = 0.768$; overall model: $r^2 = 0.541$, $F_{2,27} = 15.934$, $p < 0.001$).

4. Discussion

Results of this study demonstrate how global warming may differently affect the timing of ice-out and its advancement in boreal lakes situated within the same catchment area, lake elevation and size being the main influencing factors. This local variation in turn, was shown to govern lake settling dynamics of early migrating common goldeneye pairs. The findings of this study should be of general importance, considering that tens of millions of lakes similar in size to the lakes studied here are located north of 60°N (Verpoorter et al., 2014), being thus seasonally ice-covered (Sharma et al., 2019).

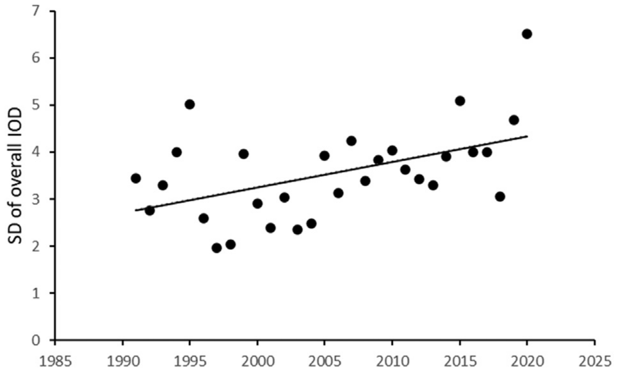

Fig. 2. Annual among-lake variation in ice-out date (measured as the standard deviation, SD, of the overall IOD) among 37 boreal lakes in southeastern Finland in 1991–2020. Trend line shows a regression through the raw SD values (see '3.1 Overall trends and within-season variation in IOD' for test statistics).

Table 2
Models to explain among-lake variation in mean IOD and in the advancement of IOD. Explanatory variables are listed in decreasing order of importance based on the independent effect, with the most important variable in bold. Independent effect of each explanatory variable represents the average contribution of the variable to the variance in the response variable over all possible models (see '2.5 Statistical analyses' for further details).

Explanatory variable	β	SD	t	p	Independent effect	
					Value	Weight
Among-lake variation in IOD						
Elevation	**25.512**	**5.747**	**4.439**	**0.000**	**0.363**	**0.784**
Vegetation index	−3.639	2.061	−1.766	0.087	0.079	0.171
Ditches	0.92	0.901	1.021	0.315	0.013	0.028
Area	0.813	1.214	0.67	0.508	0.007	0.017
Overall model: $r^2 = 0.463$, $F_{4,32} = 6.896$, $p < 0.001$						
Among-lake variation in the rate of advancement of IOD						
Area	**3.989**	**1.537**	**2.595**	**0.014**	**0.192**	**0.584**
Elevation	−10.197	7.279	−1.401	0.171	0.059	0.180
Vegetation index	1.139	2.61	0.436	0.666	0.056	0.171
Ditches	−0.388	1.142	−0.34	0.736	0.021	0.065
Overall model: $r^2 = 0.329$, $F_{4,32} = 3.926$, $p = 0.011$.						

Table 3
Models to explain among-lake variation in the within-season settling order by common goldeneye pairs. Explanatory variables are listed in decreasing order of importance based on the independent effect, with the most important variable in bold. Independent effect of each explanatory variable represents the average contribution of the variable to the variance in the response variable over all possible models (see '2.5 Statistical analyses' for further details).

Explanatory variable	β	SD	t	p	Independent effect	
					Value	Weight
IOD	**0.122**	**0.021**	**5.682**	**0.000**	**0.370**	**0.491**
Vegetation index	−0.426	0.342	−1.247	0.222	0.180	0.239
Area	−0.632	0.175	−3.606	0.001	0.169	0.225
Ditches	0.012	0.127	0.093	0.927	0.034	0.045

Overall model: $r^2 = 0.753$, $F_{4,29} = 22.150$, $p < 0.001$.

4.1. Local variation in IOD

While the advancement of IOD in northern boreal lakes has been documented in several earlier studies (references in the Introduction), the rate of advancement (3.3 days/decade) observed here is among the fastest reported so far. Given that the IOD data are from the last three decades, this finding suggests that the rate of advancement of IOD has increased, as has been suggested in some earlier studies (Hodgkins, 2013; Preston et al., 2016; Woolway et al., 2020). The finding that April temperature was important in explaining the timing of IOD supports earlier studies that air temperature in the weeks to months before IOD affect the timing of ice-out (Lopez et al., 2019; Sharma et al., 2020). That the within-season variation among lakes in IOD, explained by temperature in the overall ice melting period, showed an increasing trend with time is a new finding for boreal lakes. Even more importantly, to the best of my knowledge, these are the first results to demonstrate that relatively small lakes situated within the same catchment area may differ considerably, over an order of magnitude, in the rate of advancement of IOD. It is notable that the difference among the lakes in the rate of advancement of IOD (14.6 days) was greater than the overall advancement (9.8 days) at the study area level (i.e., mean of the lake-specific trends in IOD). Also, it is larger than the overall advancement of IOD reported in studies from other regions for a comparable time span. For example, Hewitt et al. (2018) reported that overall ice-out was 5 days earlier between 1981/2 and 2014/

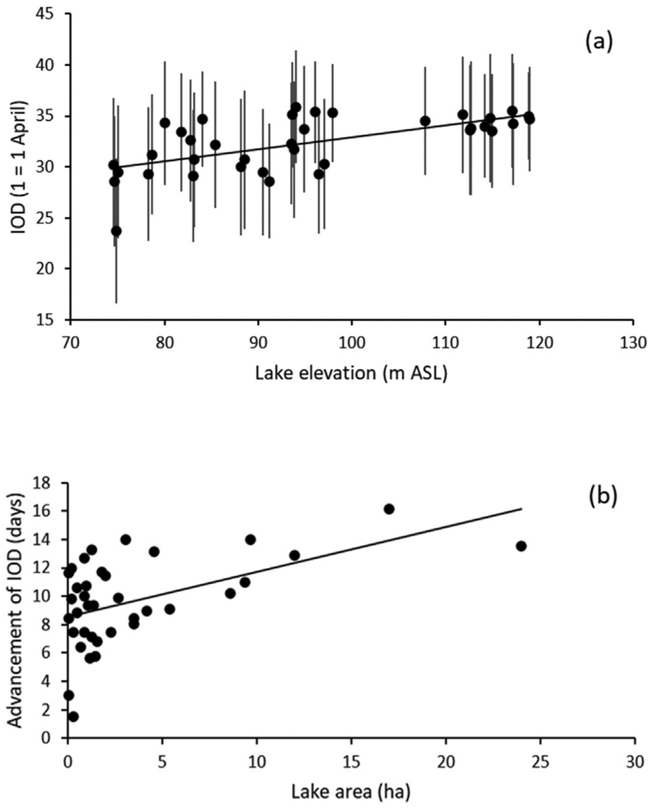

Fig. 3. Lake-specific mean (±SD) ice-out date (IOD) in relation to lake elevation (m above sea level, ASL) (a) and lake-specific advancement of IOD during 1991–2020 in relation to lake size (b). Trend lines show a regression through the raw mean IODs (a) and data points (b) (see Table 2 for test statistics).

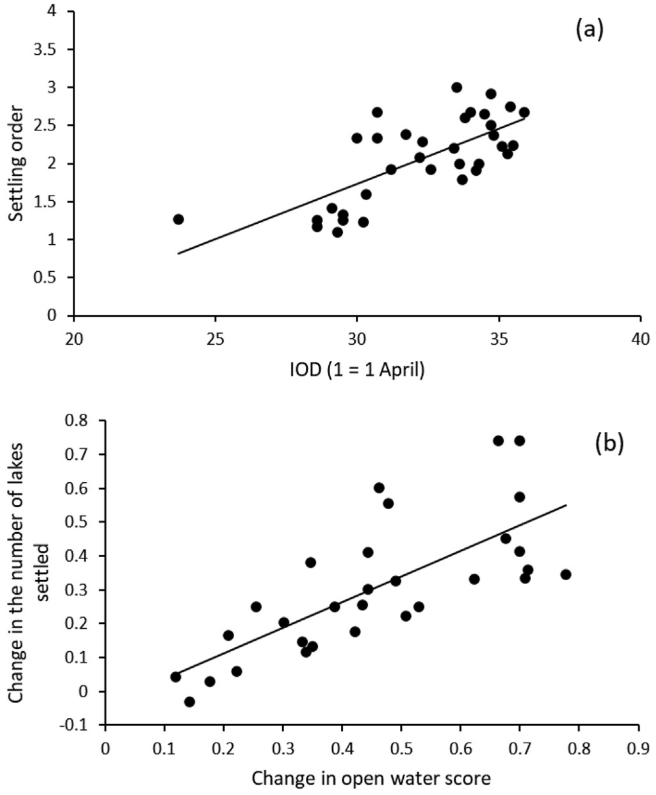

Fig. 4. Lake-specific mean settling order by common goldeneyes in relation lake-specific mean ice-out date (IOD) (a) and annual rate of increase in the number of lakes settled from the 1st to the 2nd survey in relation to the rate of ice melting between the corresponding surveys (b). Note that the means in (a) are based on the annual (1991–2020) values (see '2.4 Common goldeneye settling data' for further explanation). Trend lines show a regression through the raw data points (see '3.3 Lake settling by common goldeneye pairs in relation to variation in IOD' and Table 3 for test statistics).

5 (35 years) in seven lakes in northern Wisconsin, Canada. The increase of the within-season variation among lakes in IOD with time means that temporal heterogeneity in habitat availability has increased, a phenomenon that probably has important consequences for habitat selection of early arriving species that track closely the progress of ice melting when settling on breeding lakes (see below).

That lake elevation and size were important in explaining differences between the lakes in IOD and its advancement is a bit surprising, given that the variation for both of these variables was relatively small in the data (see Fig. 3). While elevation has been recognized important to IOD in some studies (see Sharma et al., 2020), the data in earlier studies are from mountain or alpine lakes or from geographically wide areas, covering much greater elevation gradients (Christianson et al., 2021). These are the first results to demonstrate such effects of elevation and lake size on IOD at a local scale, i.e. within a catchment area. For comparison, in a study based on satellite imagery data, Arp et al. (2013) found that IOD was explained by lake area within several lake districts in the Arctic Coastal Plane, Alaska; however, the lakes studied by these authors were much larger and covered a much wider range of sizes (min 1.6 km^2, max 836.1 km^2) than the lakes of this study. Elevation obviously is not the influential landscape feature, but it is probably mediating impacts of other factors such as variation in microclimate and in how closed is the habitat around the lake (e.g. whether the lake is surrounded by closed forests versus more open habitat such as treeless mires and fields). Further studies should address which are the specific elevation-related landscape features that affect the timing of ice-out.

4.2. IOD in the landscape context

The findings of this study bring up a previously neglected angle into the research of climate warming-caused changes in IOD: the landscape perspective. While this research approach has been previously recognized important to understand biotic and abiotic characteristics of lakes (Soranno et al., 1999; Riera et al., 2000), it has received little attention in the context of IOD research. This is probably because the research on IOD and its dynamics typically has focused more on large scale phenomena and within-lake processes but not on variation among lakes at the local scale (see Sharma et al., 2020 for a review of approaches currently used to study lake ice dynamics; further references in the Introduction). Notable exceptions to this general pattern are high-elevation mountain and alpine lakes where the importance of differences in topographic shading and snow accumulation have been recognized important in the development and duration of ice-cover (Novikmec et al., 2013; Preston et al., 2016).

However, elevation may play an important role also in lowland lakes (i.e. lakes <200 m ASL; Solheim et al., 2019), such lakes being vulnerable also to other anthropogenic stressors than climate warming. In general, lake connectivity and position in the landscape determine the degree to which a lake is prone to accumulation of harmful substances; highly connected lower elevation lakes are particularly vulnerable to negative anthropogenic impacts as they receive nutrients and pollutants through water flow from the upper parts of the catchment area (Arvola et al., 2010; Heino et al., 2021). This study revealed that IOD was earlier in lower elevation lakes. Therefore, the impact of anthropogenic stressors in those lakes may become disproportionally amplified due to climate warming-caused directional shift in IOD. For example, rising nutrient inputs and increasing temperatures may mutually intensify eutrophication symptoms in lake ecosystems (Moss et al., 2011; Shuvo et al., 2021). In lakes covered by ice in the winter, earlier ice breakup causes earlier and stronger thermal stratification and increases the period over which the lake warms over the summer months (Winder and Schindler, 2004; Austin and Colman, 2007). These changes increase the risk of algal blooms in nutrient-rich lakes (Winder and Schindler, 2004) and decrease late summer hypolimnetic dissolved oxygen levels (Hodgkins, 2013), both being phenomena that have fundamental implications to the functioning of freshwater lake ecosystems (Shuvo et al., 2021). With earlier IOD, lower elevation lakes are particularly vulnerable to the mutual effects of increasing temperature and nutrient input. All in all, research on the timing of ice-out and hydrology should more explicitly include the landscape context also for lowland lakes to enhance understanding of local drivers of IOD and, particularly, possible consequences of the differently advancing IOD in lakes within the same catchment area.

4.3. IOD and higher trophic levels: early-season lake settling dynamics of common goldeneyes

Earlier studies have shown that, at the landscape scale, among-year variation in overall settlement phenology of many waterbirds in the spring tracks among-year variation in IOD (Pöysä, 2019). This study adds to the understanding of the importance of IOD in affecting the settling dynamics of early migrating waterbirds, by showing how the progress of ice melting within a season, and differences between lakes in that process, govern lake settling by common goldeneye pairs within the landscape. Upon arrival on the breeding grounds, paired common goldeneye males display agonistic behaviour and start defending mates and territories (Savard, 1984; Eadie et al., 1995). Nest site fidelity of common goldeneye females is high, particularly if the nesting attempt in the previous year has been successful (Dow and Fredga, 1983). However, nest sites may be situated far from the first open water areas early in the spring, as is the case in this study area (Pöysä H, unpublished data). Therefore, lakes that have large ice-free areas early in the season typically accumulate early arriving common goldeneye pairs (Pöysä H, unpublished data). The increase in the number of lakes settled with the progress of ice melting within a season probably is affected by the territorial behaviour of males of pairs that have settled on lakes with large open water areas. However, it may also be that later arriving pairs settle on new lakes directly when these become accessible as the total number of pairs in the area usually increases from the 1st survey to the 3rd survey (Pöysä, 2019).

Whatever the behavioural mechanisms driving the dynamics of local distribution of breeding pairs in the early season are, the rate of the progress of ice melting governs habitat (open water) availability and, hence, plays a central role in lake use by breeding birds. Differences among lakes in the timing of ice-out introduce temporal heterogeneity to local breeding habitat availability, probably resulting in local among-lake variation in breeding success, a topic that is worth addressing in further research. It is noteworthy that the temporal heterogeneity in habitat availability early in the spring seems to be increasing, as indicated by the increase of the within-season difference between the lakes in IOD over the study period. This development may affect breeding waterbirds negatively; the effect may be counterintuitive, considering that earlier IOD per se is expected to be advantageous to open water-dependent waterbirds as it enables earlier breeding (Milonoff et al., 1998; Clark et al., 2014; Bianchini et al., 2021). For example, while there has been no overall decline in the breeding abundance of the common teal (*Anas crecca*) in the study area during 1991–2018, breeding numbers on lakes with early IOD have decreased, whereas those on lakes with late IOD have increased (Pöysä and Paasivaara, 2021). At the same time, breeding success decreased on lakes with early IOD, while it increased on lakes with late IOD (Pöysä and Paasivaara, 2021). These findings suggest that the quality of lakes with early and more advanced IOD has decreased as breeding habitat.

Lake-specific changes in IOD may also have fundamental consequences for migration decisions of waterbirds, specifically the timing of arrival. Considering that temporal heterogeneity in habitat availability may be increasing over time due to differently advancing IODs in nearby lakes, as found in this study, competition for best breeding lakes may increase. Because better habitats usually are occupied earlier than poorer ones (Fretwell and Lucas, 1970; Orians and Wittenberg, 1991; Pulliam and Danielson, 1991), differently advancing IODs can generate a ‘cascading’ competition (sensu Kokko, 1999) for early arrival, which may advance arrival dates apart from condition-dependent individual optimum dates for the onset of breeding (Kokko, 1999). The timing of breeding varies considerably among common goldeneye females (Clark et al., 2014; Messmer et al., 2021) and this variation has clear fitness consequences (Clark et al., 2014). It would be interesting to know if this variation is associated with variation in the timing of arrival and lake settling and if the relationship between the timing of arrival and the timing of breeding has changed over time.

All in all, more research is needed to understand the impacts of IOD and its advancement on lake settling dynamics and breeding success of migratory waterbirds at lake versus landscape level in the boreal areas. Shifts in lake use and changes in breeding success are to be expected, if climate warming-driven shifts in IOD differently affects the quality of nearby lakes (see above and Pöysä and Paasivaara, 2021). Furthermore, more research on impacts of climate warming-caused advancement of ice-out on the aquatic food web is needed, extending from primary producers via primary consumers to higher trophic levels, such as waterbirds and fish. Such impacts may be complex as demonstrated by Caldwell et al. (2020) for a cool-water fish, the brook trout (*Salvelinus fontinalis*): earlier ice-out increased production in littoral habitat but limited consumer accessibility to that habitat through warming water (see also Guzzo and Blanchfield, 2017). Research need is particularly urgent in the case of waterbirds, because abundances of many species in boreal Europe are declining (Lehikoinen et al., 2016; Elmberg et al., 2020; Pöysä and Linkola, 2021), but our understanding of climate warming-driven impacts on waterbirds is limited (Guillemain et al., 2013; Fox et al., 2015). Such impacts may be mediated through changes in the timing of ice-out in the breeding lakes as they have been found to affect breeding success, not only in ducks relying on invertebrate food (Clark et al., 2014; Pöysä and Paasivaara, 2021) but also in fish eating waterbirds such as the common loon (*Gavia immer*) (Bianchini et al., 2021). Changes in the duration and dynamics of the ice season in the wintering grounds of waterbirds may also be important as they have been found to affect numbers and distribution of overwintering waterbirds (Lehikoinen et al., 2013; Marchowski et al., 2017, 2020). Such distributional changes may have negative impacts on entire populations, for example if the network of current protection areas turns out to be inefficient to buffer against spatially varying anthropogenic pressures in the wintering areas (Pavón-Jordán et al., 2015; Marchowski et al., 2020).

5. Conclusions

Results of this study demonstrate how global warming may differently affect the timing of ice-out in boreal lakes even within the same catchment area. Particularly the rate of the advancement of IOD may vary considerably among nearby lakes, even more than the overall advancement of IOD at the landscape level. This local variation affects the ability of open water-dependent species to start reproduction in the spring, as exemplified here by IOD-governed lake settling dynamics of common goldeneye pairs. More research in the landscape context is needed to enhance our understanding of changes in the timing of ice-out in boreal lakes and how differently advancing IOD affects food web interactions within freshwater ecosystems and, particularly, local dynamics of organisms dependent on open water to successfully accomplish critical stages of the life cycle. All in all, the findings of this study echo recent calls (Richardson and Sato, 2015; Schulz et al., 2015; Soininen et al., 2015; Heino et al., 2021) to better integrate climate change impact research across the aquatic-terrestrial interface.

CRediT authorship contribution statement

The work has not been published previously and is not under consideration for publication elsewhere. All authors have approved the manuscript and its submission.

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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Appendix A. Supplementary material

Supplementary data to this article can be found online at https://doi.org/10.1016/j.scitotenv.2021.151397.

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