



Original Research Article

Exploring the browning of two small headwater boreal lakes over 25 years: the role of beaver floods, climate, acid recovery and forestry

Clarisse C. Blanchet^{a,b,c,*} , Aurélie Davranche^{c,d}, Petri Nummi^a,
Kimmo K. Kahilainen^c, Henrik Lindberg^e, Risto Viitala^e, Céline Arzel^b

^a Department of Forest Sciences, University of Helsinki, P.O. Box 27, Helsinki FI-00014, Finland

^b Department of Biology, University of Turku, Turku FI-20014, Finland

^c Lammi Biological Station, University of Helsinki, Pääjärventie 320, Lammi FI-16900, Finland

^d CNRS UMR 6590 ESO, University of Angers, Angers FR-49000, France

^e HAMK University of Applied Sciences, Forestry Programme, Saarelantie 1, Evo, FI-16970, Finland



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ABSTRACT

Many boreal freshwaters have become browner in the past decades, underscoring the need for long-term assessments of brownification drivers. Here, we examined long-term changes in water color (mg Pt/L), beaver activity, climate, acidifying ions concentration in precipitation, and forestry in two small boreal lakes and their catchment in 1994–2018; one lake being occupied by beavers (L. Majajärvi) and one never colonized (L. Horkkajärvi). During the study period, average annual air temperature increased (+0.049 °C per year) while average annual acidifying ion concentrations declined (−0.286 μeq SO₄^{2−}/L and −0.046 μeq NO₃[−]/L per year); annual precipitation showed no trend. Both lakes exhibited browning over time (+3.30–3.42 mg Pt/L per year). Precipitation positively influenced water color in both lakes, while annual SO₄^{2−} concentration had a negative effect. In L. Majajärvi, water color was browner during beaver floods and afterflood phases, with precipitation and beaver activity explaining a similar share of water color variability, thus underlining their similar role in mobilizing DOC from the riparian zone. In contrast, the effects of annual SO₄^{2−} concentration on water color will likely subside as other factors will drive lake browning. Forestry and air temperature showed no direct effect, potentially masked by other factors. Our results highlight beavers as ecosystem engineers able to drive water browning locally. This study demonstrates the multifaceted and complex nature of water browning and emphasizes the need for broader-scale assessments integrating both local and global drivers.

1. Introduction

The browning or brownification of many freshwaters has been studied in the past three decades in the Nordic countries. This phenomenon is the result of a combination of – changes in – climate, atmospheric acid deposition, and anthropogenic activities (see Monteith et al., 2007; de Wit et al., 2016; Krutzberg et al., 2020; Blanchet et al., 2022). Browning is defined as an increase of the color of surface waters towards yellow-brown hues over time (Graneli, 2012). The transport of terrestrial dissolved organic matter (DOM) or

* Corresponding author at: Department of Forest Sciences, University of Helsinki, P.O. Box 27, Helsinki FI-00014, Finland.
E-mail address: clarisse.blanchet@helsinki.fi (C.C. Blanchet).

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carbon (DOC) and dissolved iron (Fe) to water bodies through runoff largely contribute to the browning process (Hongve et al., 2004; Erlandsson et al., 2008; Kritzberg and Ekström, 2012; Xiao and Riise, 2021). This change of water color affects key environmental factors such as light, water temperature, and oxygen availability, which in turn strongly affect aquatic food webs, e.g. phytoplankton, biofilm, macrophytes, fish, aquatic invertebrates, host-parasite and prey-predator relationships, and pathogens (Blanchet et al., 2022). Although browning has not occurred in all boreal freshwaters and has slowed down in several regions (Eklöf et al., 2021), this phenomenon is still occurring in many lakes and streams of diverse climatic zones and freshwater habitats (see in Blanchet et al., 2022). Thus, there is an urgent need to understand the causes and consequences of browning to protect freshwater ecosystem functioning and freshwater quality.

The recovery from acidification following the decrease in atmospheric acid (sulfur and nitrogen) deposition is a well-recognized factor driving the browning of waters (Evans et al., 2005; Ekström et al., 2011; Meyer-Jacob et al., 2020). Acidification recovery enhanced the solubility and mobility of soil colored DOM, which facilitated its transport to freshwaters, potentially bringing Fe as well due to DOM-Fe complexes (Monteith et al., 2007; Neal et al., 2008; Björnerås et al., 2017; LoRusso et al., 2020; Redden et al., 2021). Climate change also contributes to the browning of waters; first by increasing soil DOM production through changes in temperature (Christ and David, 1996; Moore and Dalva, 2001; Catalán et al., 2016) and vegetation cover (Finstad et al., 2016), second by enhancing DOM leaching to surface waters through changes in precipitation amount and runoffs (Sarkkola et al., 2013; de Wit et al., 2016; Björnerås et al., 2017).

Forest management enhances the transport of DOM from terrestrial to aquatic systems (Finér et al., 2021; Nieminen et al., 2021; Holopainen and Lehtikoinen, 2022), which contributes to the long-term observed browning in the boreal region (Kritzberg, 2017; Škerlep et al., 2020; Härkönen et al., 2023). Clearcutting and site preparation have received the most attention. Clearcutting increases the leaching of DOC to surface waters through a combination of raised groundwater level (due to reduced evapotranspiration; Sarkkola et al., 2010), increase of loose organic matter (Piirainen et al., 2007), and increase of soil temperature that promotes the decomposition of organic matter (Schelker et al., 2012). Site or soil preparation is often associated with clearcutting as it is performed after a clearcut to facilitate tree establishment before replanting, and is known to enhance the leaching of DOC to surface waters (e.g. Piirainen et al., 2007; Schelker et al., 2012). There is a lack of knowledge on the impact of thinning practices (i.e. selective removal of trees) on water color, although such practices are expected to influence water DOC in the same way as clearcutting and site preparation (Bäumler and Zech, 1999; Yang et al., 2021). Also, studies in ditched peatland landscapes highlighted the contribution of forestry practices to the browning of waters (Nieminen et al., 2017; Härkönen et al., 2023).

Most studies on the causes of water browning pointed out anthropogenic activities and their consequences (e.g. climate and land-use changes) as drivers of browning (see in Creed et al., 2018; Kritzberg et al., 2020). Some “natural” drivers such as land cover can control the browning level of lakes and rivers through DOC and Fe levels (Arvola et al., 2016; Björnerås et al., 2017). Additionally, beavers (*Castor* sp.) as ecosystem engineers might promote water browning as a result of their damming activity (Vehkaoja et al., 2015; Catalán et al., 2017). Depending on habitat suitability, beavers typically dam first to fourth-order streams or the outlet of small lakes, creating new ponds or raising the lake shore level respectively. With this change from a terrestrial ecosystem to an aquatic one, the wetland area is considerably increased, and the physical, chemical, and biological conditions of the riparian zone is altered (Johnston, 2017; Nummi et al., 2018; Bashinskiy, 2020; Larsen et al., 2021). As each beaver patch goes through different stages of succession, the beaver landscape becomes a dynamic mosaic of flood-inundated and afterflood beaver patches (Naiman et al., 1988; Nummi and Hahtola, 2008; Kivinen et al., 2020), with beaver floods strongly affecting the carbon dynamics of the aquatic-terrestrial interface, thus creating biogeochemical hotspots with enhanced fluxes and reactions rates (Larmola et al., 2004; Johnston, 2017; Nummi et al., 2018).

When beavers dam a waterbody, a considerable amount of herbaceous vegetation and trees decay in the shallow inundated beaver flowage because of the anaerobic conditions caused by the raising water (Nummi, 1989; Thompson et al., 2016; Johnston, 2017). During inundation, the organic matter and nutrients originating from the dead vegetation and soil leach from the flooded area to the waterbody (Brothers et al., 2014). It induces an increase in DOC concentration in the surface water (Cirmo and Driscoll, 1993), first with low molecular weight DOC that is easily degraded by microbial consumers, then with a more humic-like DOC that promotes a brown water color (Wegener et al., 2017; Nummi et al., 2018). While DOC levels increase during the first three years of a beaver impoundment, they seem to decrease to pre-flood levels in the 4–6 next years (Vehkaoja et al., 2015) with possibly more humic DOC remaining. In contrast, a study showed that a lake did not fully recover from a flood-induced browning, with DOC levels remaining 1.5-fold higher than pre-flood levels 7 years after the browning event (Kazanjian et al., 2021). DOM composition in beaver ponds is strongly characterized by high humic content and aromaticity (Castro et al., 2023). Thus, the source of DOM in beaver flooded areas is mainly terrestrial and brown-colored regardless of its concentration in water.

Beavers were exterminated from most of their range in Eurasia and from large areas of North America too between the 16th and 19th centuries; but they returned or are returning to many parts of their former range (Whitfield et al., 2015; Halley et al., 2021). Along with the recovery of beaver populations, about 25 000 km² of new aquatic pond habitats and 550 000 km of riparian shore habitats have been created in the boreal and temperate zones (Whitfield et al., 2015). These first results call for a deeper understanding of the potential local contribution of beaver floods to water browning and its spatial extent.

In this context, this study assessed the long-term water browning of two humic lakes separately from 1994 to 2018 in the Evo area, Southern Finland, where many lakes underwent browning during our study period (Arvola et al., 2010; Arzel et al., 2020; Arvola et al., 2025). Both lakes are located in one catchment area, and hence experience similar environmental conditions, except for the colonization of beavers in one lake (L. Majajärvi), while the other lake has never been occupied by beavers (L. Horkkajärvi). First, we examined the trends of environmental variables (precipitation, air temperature, SO₄²⁻ and NO₃⁻ precipitation) of the Evo area during the study period. We expected an increase in both annual precipitation and average air temperature during the study period and a decline of both SO₄²⁻ and NO₃⁻ annual concentrations over time. Second, we evaluated the browning of the two lakes and the influence of various

environmental parameters and activities on the yearly measured water color of both lakes, one occupied by beavers, one never colonized by beavers, to assess if beaver activity can be a significant driver of lake water color change. We considered the following environmental parameters with or without beaver activity: forestry practices surfaces (thinning, clearcutting, soil preparation) within the catchment area, climate parameters (temperature, precipitation), and acidifying ions concentration (SO_4^{2-} and NO_3^- in precipitation). L. Horkkajärvi, which had not experienced any beaver flood before or during the study period, was a control site that met all environmental changes except beaver floods. While we predicted beaver activity to be a significant local driver of lake water browning in L. Majajärvi, we wanted to evaluate its significance compared to forestry practices, climate, and acid recovery, which have been proved in the scientific literature to be significant global drivers of water browning in the boreal environment. Our study intends to fill the gaps regarding the potential impacts of beaver activities on boreal forest ecosystems with a specific focus on local scale water color dynamics.

2. Material and methods

2.1. Study area

The study focused on two hydrologically connected lakes, Lake Majajärvi and Lake Horkkajärvi (3.88 and 1.15 ha; Fig. 1), located in the Evo State Forest, Southern Finland ($61^\circ 11' 34'' \text{ N}$, $25^\circ 06' 29'' \text{ E}$; Arvola et al., 2010); more specifically in the educational training forest of Häme University of Applied Sciences (HAMK). L. Horkkajärvi is a tributary lake of L. Majajärvi. Hence, its catchment (43.6 ha) is a subpart of L. Majajärvi's catchment (190.67 ha).

L. Majajärvi is located in low elevation (133.3 m a.s.l.) with maximum and mean depths of 12 and 4 m; its water is considered to be brown (227 mg Pt/L in October 2020) and it is slightly eutrophic (total phosphorus 26 $\mu\text{g/L}$, total nitrogen 805 $\mu\text{g/L}$, DOC 20.7 mg/L, Fe 0.6 mg/L; 5.76 pH in October 2020). L. Horkkajärvi is located in higher elevation (142.7 m a.s.l.) and with a higher mean depth (7.7 m) than L. Majajärvi and a similar maximum depth (12 m). L. Horkkajärvi is also a brown lake (263 mg Pt/L in October 2020) but more mesotrophic (total phosphorus 16 $\mu\text{g/L}$, total nitrogen 770 $\mu\text{g/L}$, DOC 25.5 mg/L, Fe 0.7 mg/L; 5.60 pH in October 2020). Both lake catchments are dominated by forest (96.4 and 97.5 %), mostly composed of coniferous species, with a small proportion of waterbodies and wetlands (3.6 and 2.5 %).

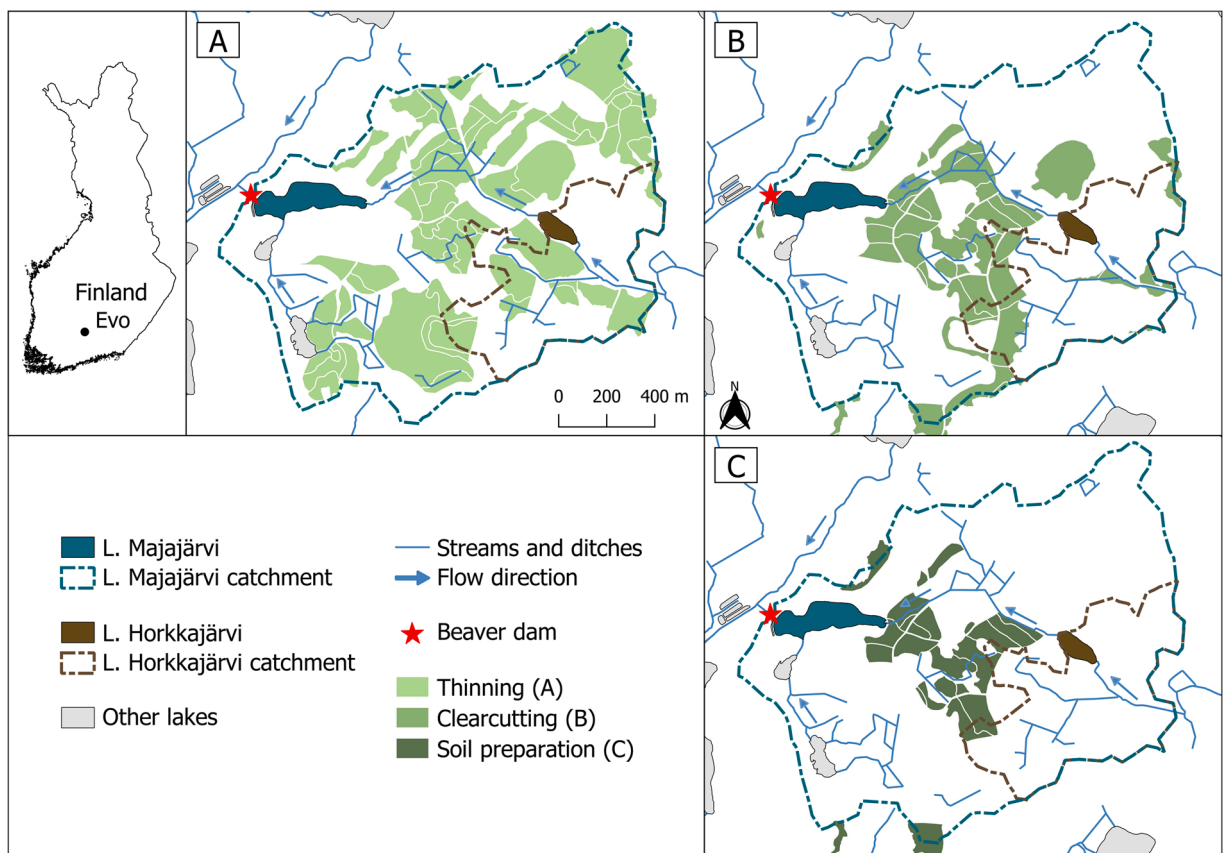


Fig. 1. Presentation of the studied lakes and their catchments (Evo area, Southern Finland), with forestry practices carried out in the catchment areas between 1994 and 2018. A) Thinning, B) Clearcutting, and C) Soil preparation (including soil harrowing, mounding, and scalping practices).

According to the Geological Survey of Finland (GTK, <https://www.gtk.fi/>), the bedrock of the entire catchment area of L. Majajärvi and L. Horkkajärvi is based on impermeable rocks (paragneiss and granodiorite; 1:200000 scale). Therefore, the lakes are mainly supplied by precipitations and surface runoff. Additionally, both catchments are predominantly covered by mineral soils, including glaciofluvial sands and till deposits (1:20000 scale). Organic soils are concentrated in the riparian area of the lakes, or in small wetland depressions along streams and ditches. Although spatially restricted, the organic soils are located in hydrologically connected zones that makes them sources of DOM during high flow events or periods of increased runoff (Gergel et al., 1999; Blaurock et al., 2022). L. Majajärvi is supplied by two inlets (one east, one south; see Fig. 1) and has one outlet located at its northwestern part, which has been frequently dammed by beavers. There are three tributary lakes draining to L. Majajärvi, including L. Horkkajärvi. L. Horkkajärvi is supplied by one inlet to its south-eastern part and has one outlet to its north-western part that is draining into L. Majajärvi situated 800 m downstream. Beaver dams have not been built in L. Horkkajärvi’s catchment during the study period.

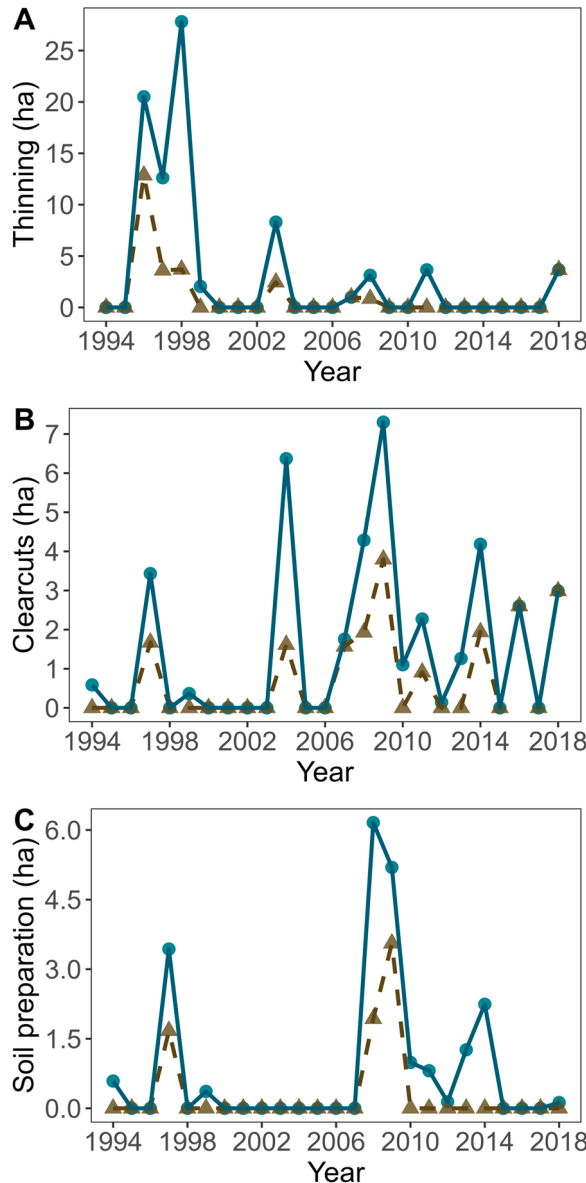


Fig. 2. Surface (in ha) of forestry practices carried out in the catchment of L. Majajärvi and L. Horkkajärvi between 1994 and 2018. A) Total surface of thinning practices per year; B) total surface of clearcuts per year; C) total surface of soil preparation carried out per year. Blue dots and solid lines are L. Majajärvi’s forestry data; brown triangles and hatched lines are L. Horkkajärvi’s forestry data.

2.2. Forestry practices data

Surfaces (in hectare) of forestry practices were provided by Häme University of Applied Sciences (HAMK) and were digitized for the period extending from 1994 to 2018. The dataset consisted of Geographic Information System (GIS) vector layers for three different types of forestry practices performed between 1994 and 2018 (Fig. 1): thinning, clear-cutting, and soil preparation practices. Soil preparation included soil harrowing, mounding, and scalping which were pooled under the category “soil preparation” to optimize statistical power. The surfaces of clearcutting, thinning, and soil preparation practices were measured for each year (Fig. 2A-C) using QGIS 3.16.6 with GRASS 7.8.5 and SAGA 2.3.2. For the forestry variables, a one-year lag was used to associate water color in the year X with forestry actions from the year X-1. This lag was defined as it is very unlikely that forestry practices have an immediate effect on water color, especially when actions were rarely carried out in the vicinity of the lakes.

2.3. Water color data

Long-term data of water color values (mg Pt/L) were provided by Lammi Biological Station (LBS): each year, the water was sampled from the surface layer of the lake, either the last week of October or the first week of November, after the autumn turnover of the lake water column and just before the lakes freeze. Samples were kept cold and in darkness until water chemistry analyses were conducted at the laboratory of LBS (about 20 km from the Evo area). Water samples were then filtered with a 0.45 µm filter prior to the color measurement. Water color was measured at 410 nm using a Shimadzu UV-1800 UV spectrophotometer, according to the Finnish standard protocol ISO 7887:2011. The water color is compared to a solution of potassium hexachloroplatinate and cobalt chloride of known concentration, which returns a water color expressed in concentration of mg of Platinum/Cobalt per Liter (mg Pt/L). A color of 0 mg Pt/L corresponds to clearwater and increasing values correspond to yellow to brown water color.

We focused on the period 1994–2018 for which estimated surfaces of forest practices were available for this study.

2.4. Climate and precipitation chemistry data

Precipitation, temperature and ion precipitation data were all retrieved from observation stations nearby the study area from the Finnish Meteorological Institute (FMI, <https://www.ilmatiiteenlaitos.fi/>). Precipitation and temperature data were retrieved from the Lammi Pappila observation station, 20 km away from the Evo area (61°03'00" N, 25°02'24" E), and ion precipitation data (SO₄²⁻, NO₃⁻) was retrieved from the Kotinen observation station, in the Evo area (61°14'23" N, 25°03'56" E, about 5 km away from the studied lakes).

Monthly precipitation was recorded for the whole study period with precipitation in mm. We calculated the annual amount of precipitation from 1994 to 2018 as a sum, for the year X, from November 1st of the year X-1 to October 31st of the year X; for instance the annual amount of precipitation of the year 1995 is calculated from November 1994 to October 1995. This sum has been done this way so that the annual precipitation corresponds to the yearly water color sampling. Monthly average air temperature data was given in Celsius degrees (°C) and the annual average was calculated in the same way as annual precipitation between 1994 and 2018, from November 1st of year X-1 to October 31st of year X. Finally, ion precipitation data (SO₄²⁻ and NO₃⁻; in µeq/L) were recorded monthly. To consider the influence of drier/wetter months – hence contributing to more or less ions in water – we calculated annual average SO₄²⁻ and NO₃⁻ concentrations based on a precipitation-weighted average using the following formula:

$$C_{\text{annual}} = \frac{\sum (C_m \times P_m)}{\sum P_m}$$

Where C_{annual} is the precipitation-weighted annual average ion concentration (in µeq/L) from November 1st of year X-1 to October 31st of year X, C_m is the monthly ion precipitation of SO₄²⁻ or NO₃⁻ (in µeq/L) and P_m is the amount of monthly precipitation (in mm). Hereafter, we refer to it as annual average SO₄²⁻ and NO₃⁻ concentrations.

2.5. Beaver activity

The beaver species found in Evo is the North American beaver, *Castor canadensis*. Eurasian (*Castor fiber*) and North American beavers have been introduced in Evo in the 1930s and 1950s (Lahti and Helminen, 1974), but only the North American beaver established in the Evo region. Beaver activity has been recorded in the Evo area since 1970 (e.g. Hyvönen and Nummi, 2008; Nummi et al., 2019; Kivinen et al., 2020). Field sessions were organized yearly to monitor the activity of beavers in Evo lakes; sightings, eatings, lodges and floods were recorded. Each year, lakes, wetlands, beaver-created ponds, and streams of the Evo area were visited to detect the presence of beaver traces. If a functioning dam was present on site and led to higher water level of the site or the maintaining of a created pond, the site was recorded as flooded.

In this study, we only focused on beaver-induced floods. L. Majajärvi has been frequently flooded by beavers (Supplementary material Table S1) while L. Horkkajärvi had never been flooded before or during the study period. Beavers dammed the outlet of L. Majajärvi (see Fig. 1), raising the water level on the shores of the lake instead of creating a new pond. Three flood states were defined as not flooded (BPN), flooded (BPF), and afterflood phase (BPA). Vehkaoja et al. (2015) demonstrated an increase in the DOC concentration of Evo lakes in the first three years of a beaver impoundment and a return to initial DOC levels within 4–6 years. However, DOC levels, and hence water color, can stay elevated for several years after water level recovery; for instance 7 years post-flood in Kazanjian

et al. (2021). Thus, we defined the afterflood phase up to 6 years after an initial flood, starting when water receded back to its original level. During 1994–2018, L. Majajärvi was flooded (BPF) in 2003, then continuously flooded from 2012 to 2018 (total of 8 years). Hence, we considered the lake to be in an afterflood phase (BPA) in 2004–2009 (6 years), and in its not flooded state (BPN) in 1994–2002 and 2010–2011 (11 years).

2.6. Statistical analysis

All statistical analyses were performed with the statistical software R (version 4.1.0; R Core Team, 2021). We used the “dplyr” (Wickham et al., 2022), “ggplot2” (Wickham, 2016), “bbmle” (Bolker et al., 2021), “DHARMA” (Hartig and Lohse, 2022; Supplementary material Fig. S2A-B), and “relaimpo” (Grömping, 2006) R packages for data sorting, graphs, model selection and interpretation, and residuals diagnostics. Explanatory variables were all centered and scaled prior to analysis.

Changes of environmental parameters over the study period – Following the requirements for normality, we evaluated changes in environmental parameters (precipitation, temperature, and SO_4^{2-} and NO_3^- concentrations) and their importance in our study area between 1994 and 2018 using ordinary least square linear regression models (LM).

Browning of L. Majajärvi and L. Horkkajärvi – Before investigating the drivers influencing water color changes of the lakes, we examined if both lakes underwent browning over the study period. The response variable (water color) fulfilled the requirements of independence and normality for both lakes (Kolmogorov-Smirnov test; L. Majajärvi: $D = 0.119$, $p = 0.880$; L. Horkkajärvi: $D = 0.106$, $p = 0.947$). Hence, we fitted an ordinary least square linear regression model (LM). To explain the water color variation of L. Majajärvi and L. Horkkajärvi, the pre-selection of variables to include in the models was based on a correlation threshold (ρ) of 0.6 (Supplementary material Fig. S3A-B) to avoid collinearity issues. All variables correlated above this threshold were not added in the same model formulas in order to avoid variable redundancy. After computing model formulas, the most fitting formula was selected based on the Akaike Information Criterion (AIC); the selection was based on the δAIC , which ranks the models according to their AIC scores (“ICtab” function). One model was retained for L. Majajärvi and one for L. Horkkajärvi. Hence, we used ordinary least square multiple linear regression models to test the potential effect of environmental variables on the color of L. Majajärvi and L. Horkkajärvi separately. Predictor significances were evaluated using type II F-tests (“drop1” function). For each fitted model, the relative contribution of each explanatory variable to the total explained variance (multiple R^2) was extracted using the “calc.relimp” function with the Lindeman, Merenda, and Goldmethod (lmg) method. The multiple R^2 is partitioned between the variables and accounts for both their unique and shared contribution (Grömping, 2006).

Our aim was not to develop predictive models but rather identify the significant drivers of changes in water color. Hence, we did not perform model selection to keep significant variables only. Dropping predictors based on significance has also been widely criticized as it can exclude true causal variables that appear non-significant, select falsely significant variable, and increase overfitting (Whittingham et al., 2006; Mundry and Nunn, 2009; Harrell, 2010). Thus, we present results about all the explanatory variables in the

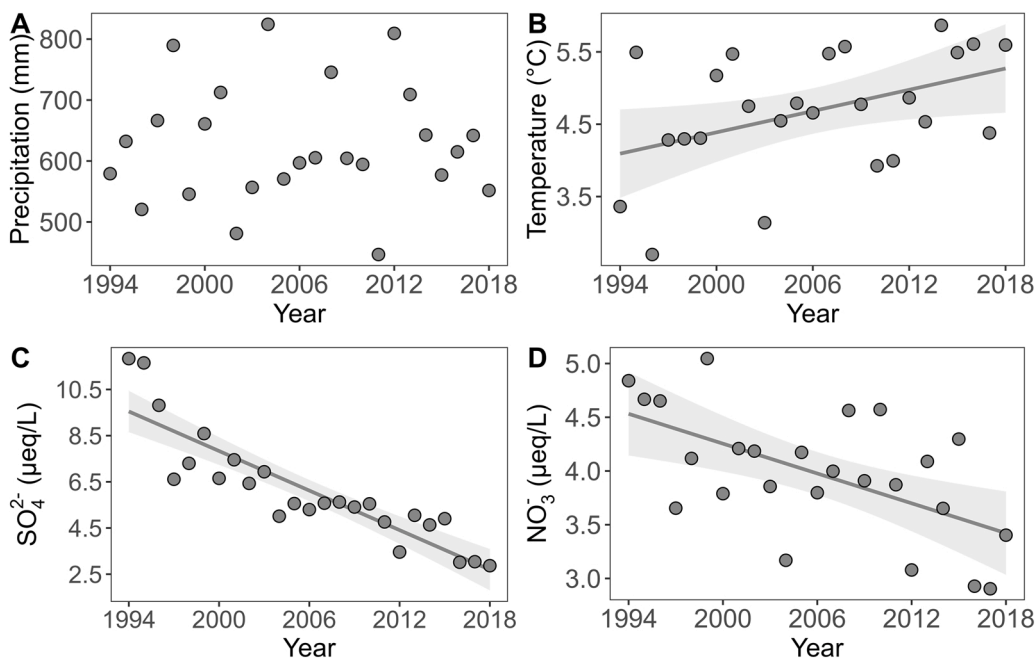


Fig. 3. Evolution of the A) annual amount of precipitation (mm), B) average annual air temperature ($^{\circ}\text{C}$), C) average annual SO_4^{2-} concentration ($\mu\text{eq/L}$), and D) average annual NO_3^- concentration ($\mu\text{eq/L}$) between 1994 and 2018 in the Evo area. Linear regression lines ($\pm 95\%$ CI) are visible when a significant relationship was found.

linear regressions.

3. Results

3.1. Change of environmental parameters over the study period

During the study period, the annual amount of precipitation varied from 446.60 mm to 824.30 mm, with an average amount of 627.18 ± 96.48 mm, and did not increase over time (LM: $p = 0.982$; Fig. 3 A). In contrast, the average annual air temperature considerably increased (LM: slope = 0.049 ± 0.021 , $p = 0.029$, $R^2 = 0.155$; Fig. 3B) and varied between 2.70 °C and 5.87 °C, with an average temperature of 4.68 ± 0.83 °C. Additionally, the yearly SO_4^{2-} concentration strongly decreased (LM: slope = -0.286 ± 0.031 , $p < 0.001$, $R^2 = 0.779$; Fig. 3 C), and varied between 2.868 and 11.835 $\mu\text{eq/L}$ with an average concentration of 6.121 ± 2.37 $\mu\text{eq/L}$. NO_3 concentration also decreased significantly over time (LM: slope = -0.046 ± 0.013 , $p = 0.002$, $R^2 = 0.313$; Fig. 3D), and varied from 2.904 to 5.046 $\mu\text{eq/L}$ with an average value of 3.977 ± 0.58 $\mu\text{eq/L}$.

3.2. Browning of L. Majajärvi and L. Horkkajärvi

Both lakes have become browner over time (L. Majajärvi: intercept = 192.02 ± 16.37 , slope = 3.42 ± 1.17 , $p = 0.008$, $R^2 = 0.24$; L. Horkkajärvi: intercept = 234.97 ± 20.15 , slope = 3.30 ± 1.44 , $p = 0.03$; Fig. 4 A) at a rate of 3.42 ± 1.17 and 3.30 ± 1.44 mg Pt/L per year between 1994 and 2018 for L. Majajärvi and L. Horkkajärvi respectively. The water color of L. Majajärvi ranged between 146 and 335 mg Pt/L, while the color of L. Horkkajärvi ranged between 146 and 396 mg Pt/L in 1994–2018.

According to the correlation threshold ($\rho = 0.6$), annual SO_4^{2-} and NO_3 concentrations were highly correlated ($\rho = 0.766$). Surfaces of clearcuts and soil preparation practices were also significantly correlated in both L. Majajärvi and L. Horkkajärvi catchments (respectively $\rho = 0.676$ and $\rho = 0.625$). These correlations limited the possible model formulas to 4 per lake (Table 1). In both L. Majajärvi and L. Horkkajärvi, the same model formula was selected and was thus used as the most fitting model. The model formula included the surface of thinning and soil preparation practices, the annual amount of precipitation, the annual average air temperature, and the annual average SO_4^{2-} concentration between 1994 and 2018 (Table 2). Beaver activity was only included in the model of L. Majajärvi as L. Horkkajärvi was not colonized. The linear models explain 65.27 % of L. Majajärvi's water color variation ($F = 7.443$; $p < 0.001$, multiple $R^2 = 0.754$, adjusted $R^2 = 0.653$) and 33.86 % of the variation of the color of L. Horkkajärvi ($F = 3.457$, $p = 0.022$, multiple $R^2 = 0.476$, adjusted $R^2 = 0.339$).

The observed browning seems to be mainly due to the annual amount of precipitation in L. Horkkajärvi (slope = 27.95 ± 9.78 , $F = 8.16$, $p = 0.01$; Fig. 4B) as it contributes to 24.59 % out of 47.64 % of the total variance explained (Fig. 5 A), followed closely by the annual average SO_4^{2-} concentration (slope = -25.72 ± 10.31 , $F = 6.23$, $p = 0.02$; Fig. 4 C) that contributed to 19.81 % to the total

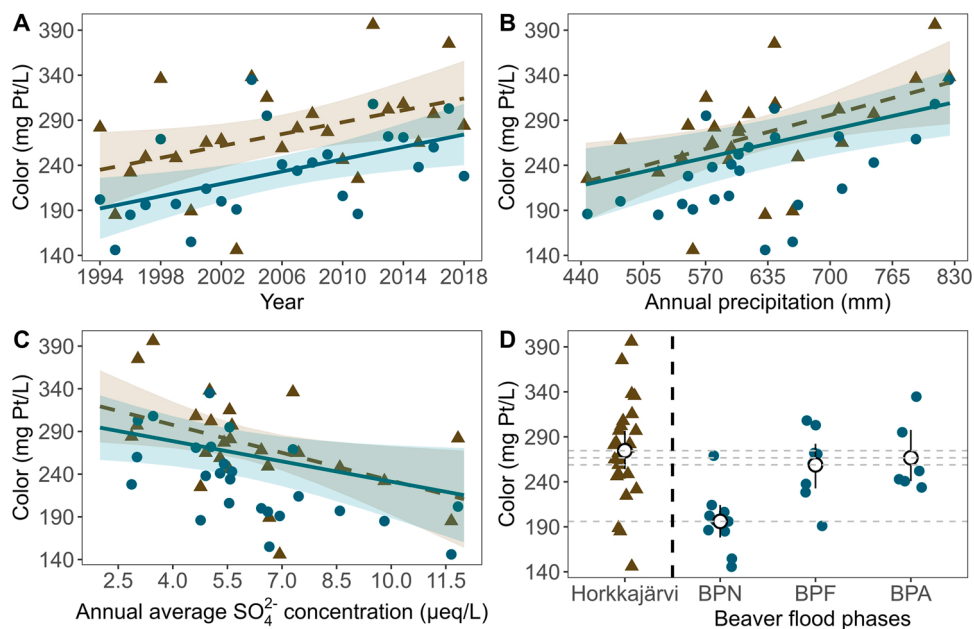


Fig. 4. Prediction of water color (mg Pt/L) of L. Majajärvi and L. Horkkajärvi according to A) years from 1994 to 2018, B) the annual amount of precipitation (mm), C) the average annual SO_4^{2-} concentration ($\mu\text{eq/L}$), and D) beaver activity (BPN = no flood, BPF = flooded, BPA = afterflood phase) compared to L. Horkkajärvi's color (grey dashed lines indicate the mean water color of each category). L. Majajärvi is represented by blue dots and solid regression line (± 95 % confidence interval) and L. Horkkajärvi by brown triangles and dashed regression line (± 95 % CI). Note that the intercepts differ from Table 2, as water color predictions show partial effects, which consider non-focal variables.

Table 1

List of possible model formulas to explain at best the variation of the water color of L. Majajärvi and L. Horkkajärvi. The most fitting formula for each lake was selected based on the δ AIC and is bolded in the table. *Clearcut* = total surface of clearcuts (in ha) carried out in a year, *SP* = total surface of soil preparation (in ha) carried out in a year, *Thinning* = total surface of thinning (in ha) carried out in a year, *Precipitation* = annual amount of precipitation (in mm), *Temperature* = average annual air temperature (in °C), SO_4^{2-} = average annual SO_4^{2-} concentration in precipitation (in μ eq/L), NO_3 = average annual NO_3 concentration in precipitation, *Beaver* = beaver activity (BPN, BPF, BPA).

Model formula	df	AIC	δ AIC	R ²
<i>L. Majajärvi</i>				
SP + Thinning + Precipitation + Temperature + SO_4^{2-} + Beaver	9	246.777	0.0	0.653
Clearcut + Thinning + Precipitation + Temperature + SO_4^{2-} + Beaver	9	248.636	1.9	0.626
SP + Thinning + Precipitation + Temperature + NO_3 + Beaver	9	251.611	4.8	0.579
Clearcut + Thinning + Precipitation + Temperature + NO_3 + Beaver	9	252.423	5.6	0.565
Null model	2	267.836	21.1	-
<i>L. Horkkajärvi</i>				
SP + Thinning + Precipitation + Temperature + SO_4^{2-}	7	269.302	0.0	0.339
Clearcut + Thinning + Precipitation + Temperature + SO_4^{2-}	7	269.45	0.1	0.335
SP + Thinning + Precipitation + Temperature + NO_3	7	273.185	3.9	0.227
Clearcut + Thinning + Precipitation + Temperature + NO_3	7	273.223	3.9	0.226
Null model	2	275.477	8.1	-

Table 2

Coefficient estimates of the final linear models investigating the changes of the water color of L. Majajärvi and L. Horkkajärvi. The Beaver variable in L. Majajärvi's linear model has three modalities (BPN, BPF, BPA); the reference level of the Beaver variable in the intercept is the BPA modality. Note that the estimates of the quantitative predictors are scaled and thus expressed per 1 standard deviation of each predictor. *SP* = total surface of soil preparation (in ha) carried out in a year, *Thinning* = total surface of thinning (in ha) carried out in a year, *Precipitation* = annual amount of precipitation (in mm), *Temperature* = average annual air temperature (in °C), NO_3 = annual NO_3 precipitation (in μ eq/L), *Year* = 1994–2018, *Beaver* = beaver activity (BPN, BPF, BPA).

Variable	Coefficient	SE	t-value	p-value
<i>L. Majajärvi</i>				
Intercept	261.89	12.83	20.41	< 0.001
SP	-7.41	6.32	-1.17	0.257
Thinning	-0.80	7.13	-0.11	0.912
Precipitation	22.90	6.47	3.54	0.003
Temperature	-10.92	7.43	-1.47	0.159
SO_4^{2-}	-18.71	8.39	-2.23	0.039
Beaver No	-51.65	18.30	-2.82	0.277
Beaver Flooded	-19.01	16.91	-1.12	0.012
<i>L. Horkkajärvi</i>				
Intercept	274.60	9.16	29.98	< 0.001
SP	-3.65	9.43	-0.39	0.703
Thinning	-1.14	10.84	-0.11	0.917
Precipitation	27.95	9.78	2.86	0.010
Temperature	-4.84	11.70	-0.41	0.684
SO_4^{2-}	-25.72	10.31	-2.50	0.022

variance explained (Fig. 5 A). In L. Majajärvi, annual precipitation (slope = 22.91 ± 6.5 , $F = 12.53$, $p = 0.003$) was the main driver while considering unique contribution only, then followed by annual average SO_4^{2-} concentration (slope = -18.71 ± 8.39 , $F = 4.98$, $p = 0.039$), and beaver activity ($F = 3.99$, $p = 0.038$; Fig. 4D). However, if predictors unique and shared contributions were considered, beaver activity was the main driver of browning in L. Majajärvi, with 28.34 % out of 75.4 % of the variance explained respectively (Fig. 5B), compared to 22.5 % for annual precipitation amount and 20.27 % for SO_4^{2-} concentration. The water color of L. Majajärvi was on average 196.0 ± 9.6 mg Pt/L when the lake was not flooded, 258.9 ± 13.8 mg Pt/L when flooded, and 266.7 ± 16.3 mg Pt/L when the lake was in an afterflood phase. A post-hoc test confirmed the water color of L. Majajärvi was substantially browner in flooded and afterflood years compared to years not experiencing beaver activity (respectively $p = 0.003$ and $p = 0.003$; pairwise t -test). In contrast, the water color of L. Majajärvi was not significantly different between flood and afterflood phases ($p = 0.999$).

The average air temperature did not significantly affect the color of L. Majajärvi ($p = 0.16$) or L. Horkkajärvi ($p = 0.749$). We also did not find any significant effect of both types of forestry practices on the color of L. Majajärvi and L. Horkkajärvi, whether it was soil preparation (respectively $p = 0.26$, and $p = 0.7$) or thinning practices (respectively $p = 0.91$, and $p = 0.92$). Together, the three non-significant variables accounted for only 4.3 % of the water color variance explained in L. Majajärvi, and 3.2 % in L. Horkkajärvi (Fig. 5), supporting the idea that these variables do not play a meaningful role in water color changes in our study.

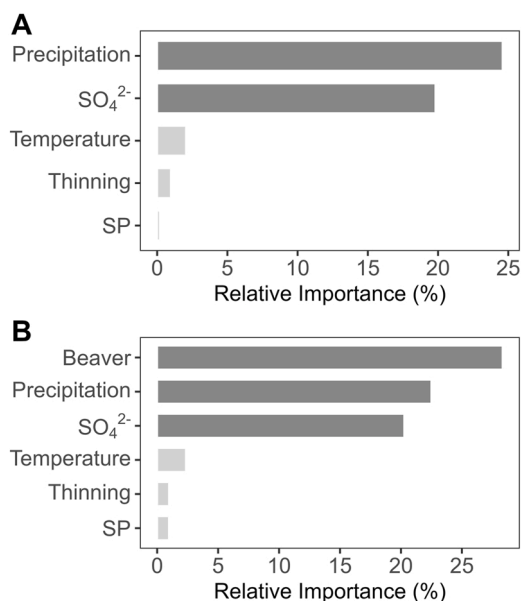


Fig. 5. Relative importance (%) of each predictor explaining water color changes in A) L. Horkkajärvi, and B) L. Majajärvi over the study period, based on explained variance decomposition. Dark gray bars indicate significant variables in the linear regression models and light grey bars represent non-significant variables. *Precipitation* = annual amount of precipitation, *Year* = 1994–2018, *NO₃* = annual NO₃ precipitation, *Temperature* = average annual air temperature, *Thinning* = total surface of thinning carried out in a year, *SP* = total surface of soil preparation carried out in a year, *Beaver* = beaver activity.

4. Discussion

4.1. Water browning over time

Result shows that both studied lakes turned browner between 1994 and 2018 at a rate of 3.42 ± 1.17 (L. Majajärvi) and 3.30 ± 1.44 mg Pt/L per year (L. Horkkajärvi). This browning is true for many other lakes in the Evo area (Arvola et al., 2010; Arzel et al., 2020; Arvola et al., 2025) and in boreal areas in general (de Wit et al., 2016; Isidorova et al., 2016; Rääke et al., 2024). In the same study area, Arzel et al. (2020) found an increase of lakes water color by 1.8 between 1990 and 2008. Another study estimated that TOC (90–95 % of DOC) concentration of Finnish rivers, stream, lakes, and coastal areas increased by respectively 2.1, 1.2, 1.2, and 1.8 mg/L between 1990 and 2020 (Rääke et al., 2024). In more than 400 Fennoscandian lakes and rivers, the median increase of total organic carbon was 1.4 % per year (range between 0.8 % and 2 %) in 1990–2013 (de Wit et al., 2016). Weyhenmeyer et al. (2016) modelled the fate of 6347 Swedish lakes and rivers using the worst-case climate scenario until 2030 and predicted a 1–7-fold increase in water color. Their modelling showed the extreme sensitivity of small headwater lakes to browning compared to larger lakes or rivers. Hence, our results align with the global understanding that browning is a common trend and that small lakes fed by surface water are strongly affected by browning.

It should be noted that the modest explanatory power of time (*Year*) to explain water color changes (adjusted $R^2 = 0.15$ – 0.24) indicates a substantial interannual variation in the study lakes, also visible in Fig. 4 A. While part of this unexplained variance may stem from the influence of the drivers analyzed in our study (e.g. precipitation amount, acidifying ion concentration, beaver activity), it is likely that lake-specific watershed features contribute to interannual variations. In particular, water retention time (WTR) is known to influence both the delivery and processing of DOM within lakes (Jiang et al., 2023), thus impacting water color responses. Lakes with short WTR tend to be more sensitive to browning than lakes with longer WTR that exhibit slower and buffered responses (Köhler et al., 2013). Although direct WTR measurements were not available for our study lakes, simple water-balance estimates indicate that L. Majajärvi and L. Horkkajärvi have WTRs of approximately 2.0–2.7 months and 5.8–6.7 months, respectively (Supplementary material Text S1), which are considered short. Both lakes also have high drainage ratio (catchment area:lake area; L. Majajärvi: 49.1, L. Horkkajärvi: 37.9), indicating great sensitivity to catchment inputs delivered via runoff (Jones et al., 2018; Oleksy et al., 2022). This combination of short WTR and high drainage ratio likely contribute to the strong interannual variation in water color observed in our study lakes, and also implies strong seasonal variation. This further suggests that annual sampling may miss important dynamics, especially in such rapidly flushed systems. In this study, however, water color was always measured at the same time of year, after the autumn turnover when the water was fully mixed, a standard approach that reduces seasonal bias and variance between years (Puro-Tahvanainen et al., 2011). Nevertheless, annual sampling does not capture the event-driven pulses or seasonal fluctuations. Future studies should therefore incorporate higher temporal sampling resolution and a higher set of lakes, while considering watershed features – such as WTR and drainage ratio – that determine the sensitivity of lakes to environmental stressors.

4.2. Water browning and acid recovery

During the 25 years study period, the annual average SO_4^{2-} concentration strongly and steadily decreased (ca. $-0.3 \mu\text{eq/L}$ on average per year), which was correlated to the browning of both lakes. Many studies linked an increase of DOC concentration in freshwaters with declining sulphur deposition/precipitation (Evans et al., 2005; Monteith et al., 2007; Vuorenmaa et al., 2014; Redden et al., 2021) and a change of composition towards browner components (Ekström et al., 2011), the so-called acid recovery. This is mainly due to the increasing DOM mobility and solubility in soils during recovery from acidification, causing a greater transport of colored DOM to surface waters (Monteith et al., 2007; Meyer-Jacob et al., 2020). In both lakes, the effect of declining NO_3^- concentration on water color was not investigated, but its effects may not be as straightforward as recovery from SO_4^{2-} , since the effect of nitrogen on soil and water quality depends on the prevailing levels of ecosystems N saturation and can have contrasting effects (Sawicka et al., 2017).

All in all, while acid recovery-driven browning may be a return to pre-industrial DOC levels (i.e. 1850s), current lake DOC levels in low acid deposition areas often surpass pre-industrial concentrations (Meyer-Jacob et al., 2019). Southern Finland is considered a moderate to low deposition area in a global context, especially if compared to Central-Western Europe and North America (Vet et al., 2014; Vuorenmaa et al., 2018; de Wit et al., 2021). In this study, the recovery from acidification may have more contributed to browning in the 1990s and early 2000s compared to more recent decades (Arvola et al., 2025). Thus it is likely that, in our study area, browning is a result of multiple other environmental drivers such as climate – here precipitation – especially in the studied lakes with historically moderate deposition (Meyer-Jacob et al., 2020; Xiao et al., 2020).

4.3. Water browning and rainfall

In both studied lakes, the annual amount of precipitation was a major factor driving changes in water color. The contribution of rainfall has already been known for decades (e.g. Hongve et al., 2004; de Wit et al., 2016); it may be explained by DOC leaching at its maximum during precipitations, that raises the water table and increases the hydrological connections between organic soils and water bodies (McDowell and Likens, 1988; Hongve et al., 2004; Laudon et al., 2011). This process was highlighted as a global driver of DOC export to freshwaters (de Wit et al., 2016; Weyhenmeyer et al., 2016), especially from the riparian area that is a major provider of DOC (Ledesma et al., 2015, 2018; Ploum et al., 2021). de Wit et al. (2016) also highlighted that precipitation patterns are a strong factor driving water browning, especially in areas with a median annual precipitation of about 700 mm or less (“dry category”). In the Evo area, annual precipitation varied from 447 mm to 824 mm with a median amount of 605 mm between 1994 and 2018, which falls in this category. While annual precipitation did not increase significantly during our study period, it is expected to become significant by 2040 s in the Evo area, with a 1–3 % increase per decade (Jylhä et al., 2014), and a 10 % rise in precipitation is estimated to increase the mobilization of organic matter from soils to freshwaters by at least 30 % (de Wit et al., 2016). While increased evapotranspiration due to warming may partially offset the effects of higher precipitation, studies suggest that enhanced precipitation generally increase runoffs despite higher temperatures, especially in areas dominated by coniferous forest (Creed et al., 2014). We can therefore expect precipitation to play a major part in the current and future browning of the lakes in the Evo area. The boreal areas in general are also highly likely to follow similar trends given the projected global increase in precipitations (Jylhä et al., 2004; Ruosteenoja and Jylhä, 2021).

4.4. Water browning and beaver floods

So far, this study documented the browning of two boreal lakes over more than two decades and linked it with precipitation quantity and declining annual average SO_4^{2-} concentration. We also investigated the ecological aspects of browning through beaver effects on water quality (see Grudzinski et al., 2022). Beaver damming activities appear as an important local driver, where beaver-induced floods (BPF) and afterflood phases (BPA) substantially increased the color of the beaver lake. Although annual precipitation had a higher unique contribution than beaver activity to the model's variance, the combined unique and shared contribution of beaver activity indicates that it was as important as annual precipitation. Hence, beaver activity seems to play a major role in the water color variation of L. Majajärvi over the 25-year study period.

Beaver engineering can cause significant changes in the physical habitat. While no studies have explicitly demonstrated long-term browning by beavers (but see Blanchet et al., 2022), their effects on DOC are well documented. Beaver-engineered habitats generally contain more DOC than beaver-free habitats (Cazzolla Gatti et al., 2018; Lynch et al., 2019; Ciudiené et al., 2020). In the Evo area, beaver activity increased DOC concentration in small lakes (Vehkaoja et al., 2015), consistent with the browning we observed in L. Majajärvi during flood phases. Similarly, a 30-year increase in DOC levels was linked to beaver recolonization and wetland restoration in a German catchment (Smith et al., 2020).

By cutting trees for foraging and damming, beavers add a substantial amount of organic material such as plant debris and leaf litter (Hodkinson, 1975; Nummi, 1989; Johnston, 2017), while the flooding of originally terrestrial areas promotes leaching of soil DOC (Naiman et al., 1994; Rasilo et al., 2015). In the flooded area surroundings, evapotranspiration is reduced since less water is transferred from the ground to the atmosphere by the trees and the herbaceous vegetation. In turn, groundwater levels increase (Smith et al., 2020) enhancing surface water connectivity and mobilizing riparian DOC to water bodies. As riparian areas are major sources of terrestrially-derived DOC in streams and lakes (Winterdahl et al., 2011; Rasilo et al., 2015), beavers may mobilize DOC from the riparian area in a way comparable to precipitation events. This may explain why the relative importance of beaver activity increased when shared contributions to variance were considered, and suggest that its effects are closely linked to precipitation patterns.

Moreover, damming increases water residence time, which likely helps maintaining high DOC concentration in flooded areas by reducing DOC downstream export (Hanson et al., 2011).

Beaver floods also affect DOM quality, as inundated soils and decaying materials enrich the flooded area with highly colored and refractory DOM (Catalán et al., 2017; Castro et al., 2023). Strong UV absorption in brown waters (Thrane et al., 2014; Williamson et al., 2015) further limits photochemical removal processes of DOM (see in Tranvik et al., 2009), leaving a substantial part of unprocessed DOM in the ponds (Younes and Berggren, 2024). Thus, even if DOC concentration may decline after a few years, the remaining fraction is largely refractory colored DOC, maintaining the browner color of beaver-occupied lakes like L. Majajärvi. Flood events may therefore cause long-lasting changes in water chemistry, even after water recede to their initial levels (Kazanjian et al., 2021).

During the study period, the first flood in L. Majajärvi occurred in 2003, when water color rose from 191 to 335 mg Pt/L, paralleled by an increase in L. Horkkajärvi (146–338 mg Pt/L). A similar pattern occurred in 2012–2013, with high amounts of annual precipitation (809.4 mm in 2012 and 709.1 mm in 2013) and another flood in 2012. L. Horkkajärvi, as a small tributary-free lake, is highly sensitive to environmental changes such as precipitation (Rasmussen et al., 1989; Weyhenmeyer et al., 2016), which may explain the steep increase in water color. In L. Majajärvi, the additive effects of beaver flooding and precipitation likely explain the rise on water color, since both mobilize riparian DOC. Moreover, as L. Majajärvi has three tributary lakes that retain DOC (Mattsson et al., 2005; Larson et al., 2007; Arvola et al., 2016), the effect of precipitation alone should be buffered, while flooding acts directly on the lake.

Although beaver-induced floods may promote browning, the effects appear to be limited to the dammed area, with minor effects on downstream waterbodies (Devito et al., 1989; Kothawala et al., 2006; Vehkaoja et al., 2015; Koschorreck et al., 2016). For example, Čiuldiene et al. (2020) reported DOC concentration 2.7 times higher in beaver ponds than downstream. In that respect, beaver ponds resemble natural wetlands that retain DOC (Mattsson et al., 2005; Larson et al., 2007). Similarly, DOC and carbon accumulation in sediments are about two times higher in dammed versus unoccupied streams (Cazzolla Gatti et al., 2018). Thus, at the landscape and watershed scales, the browning of beaver-dammed waterbodies may be locally limited (Wegener et al., 2017).

4.5. Water browning and air temperature

The annual air temperature increased considerably in the Evo area during the study period (0.049°C per year, ca. 1°C over 25 years) at a rate comparable to other boreal regions and faster than other climatic zones and the global average (Burrell et al., 2022; Rantanen et al., 2022; IPCC, 2023). Such warming is usually associated with ecological and environmental impacts, including alteration in tree species distribution (Dyderski et al., 2018) and growing season (Hänninen and Tanino, 2011), longer lake ice-free seasons (Mishra et al., 2011), warmer water temperature (O'Reilly et al., 2015) and finally water browning (Lepistö et al., 2021). However, this result must be interpreted with caution as the year explains 15.51 % of the variance of annual average air temperature, which might be due to the strong interannual variation.

Despite this marked increase, we found no significant effect of air temperature on lake water color. This contrasts with other Finnish studies reporting air temperature as a key driver of browning (e.g. Lepistö et al., 2021; Räike et al., 2024). For example, Räike et al. (2024) showed that temperature was a more important driver of browning than precipitation in 100 Finnish riverine catchments. Nevertheless, other studies also did not find a significant effect of air temperature on DOC (Hudson et al., 2003; Intiazy et al., 2025) and suggested that results may strongly depend on the studied environment or that effects on DOC production may be more gradual through changes in vegetation growth and litterfall. We believe the role of temperature on the browning of waterbodies may be more visible on larger scales, may have a delayed effect, or that we could not detect it because its influence on DOC fluxes and color could be more seasonal (Miller et al., 2001; Broder et al., 2017; Gutierrez Lopez and Laudon, 2023). We could not test this seasonal aspect as we only had yearly color data for both lakes.

4.6. Water browning and forestry activities

Forestry activities have been shown to enhance DOC leaching into surface waters (e.g. Schelker et al., 2012, 2014; Nieminen et al., 2015; Kļaviņa et al., 2021), but we did not find a significant effect on the color of L. Majajärvi and L. Horkkajärvi over the study period. Several factors may explain this lack of effect. First, many studies highlighting the effect of forestry (mostly clearcutting) practices on DOC fluxes occurred close to the waterbodies (Schelker et al., 2012, 2014; Nieminen et al., 2015), while in our study, operations were distributed across the catchment and rarely close to the shorelines. Moreover, Schelker et al. (2014) demonstrated that at least 11–25 % of a catchment would need to be clearcut in a year for DOC increase to be significant, whereas cutting never exceed 4 % in both lakes catchments (Supplementary material Table S4). Second, the increased annual average air temperature over the study period without a corresponding change in annual precipitation likely reduced runoff via increased evapotranspiration in forestry plots (Abtew and Melesse, 2013; Shi et al., 2022). Forestry effects may therefore be more visible during wetter years with stronger runoffs (Hongve et al., 2004; Strock et al., 2016). Finally, most forestry practices were carried out on mineral soils, where forestry has less impact compared to actions on drained or pristine peatlands (Finér et al., 2021; Härkönen et al., 2023 and references therein). Hence, forestry effects on water color were probably buffered.

5. Conclusions and perspectives

Over 25 years, both lakes became browner over time, consistent with trends across the boreal region and beyond. Seasonal fluctuations in DOM inputs are expected, particularly in our study lakes. Although the sampling design ensured reliable comparison across

years, it does not capture short-term color dynamics. Higher temporal resolution would therefore be necessary to fully assess seasonal variability in rapidly flushed lakes, in addition to higher spatial sampling resolution. Annual precipitation was a major driver, confirming that precipitation patterns are major contributors to browning, particularly in boreal areas facing wetter conditions under climate change. The decline of annual average SO_4^{2-} concentration over time also contributed to the browning of the lakes, although this effect is expected to diminish in the future as other drivers will dominate. Air temperature and the studied forestry practices were not significant, but we do not exclude their potential impact that could be more relevant at broader scales or in other contexts. In L. Majajärvi, beaver activity influenced water color as much as annual precipitation. Periods of beaver activities (i.e. beaver floods and afterflood phases) coincided with browner waters, suggesting that beaver-induced flooding mobilizes riparian DOC in a similar way as precipitation events. Experimental approaches, such as artificial flooding of terrestrial soils, could help quantifying the effects of flooding dynamics on DOM concentration, composition, and water color. Overall, our results show that precipitation, acid recovery and beaver activity determine lake browning on a local to global scale. Accounting for these interactions and considering catchment features will help to improve our understanding of future water color changes in boreal freshwaters – and beyond – under global change pressures.

Ethical statement

This study did not involve human subjects, animal experimentation, or the use of endangered or protected species, and thus did not require ethical approval.

All data were collected and handled in accordance with relevant institutional, national, and international guidelines.

All authors confirm that the research was conducted with integrity and transparency, and that the work presented is original, with proper acknowledgment of financial sources.

CRediT authorship contribution statement

Clarisse C. Blanchet: Writing – original draft, Visualization, Project administration, Methodology, Funding acquisition, Formal analysis, Data curation, Conceptualization. **Petri Nummi:** Writing – review & editing, Supervision, Resources, Funding acquisition. **Aurélie Davranche:** Writing – review & editing, Supervision, Methodology, Conceptualization. **Henrik Lindberg:** Writing – review & editing, Resources. **Kimmo K. Kahilainen:** Writing – review & editing, Supervision, Resources. **Céline Arzel:** Writing – review & editing, Supervision, Resources, Project administration, Funding acquisition, Conceptualization. **Risto Viitala:** Writing – review & editing, Resources.

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. Supporting information

Supplementary data associated with this article can be found in the online version at [doi:10.1016/j.gecco.2025.e03960](https://doi.org/10.1016/j.gecco.2025.e03960).

Data availability

Data will be made available on request.

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