



Ecology and extent of freshwater browning - What we know and what should be studied next in the context of global change



Clarisse C. Blanchet^{a,b,*}, Céline Arzel^a, Aurélie Davranche^c, Kimmo K. Kahilainen^d, Jean Secondi^{e,f}, Sami Taipale^g, Henrik Lindberg^h, John Loehr^d, Sanni Manninen-Johansenⁱ, Janne Sundell^d, Mohamed Maanan^j, Petri Nummi^b

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

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

^c CNRS UMR 6554 LETG, University of Angers, 2 Boulevard Lavoisier, FR-49000 Angers, France

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

^e University of Lyon, Université Claude Bernard Lyon 1, CNRS, ENTPE, UMR 5023 LEHNA, F-69622, Villeurbanne, France

^f Faculty of Sciences, University of Angers, F-49000 Angers, France

^g Department of Biological and Environmental Science, University of Jyväskylä, P.O. Box 35, FI-40014 Jyväskylä, Finland

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

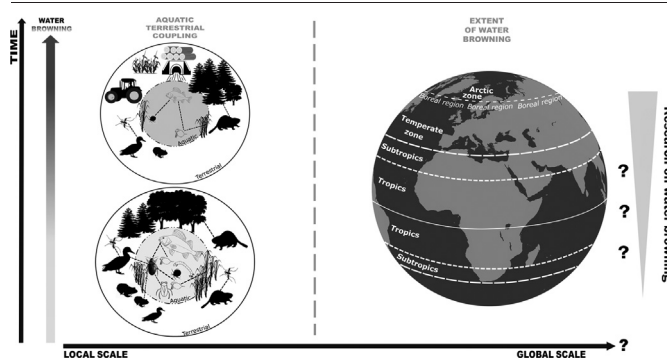
ⁱ Vanajavesi Center, Perttulantie 84, FI-13430 Hämeenlinna, Finland

^j UMR CNRS 6554, University of Nantes, F-44000 Nantes, France

HIGHLIGHTS

- Browning studies overlooked freshwater habitats like small and temporary wetlands.
- Macrophytes, invasive species, and food webs are disregarded in browning studies.
- Browning and the aquatic-terrestrial habitat coupling should be investigated.
- Browning is a more global phenomenon than current focus on boreal zones suggests.
- Remote sensing offers great potential to investigate browning at a global scale.

GRAPHICAL ABSTRACT



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ABSTRACT

Water browning or brownification refers to increasing water color, often related to increasing dissolved organic matter (DOM) and carbon (DOC) content in freshwaters. Browning has been recognized as a significant physicochemical phenomenon altering boreal lakes, but our understanding of its ecological consequences in different freshwater habitats and regions is limited. Here, we review the consequences of browning on different freshwater habitats, food webs and aquatic-terrestrial habitat coupling. We examine global trends of browning and DOM/DOC, and the use of remote sensing as a tool to investigate browning from local to global scales. Studies have focused on lakes and rivers while seldom addressing effects at the catchment scale. Other freshwater habitats such as small and temporary waterbodies have been overlooked, making the study of the entire network of the catchment incomplete. While past research investigated the response of primary producers, aquatic invertebrates and fishes, the effects of browning on macrophytes, invasive species, and food webs have been understudied. Research has focused on freshwater habitats without considering the fluxes between aquatic and terrestrial habitats. We highlight the importance of understanding how the changes in one habitat may cascade to another. Browning is a broader phenomenon than the heretofore concentration on the boreal region. Overall, we propose that future studies improve the ecological understanding of browning

* Corresponding author at: Department of Forest Sciences, P.O. Box 27, University of Helsinki, FI-00014 Helsinki, Finland.

E-mail address: clarisse.blanchet@helsinki.fi (C.C. Blanchet).

through the following research actions: 1) increasing our knowledge of ecological processes of browning in other wetland types than lakes and rivers, 2) assessing the impact of browning on aquatic food webs at multiple scales, 3) examining the effects of browning on aquatic-terrestrial habitat coupling, 4) expanding our knowledge of browning from the local to global scale, and 5) using remote sensing to examine browning and its ecological consequences.

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1. Introduction

Over the last three decades, surface waters have become browner throughout the Northern Hemisphere (Monteith et al., 2007) raising concerns about the processes in action, its spatial extent and the consequences for water quality and aquatic trophic webs. The change in water color toward browner hues is known as the “brownification” process or “browning”. Since no consensus exists on a preferred term to describe the increase in water color, we refer to it as (water) browning throughout this article.

Browning of surface waters refers to an increase in water color toward yellow-brown hues (Graneli, 2012). Water color is strongly related to dissolved organic matter (DOM) or carbon (DOC) of terrestrial origin (Weyhenmeyer et al., 2014; Kritzberg, 2017). DOM originates from decomposition processes of dead organisms, such as microorganisms, animals, and plants in both aquatic and terrestrial habitats. DOM is a natural component of water and includes any compounds that can pass through a 0.45 µm mesh (Evans et al., 2005). Therefore, the composition of DOM varies between different environments. In general, DOM is composed of a small proportion of low molecular weight compounds, such as amino acids, and a larger proportion of high and medium molecular weight humic and fulvic acids, commonly referred as humic substances. DOM absorbs light in the ultraviolet and in the short wavelengths of visible light, which gives a yellow-brown color to DOM-rich waters (Evans et al., 2005).

DOC is the primary component of DOM. It plays an important role in surface waters' biogeochemistry and ecology, e.g., food web dynamics and structure, carbon budgets and acid-base chemistry (Salonen et al., 1983; Hruška et al., 2003; Cole et al., 2007; Jansson et al., 2007). Browning and lake productivity tend to have a unimodal relationship, where initial increment of DOC tends to boost biological productivity until a concentration of about 5 mg/L is reached, whereafter subsequent browning tends to

decrease productivity (e.g., Finstad et al., 2014; Seekell et al., 2015). In lakes, water color is often measured with absorbance coefficients at 254 and 440 nm (e.g., Köhler et al., 2013; Fasching et al., 2014); and is considered brown when DOC concentration exceeds 10 mg/L. However, the browning of waters may be greater than the increase in DOM/DOC content in waters (Hongve et al., 2004; Erlandsson et al., 2008). Concurrent increases in DOM and dissolved iron (Fe) concentrations in surface waters have been observed in the arctic, boreal and temperate zones and associated to changes in water color (e.g., Kritzberg and Ekström, 2012; Sarkkola et al., 2013; Brezonik et al., 2019; Xiao and Riise, 2021). DOM and Fe molecules can form stable complexes that are difficult to process by aquatic organisms, and contribute to the browning process (see in Maranger and Pullin, 2003; Sarkkola et al., 2013; Weyhenmeyer et al., 2014; Lei et al., 2020).

Browning of waters usually refers to the increased amount of terrestrially derived DOM and more recently Fe in surface waters. In contrast, changes in DOM composition have been less studied in regards to browning; but gained more interest in the last ten years (e.g., Jane et al., 2017; Xenopoulos et al., 2021) since it plays an important role in water color changes. Higher proportions of humic substances can partly explain water browning. Humic substances are more aromatic – possessing strong chemical stability – with large size and high molecular weight (Martin-Mousset et al., 1997; Ekström et al., 2011). All these characteristics make DOM less photochemically and biologically degradable, i.e. refractory/recalcitrant DOM (Ågren et al., 2008; Hansell, 2013), as bacteria for instance preferentially use low molecular weight DOM such as carbohydrates and amino acids (Berggren et al., 2010). Moreover, the degradation efficiency of aquatic consumers usually decreases with DOM age (Raymond and Bauer, 2001), whereas fresh DOM from catchment vegetation can significantly boost the system productivity (Lennon and Pfaff, 2005). The seasonal and annual variations of DOM and Fe concentrations have only been

demonstrated in the last 20 years (Laudon et al., 2004; Dawson et al., 2008; Haaland et al., 2010; Finstad et al., 2016). Hence, the understanding of the change in DOM composition and concentration must be improved.

No single mechanism can explain water browning (Temnerud et al., 2014; Škerlep et al., 2020) that is likely to greatly impact both ecological and societal aspects. Water browning affects food webs, e.g., prey-predator interactions or primary production (Karlsson et al., 2009; Ranåker et al., 2012; Kritzberg et al., 2020), and ecosystems services of aquatic ecosystems, e.g., fish production, drinking water quality, and recreation services (Solomon et al., 2015; Kritzberg et al., 2020).

In this review, we focus on the diversity of ecological consequences of water browning on trophic levels of aquatic ecosystems, highlight knowledge gaps regarding the effect of browning on aquatic-terrestrial habitat coupling, and investigate the potential of browning as a more global phenomenon than currently presented. We aim to set research directions to improve our understanding of the browning phenomenon and its impact on ecosystem functioning. Specifically, our objectives are to review the consequences of browning on 1) different freshwater habitats, 2) food webs, 3) aquatic-terrestrial habitat coupling, present 4) browning and the DOM/DOC increase in different regions of the world, and finally 5) examine tools such as remote sensing to investigate the extent of browning from local to global scales.

2. Ecology of water browning

2.1. Browning alters lakes and rivers: what about other freshwater habitats?

Water browning alters directly and indirectly many characteristics of freshwater habitats, such as their optical and thermal conditions, oxygen availability, bioavailability of pollutants in water, and greenhouse gases sequestration and emission (Table 1). However, studies have focused on lakes, rivers, or controlled experiments (e.g., respectively Arzel et al., 2020, Berggren and Al-Kharusi, 2020, and Ekström et al., 2011; Fig. 1). Freshwaters encompass a wide diversity of other habitats, including small and temporary wetlands, which are not defined in regulations globally. There are many different temporary wetland types (e.g., alpine pool, prairie pothole, vernal pool); but they are all small, shallow, and they often dry annually (Calhoun et al., 2017). The unique features of these wetlands make them biodiversity hotspots for many species, such as aquatic invertebrates (Colburn et al., 2007), semi-aquatic amphibians (Snodgrass et al., 2000; Gibbons et al., 2006) or waterbirds (Nummi et al., 2019, 2021), and terrestrial moose (*Alces alces*) or hares (*Lepus* sp.) (Dixneuf et al., 2021).

Browning may have direct and indirect consequences on aquatic and semi-aquatic species (see Sections 2.2 and 2.3) Hence, we may expect that the degradation of small and temporary wetlands due to browning will have drastic consequences on their inhabitants and users. However, no studies have focused on the potential browning of temporary wetlands; although one paper mentioned a concomitant increase of the water color and DOC concentration of temporary ponds in Spain (Fig. 1A and B; Serrano, 1994). Additionally, several papers investigated the DOC/DOM characteristics of temporary wetlands (e.g., Yu et al., 2015; Chow et al., 2016). The importance of small and temporary wetlands is now recognized (Zedler, 2003; Calhoun et al., 2017; Ramsar Convention on Wetlands, 2018). Research on such habitats should thus now investigate how browning may modify them and their communities; it would improve knowledge on the processes of browning and help targeting good integrated watershed management strategies, including networks of all wetland types.

2.2. Browning affects aquatic food webs

The impacts and major role of light, temperature and chemistry on primary production, prey-predator interactions, and food web structure in aquatic environments are well known (Grant, 1986; Wissel et al., 2003; Ask et al., 2009; Ranåker et al., 2012). Hence, most research investigating the ecological consequences of browning focused on the response of primary producers (e.g., Ask et al., 2009; Forsström et al., 2013; Seekell et al., 2015) and planktonic communities (e.g., Estlander et al., 2017; Saebelfeld et al., 2017; Williamson et al., 2020), especially in lakes. Other studies showed the different responses of fishes to browning (Hedström et al., 2017; Hayden et al., 2019; van Dorst et al., 2020) or the direct link between a 20-year decline of aquatic macroinvertebrates and browning of boreal lakes (Arzel et al., 2020). However, there is far less knowledge regarding the effects of browning on macrophytes, invasive species, and food webs.

2.2.1. Macrophytes

Although plants can benefit from browning through the attenuation of UV-B penetration, CO₂ provisioning and binding of harmful metals (Scully et al., 1995; Sobek et al., 2003; Wang et al., 2010), further browning and subsequent change in light regime may cause submerged macrophyte decline (Reitsema et al., 2020) due to a decrease of their maximum growing depth (Bociag, 2003; Reitsema et al., 2018), particularly if associated with climate warming (Choudhury et al., 2019; Reitsema et al., 2020). However, Nagengast and Gąbka (2017) showed that submerged macrophyte

Table 1

Effect of water browning on the characteristics of surface waters (↓ = decrease, ↑ = increase).

Water characteristics affected by browning	Effect of browning	References
Optical conditions	<ul style="list-style-type: none"> • ↓ Ultraviolet exposure and visible light penetration through the water column • Red colors become the most penetrating wavelengths in high-DOM lakes 	Kirk, 1983; Jones, 1992; Kirk, 1994; Thrane et al., 2014; Williamson et al., 2015
Thermal conditions	<ul style="list-style-type: none"> • Stronger thermal stratification and shallower thermocline in high-DOM lakes • Less likely to happen in shallow lakes that have enough mixing energy to prevent thermal stratification 	Houser, 2006; Read and Rose, 2013; Solomon et al., 2015; Williamson et al., 2015; Strock et al., 2017; Pilla et al., 2018
Oxygen (O ₂) availability	<ul style="list-style-type: none"> • Dissolved O₂ depletion due to ↑ microbial respiration and loss of benthic primary producers • Browning-related steeper thermal stratification prevents the mixing of oxygenated water to deeper parts of the waters • Browning-anoxia feedback loop: release and ↑ solubility of DOC, iron (Fe) and phosphorus 	Roehm et al., 2009; Foley et al., 2012; Brothers et al., 2014; Knoll et al., 2018; Berggren and Al-Kharusi, 2020
Greenhouse gases sequestration and emission	<ul style="list-style-type: none"> • DOC concentration positively correlated to CO₂ efflux and total in-lake production • Net contribution of browning to CO₂ emissions from lakes ambiguous: balance between DOC mineralization and burial depends on lake biogeochemistry • ↑ Dissolved methane in lakes 	Hanson et al., 2011; Furlanetto et al., 2012; Ferland et al., 2014; Vachon et al., 2017; Zhou et al., 2018; Allesson et al., 2021
Bioavailability of pollutants in water	<ul style="list-style-type: none"> • ↑ Concentration of arsenic and vanadium linked to ↑ concentration of DOC-Fe complex in surface waters • Concomitant ↑ in water color and mercury burial in lakes, and ↑ in-lake methylation by browning-induced anoxic conditions • ↑ Bioavailability of organic pollutants in water by sorption processes 	Wällstedt et al., 2010; Oni et al., 2013; Ripszam et al., 2015; Isidorova et al., 2016; Ahonen et al., 2018; Kozak et al., 2021

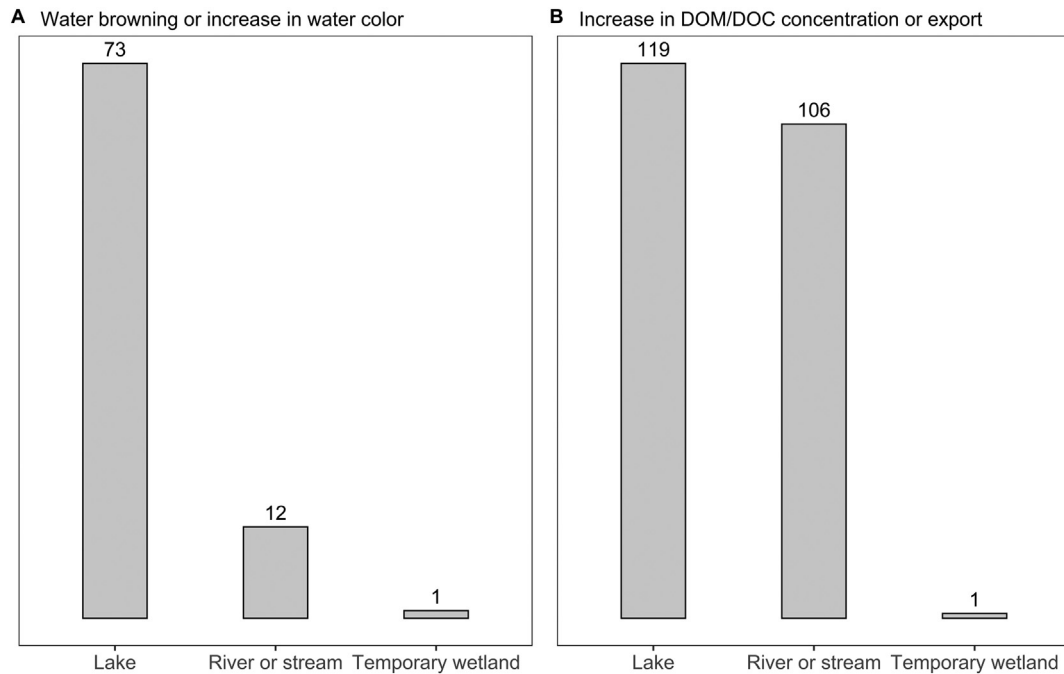


Fig. 1. Number of publications mentioning A) water browning (and synonyms) or an increase in water color in different freshwater habitats, and B) an increase in DOM/DOC concentration or export to waters in different freshwater habitats. Some articles mention both water browning and an increase in DOM/DOC concentration or export, in these cases they are counted in both panels A and B. Advanced search was carried out using Web of Science Core Collection on 12/11/2021; the search terms are provided in the supplementary material (S1).

occurrence depends on water color in Polish lakes. If they might initially benefit from increased temperature and browning, they are expected to collapse after a certain threshold (Choudhury et al., 2019), programming a potential global decline with browning expansion and reinforcement. Macrophyte decline might induce a homogenization effect with a reduction of structurally complex littoral habitats (Hilt et al., 2013), which might in turn disturb higher trophic levels in freshwaters (Scharnweber et al., 2016). In addition, a decline in *Carex* and even stronger in *Equisetum* macrophytes was noted between the 1990s and the 2010s in boreal lakes (Suhonen et al., 2011; Pöysä et al., 2017). Although water browning was not directly linked to the decline of these emergent macrophytes in these studies, it should be further investigated, like the unexplored response of floating macrophytes to browning.

2.2.2. Invasive species

In some cases, water browning may have more influence on lake invasion by non-native macrophytes than climate warming if it negatively affects the growth of the native plants and its capacity to resist invasion or compete (Mormul et al., 2012). Nevertheless Xu et al. (2018) found contrasting results, highlighting the need for further research in different environments. Jellyfish invasions in the Southern Hemisphere are limited by the sensitivity of medusa stage to UV radiation; browning is thus expected to provide favorable conditions for invasion of lakes (e.g., *Craspedacusta sowerbii* in Caputo et al., 2018). Moreover, Gallardo et al. (2016) noted increasing organic matter content in invaded freshwater habitats by invaders of different trophic positions (e.g., primary producers, filter collectors), which may be due to additional loadings such as excretion and changing hydrological conditions. Such increase may lead to water browning, for example via top-down effects by introduced or invasive fish (e.g., Milardi et al., 2019). Severe browning is related to increasing levels of anoxia that may promote the invasion of low oxygen tolerant invasive species. Such could be predatory invertebrates (such as *Chaoborus*), or fishes (such as Crucian and Prussian carps) with a potential for ecosystem-level effect; but we are not aware of such studies directly related to browning. Similarly, there is very little research accounting for the potential effect of invasive species on browning. Invasive species usually have their highest effects

far outside of their native range. Different species have been frequently introduced in South America, like the North American beaver (*Castor canadensis*) and African hippopotamus (*Hippopotamus amphibius*). They have caused an enhanced transfer of DOM from terrestrial to aquatic ecosystems, potentially contributing to browning, thus influencing habitats for other species (e.g., Westbrook et al., 2017; Shurin et al., 2020). Introduced ungulates, such as game species (e.g., deer) could indirectly cause browning via their browsing effects; they have potential to alter riparian vegetation, and in turn carbon fluxes to water (Opperman and Merenlender, 2000). All in all, the impact of water browning on invasive species and vice versa has received little attention and requires further research.

2.2.3. Food webs

Browning influences the productivity of food webs nonlinearly: it initially increases the overall biomass, but subsequently starts to reduce it (Karlsson et al., 2009, 2015; Seekell et al., 2015). While such changes are documented, especially in algal communities and fish biomass (Karlsson et al., 2009; Finstad et al., 2014; van Dorst et al., 2020), very few studies included most or all different trophic levels to measure how a browning gradient in nature influences overall biomass, energy flows and transfer. When considering browning gradients and food webs together, one issue is the multiplicity of simultaneous processes, since browning is associated with increasing levels of nitrogen and phosphorus that give a net boost to food webs (e.g., Hayden et al., 2019; Keva et al., 2021). However, semi-natural experiments have used terrestrial carbon additions in small ponds or lakes, using various tracers (e.g., sugar) or isotopically different terrestrial plants (e.g., maize), to track how additional carbon is transferred upwards in food webs (e.g., Pace et al., 2004; Carpenter et al., 2005; Taipale et al., 2008; Scharnweber et al., 2014; Jones et al., 2018). They mainly suggest a relatively high carbon transfer up to fish, but there is often a very clear contrast to natural conditions where terrestrial-derived dissolved organic carbon is often of residual quality, meaning not available or not preferred by upper trophic level consumers (e.g., Brett et al., 2017). Studies about lake food webs along browning gradients are scarce and even less is known about small and temporary wetlands. Their hydroperiodicity and

varying food web structure, usually without fish predators, strongly deviate from lakes. Browning may therefore impact food webs differently pending on freshwater habitat types. Moreover, their small size makes them more influenced by the surrounding terrestrial habitats, with which they are likely linked through bidirectional fluxes of elements and organisms.

2.3. Browning calls for an aquatic-terrestrial habitat coupling approach

Terrestrial and aquatic habitats are inherently connected via fluxes of elements and organisms, but most studies focus on habitats separately (e.g., Poliss et al., 1997; Soininen et al., 2015). Many animals are living at the interface of terrestrial and aquatic habitats, providing important insights to understand how changes in one habitat may cascade to another. Furthermore, aquatic-terrestrial coupling is likely bidirectional and should be viewed as feedback loops since many organisms use both habitats during their lifecycle.

2.3.1. Amphibians

To our knowledge, no research has been carried out to investigate the potential impact of browning on amphibian populations. Amphibians provide ecosystem services (Hocking and Babbitt, 2014) from cultural services to structural and functional supporting services (i.e., influence ecosystem structure through bioturbation, and ecosystem functions such as nutrient cycling through waste excretion, respectively). They also have an unfavorable conservation status worldwide (Stuart et al., 2004). Water browning is expected to extend and intensify in ponds and small lakes which are the breeding habitats of most Palearctic amphibians (Bolocho et al., 2020). It is therefore important to assess the potential effects of this phenomenon on this group. The reduction in light intensity may be detrimental to species or stages using vision to forage underwater. The predictions are not obvious for tadpoles that feed on phytoplankton but also on biofilm (Altig et al., 2007) if the proportion of autotroph bacteria increases in lentic ecosystems. Less ambiguous is the fact that humic acids can, on one hand, interfere with olfaction in fish (Fisher et al., 2006), thus potentially decreasing their predation pressure on tadpoles; but on the other hand, impair the tadpole's ability to recognise dragonfly predators (Polo-Cavia et al., 2016).

The larval stages of amphibians may benefit from the attenuation of UV-B radiation due to browning. UV radiation is harmful to amphibians especially during their development (Bancroft et al., 2008; Londero et al., 2019). For instance, in the boreal species *Rana temporaria*, embryos exposed to UV-B displayed a higher frequency of developmental anomalies, late metamorphosis and smaller size than controls (Pahkala et al., 2001). In addition to the effects on foraging and development, the changes in the photic environment induced by browning (Scully et al., 2003; Nydahl et al., 2019) are expected to affect social interactions of species that mate in water and partly rely on visual communication with bright UV-reflecting color patches and exaggerated morphological traits like European newts. A reduction of light transmission in turbid water seems to limit the expression of sexual traits of *Lissotriton helveticus* males even if the underlying mechanism is not identified (Secondi et al., 2007) but a reduction of the food acquisition rate is a possible cause (Baker, 1992). Newts display a complex courtship usually on the pond bottom that includes visual and olfactory components (Halliday, 1977). *Lissotriton vulgaris* females assess the UV component of the ventral coloration of males and spend more time close to a male when UV radiation is available (Secondi et al., 2012). The lack of UV in brown waters was shown to affect species recognition between *L. vulgaris* and *L. helveticus* in the lab (Secondi and Théry, 2014). When visual cues are not available females may give more weight to olfactory information as observed in the Alpine newt though (Denoël and Doellen, 2010). However, humic acids may interfere with olfactory communication in water breeding amphibians like newts, as demonstrated in fish (Mesquita et al., 2003; Fisher et al., 2006). Finally, humic acids have been shown experimentally to have a hormone-like effect in fish and amphibians causing a slight feminization (Steinberg et al., 2004). Thus, a change in water color may reduce the ability for individuals to acquire food, detect predators, express sexual traits involved in mate selection,

assess potential mates, and affect the expression of sexual hormones. These issues have not been investigated in amphibians yet. Nevertheless, negative consequences on individual fitness and population growth may be expected. It is noteworthy that many amphibian species breed in naturally stained water and seem to sustain viable populations, even *Lissotriton* newts where sexual selection for visual traits is strong. Particular attention should be given to areas where clear waters were dominant and are now browning. There, locally adapted populations may be more at risk than populations that have been living in heterogeneous environments where water bodies with different levels of browning have been co-occurring for a long time, for instance in mixed landscapes with forest and open areas. This concern should be rapidly addressed as clear lakes are more sensitive to browning than brown lakes (Knoll et al., 2018; Williamson et al., 2020).

2.3.2. Waterbirds

In the boreal environment, the abundance of waterbirds feeding on fishes, plants and invertebrates showed a positive relation with clear water and macrophyte percentage cover (Hansson et al., 2010). The impact of browning on waterbirds has not been demonstrated yet, but water browning causes macrophyte decline (Reitsemma et al., 2018). The decline (richness and abundance) of ducks with an insectivorous diet over the past 25 years (Pöysä et al., 2019; Elmberg et al., 2020) could also be linked to the concomitant decline of aquatic invertebrates associated with water browning (Arzel et al., 2020). The different compartments of lake food webs are interrelated, so disturbances on one level can greatly impact others, potentially leading to changes from local to large scale. Fennoscandian lakes are the main breeding area of migratory ducks in Europe (European Commission, 2001). A decline in duck breeding success over the boreal environment, as a direct or indirect result of browning, could lead to strong consequences on their population dynamics. Insectivores are one of the largest guilds of predators (Nyffeler et al., 2018). A decline in insects will surely negatively impact their predators through trophic cascades. For instance, the Diptera family, in which many species have an aquatic larval stage, represents at least 20% of the diet of predators of distinct taxa, e.g., birds, bats and invertebrate predators such as Odonates (Vesterinen et al., 2020). A general decline of biomass or abundance in this taxon may thus have profound and global consequences in the tree of life as the insect resource is shared by so many predator groups.

2.3.3. Pathogens

At the global scale, browning may also affect drinking water quality, and increase the risk of pathogen persistence by reducing the potential for solar UV inactivation of pathogens (Williamson et al., 2017). Waterborne pathogens are one of the most frequent sources of infectious diseases. For example, the United States counts between 12 and 19 million people infected annually (Trtanj et al., 2016; Williamson et al., 2017). Waterborne pathogens of humans and wildlife include bacteria, fungi, protozoans and viruses. Among them, slow and high pathogenic avian influenza persistence in the aquatic environment is expected to be promoted by climate change with an increase in temperatures (see in Dalziel et al., 2016); but studies overlooked browning processes also linked to climate change. Many studies demonstrated the importance of solar radiation in the inactivation of the four types of pathogens in surface waters (King et al., 2008; Overholt et al., 2012; Mattle et al., 2015; Nguyen et al., 2015). Pathogen vectors, e.g., mosquitoes, are also sensitive to natural solar UV radiation (Berry et al., 2020), through a decrease in larval survivorship. Browning decreases UV-B penetration (Williamson et al., 2016), hence its solar inactivation potential (SIP) in the water column, which can favor the survival of pathogens. For example, Williamson et al. (2015) showed that the long-term increase of DOM in lake Giles in North America and the concurrent increased UV absorption led to a two-fold diminution of SIP. Similarly, DOM provides a refuge for mosquito larvae to UV radiation, which increases habitat suitability (Berry et al., 2020).

Climate change projections predict increased heavy precipitation events, which will translate into an enhanced release of DOM into surface waters, especially in highly disturbed catchments (Ren et al., 2016). Further research is

needed to efficiently target relevant management and treatment efforts against pathogens; focus should be on high-DOM waters and future increased precipitation zones where pathogens are highly expected to thrive.

2.3.4. Flows of energy and organisms between terrestrial and aquatic environments

Browning may impact strongly and in multiple ways energy sources and flows in aquatic environments, but may also alter the fluxes from aquatic to terrestrial environments. Terrestrial leaves may be an alternative carbohydrate source for herbivorous zooplankton, which can use terrestrial carbohydrates for their fatty acid synthesis under phytoplankton deficiency (Taipale et al., 2016a). However, the fate of other terrestrial origin biomolecules (e.g., amino acids) in the aquatic food webs is not known, and most of current knowledge is related to indirect consequences. For example, browning has a great impact on the phytoplankton composition, and the synthesis and transfer of physiologically essential long-chain polyunsaturated fatty acids (PUFA), such as eicosapentaenoic acid (EPA, 20:5 ω 3) and docosahexaenoic acid (DHA, 22:6 ω 3) (Taipale et al., 2016b; Strandberg et al., 2016); PUFA are required for optimal growth and reproduction of zooplankton, fish and mammals (Arts et al., 2009). Since EPA and DHA are synthesized only by certain phytoplankton taxa (Taipale et al., 2016b), changes in the phytoplankton community influence EPA and DHA availability for herbivorous zooplankton, and their transfer in the food web. Browning might have opposite impacts on the phytoplankton composition in different climatic zones and biomes. Consequences in nutritional quality of seston might thus differ markedly between these zones. For example, Senar et al. (2019) found that browning favored cyanobacteria and decreased sestonic EPA and DHA content in temperate lakes. However, in boreal lakes, strong browning is known to inhibit cyanobacteria (Taipale et al., 2016b; Senar et al., 2021), but favor the raphidophyte *Gonyostomum semen* (Lepistö et al., 1994; Lebrecht et al., 2018) which might result in an apparent increase on EPA even though *G. semen* is too large to be consumed by most zooplankton (Gutseit et al., 2007; Strandberg et al., 2020).

Zooplankton studies are scarce, but current results suggest that herbivorous cladocerans and calanoids are able to detect high quality alternative diets, and thus mitigate browning-induced lower nutritional quality of seston (Taipale et al., 2016a; Senar et al., 2019). However, the low availability of high-quality algae may limit zooplankton biomass production (Taipale et al., 2019). Moreover, the negative impact of browning on the nutritional quality of seston and zooplankton was recently identified in the productivity gradient of subarctic lakes (Keva et al., 2021), and was mostly explained by the structural changes in the zooplankton community. Altogether, two separate studies have shown that browning decreases nutritional quality of perch for human consumption by leading to lower EPA and DHA and higher mercury content (Taipale et al., 2016b; Strandberg et al., 2017).

Recent studies have also shown the impact of PUFA on the survival of insectivore bird chicks (Twining et al., 2016), which makes aquatic ecosystem insect fluxes important PUFA sources also for insectivorous birds. While the hatching of aquatic insects will have direct important effects on birds and riparian insects, there might be a feedback loop via terrestrial insects and bird faeces back to the aquatic environment (Scharnweber et al., 2014). Aquatic invertebrate communities are strongly structured by selective fish predation that may change the insect fluxes to terrestrial habitats (Gratton et al., 2008; Milardi et al., 2019), and may even cause trophic cascades in riparian terrestrial habitats (Knight et al., 2005). Insect flux also contains both harmful and beneficial substances (Chaves-Ulloa et al., 2016; Popova et al., 2017), differing between ecosystems. Moreover, very little is known on how potential changes in the synthesis and transfer of essential biomolecules in freshwater food webs influence consumers in the interface of aquatic and terrestrial ecosystems (but see Taipale et al., 2016b); for instance, the consequences on animals feeding on aquatic resources such as waterbirds or semi-aquatic mammals is not known and calls for future research.

2.3.5. Beavers as promoters of browning

While the causes of browning are mainly attributed to human activities (see Section 3.1), natural disturbances such as beaver-induced floods may

also substantially contribute to the process. Beavers (*Castor* sp.) are known as ecosystem engineers to cause significant patch disturbance in boreal riparian ecosystems (Remillard et al., 1987; Nummi and Kuuluvainen, 2013; Kivinen et al., 2020). By damming, and the ensuing flooding, beavers cause the death of herbaceous vegetation and trees because of the anaerobic conditions of roots caused by the flood (Thompson et al., 2016; Johnston, 2017). Organic matter and nutrients coming from the dead plants and soil are then flushed from the flood zone to the dammed water body, hence affecting the biogeochemical conditions of the water (Vehkaoja et al., 2015; Nummi et al., 2018). Vehkaoja et al. (2015) showed that beaver lakes had higher DOC concentrations than non-beaver lakes in small boreal lakes, with an increase in DOC concentration within the three first years of beaver impoundment. DOC concentrations returned to their pre-flooding level after 4–6 years. Blanchet (2020) observed the same pattern with higher water color measured in lakes recently flooded, i.e. three years, compared to lakes without beaver activity or with older flood events. In the first impoundment years, DOC arriving in water bodies comes from the decaying plants (Hodkinson, 1975; Nummi, 1989) and is mainly composed of low molecular weight molecules that could be easily processed microbially. The following impoundment years, however, bring DOC with terrestrial characteristics to the waterbody (Rasilo et al., 2015), i.e. refractory and aromatic molecules with high molecular weight which are less efficiently used by organisms and mainly removed by photochemical reactions. Although DOC concentrations usually return to their pre-flood level (Vehkaoja et al., 2015), the remaining DOC may be composed of more colored molecules, hence contributing to the browning phenomenon. Newly established beaver ponds, in particular, may contribute more to browning in comparison to old beaver ponds as they have more humic-like DOM (Catalán et al., 2017).

While the immediate effects of beavers on water chemistry and aquatic animals are known, there is far more limited understanding of riparian changes and potential feedback loops back to aquatic habitats. These aspects are important to consider, as beavers were hunted to the brink of extinction between the 16th and 19th centuries in Eurasia, leaving only eight isolated populations from France to Mongolia by the end of the 19th century (Nolet and Rosell, 1998). They were reintroduced in the 20th century which led to a successful recovery of some beaver populations and their gradual return to their previous distribution area (Whitfield et al., 2015; Halley et al., 2021). Their increasing population, for instance, resulted in increased DOC concentrations in streams in a 30-year study in Germany (Smith et al., 2020). Therefore, the recent and current population increase of beavers and their substantial role in the biogeochemistry of headwater bodies and the riparian zone are strong arguments to include them in research on water quality, especially in the boreal landscape where beavers are largely distributed, and in areas where they are non-indigenous.

3. Drivers and subsequent spatial extent of water browning

3.1. Main drivers of water browning

Over the past two decades of studies, no single mechanism but rather a combination of several drivers can explain water browning (Temnerud et al., 2014; Škerlep et al., 2020; Xiao et al., 2020), such as acid recovery, weather patterns and land-use (Hongve et al., 2004; Monteith et al., 2007; Björnerås et al., 2017; Kritzberg, 2017), which evolve at different timescales. Most of the research investigating the causes of browning was carried out on lakes and rivers (e.g., de Wit et al., 2016; see Fig. 1A and B). As mentioned in Section 2.1, browning processes in small and temporary wetlands remain unknown, although they are connected to other freshwaters via surface and subsurface hydrologic connections (Ameli and Creed, 2017). Research on browning of surface waters should thus include aquatic networks at the catchment scale at least, to get a more holistic view of the processes.

As several reviews already addressed the potential mechanisms of browning (e.g., Evans et al., 2005; Creed et al., 2018; Kritzberg et al., 2020), we provide a summary of water browning drivers in Table 2 to concentrate

Table 2

Summary of the main past and present factors driving water browning over time (↓ = decrease, ↑ = increase).

Driver	Effect(s)	References
Acid recovery ↓ Acid deposition	<ul style="list-style-type: none"> • ↑ DOM mobility and solubility in soils, and ↑ transport to aquatic systems • Changes in DOM composition toward more colored molecules 	Monteith et al., 2007; LoRusso et al., 2020; Meyer-Jacob et al., 2020; Redden et al., 2021
Climate (change) ↑ Precipitation	<ul style="list-style-type: none"> • ↑ Water table and ↑ connectivity between organic soils and surface waters: DOM leaching • 10% ↑ in precipitation estimated to ↑ mobilization of organic matter from soils to freshwaters by at least 30% 	Hongve et al., 2004; Laudon et al., 2011; de Wit et al., 2016; Mahdiyian et al., 2021
↑ Temperature	<ul style="list-style-type: none"> • ↑ Export of DOM to freshwaters: stimulation of soil biological activity ↑ organic matter decomposition and DOM solubility • 2 °C ↑ in temperature estimated to ↑ organic matter decay rates up to about 10%, mainly through changes in runoff 	Christ and David, 1996; Moore and Dalva, 2001; Dawson et al., 2008; Catalán et al., 2016
Permafrost thawing (due to ↑ temperatures)	<ul style="list-style-type: none"> • ↑ DOM concentration in waters • Change in DOM composition: mobilization of ancient DOM from deeper soil layers with lower degradation efficiency 	Feng et al., 2013; Ewing et al., 2015; Ward and Cory, 2015; Wauthy et al., 2018; Ma et al., 2019
Land cover Forest cover Wetland cover	<ul style="list-style-type: none"> • Coniferous forests = sources of DOC and Fe in freshwaters • Wetlands = major contributors of DOM to surface waters • Peatland cover can account for 78% of DOC catchment export to lakes on the long-term 	Finstad et al., 2016; Björnerås et al., 2017 Dillon and Molot, 1997; Mattsson et al., 2005; Arvola et al., 2016
Land use Agriculture	<ul style="list-style-type: none"> • Soil degradation and water flow modification: releases DOM, excess nutrients, and pesticides to freshwaters 	Karlen et al., 1997; Ogle et al., 2005; Graeber et al., 2012
Afforestation	<ul style="list-style-type: none"> • Accumulation of soil organic carbon (due to ↑ in forest cover) and its export to surface waters, especially if coniferous trees • Considered as contributing to long-term browning on the centennial timescale 	Meyer-Jacob et al., 2015; Kritzberg, 2017; Škerlep et al., 2020
Clearcutting and site preparation practices	<ul style="list-style-type: none"> • ↑ DOM leaching through multiple factors: ↑ groundwater level, ↑ loose organic matter due to topsoil disturbance, and ↑ organic matter decomposition rate (due to ↑ soil temperature) • Effect of harvesting and preparation practices potentially of short-term 	Piirainen et al., 2007; Laudon et al., 2009; Winkler et al., 2009; Sarkkola et al., 2010; Schelker et al., 2012; Glaz et al., 2015
Peatland drainage	<ul style="list-style-type: none"> • ↑ Export of DOM to surface waters due to ↑ decomposition of surface peat • Release of old DOM (up to several thousands of years; less efficiently used than modern DOM) by their mobilization from deeper parts of the soil 	Hulatt et al., 2014a, 2014b; Marttila et al., 2018; Finér et al., 2021; Nieminen et al., 2021
Interplay between acid deposition, climate change, and land use “Greening” phenomenon (i.e., ↑ vegetation productivity due to ↑ growing season, biomass, and cover)	<ul style="list-style-type: none"> • ↑ DOM concentration in surface waters due to ↑ export of DOM from catchments • DOM export in arctic and boreal waters estimated to ↑ by 65% in the next hundred years, primarily because of greening 	Larsen et al., 2011; Finstad et al., 2016; Zhu et al., 2016; Kritzberg, 2017

here below on the actual and potential extent of browning following these drivers.

3.2. Spatial extent of water browning processes

The main factors identified that affect browning processes include acid recovery, climate change (heavier precipitation events and increasing temperatures, melting of permafrost), land cover, land use, and catchment greening. The combination of several of these factors has mainly caught researchers' attention in the Northern Hemisphere (Fig. 2). In the articles cited in this review, evidence of long-term browning has only been demonstrated in the Northern Hemisphere through different processes (Fig. 2A, B, and C), with a clear focus on cold and temperate regions (Fig. 2D). Our work shows that the semantic of water browning remains unclear globally (Fig. 2A, B, C). This is due to the imbrication of diverse processes at its origin. This makes it difficult to get an overview of its extent at the global scale, although evidence of processes linked to browning waters can be found from cold to tropical regions.

3.2.1. Cold regions

Here we focus on the comparatively cold regions of the globe that contain the climate zones (e.g., polar and subpolar) or biomes (e.g., boreal) typical to the region. In the Northern Hemisphere, the increase in water color and DOM concentration in arctic lakes and rivers is mainly due to the greening of tundra (Fraser et al., 2011; Epstein et al., 2012), as well as climate change and its consequences on permafrost (Ma et al., 2019) and peatlands (Dillon and Molot, 1997; Minayeva et al., 2016). Wetlands cover 60% of the

Arctic zone, most of which are peatlands (Minayeva and Sirin, 2009). Climate change predictions project a faster warming in the Arctic compared to other climate zones (IPCC, 2014), with increasing precipitation events, which will result in permafrost loss; it will in turn degrade arctic peatlands and facilitate the export of aromatic, high molecular weight, colored DOM (Frey and Smith, 2005; Ewing et al., 2015; Minayeva et al., 2016). In the Southern Hemisphere, no research has investigated a possible browning trend in Antarctic surface waters. Nevertheless, the literature on DOC suggests a generally very low concentration in Antarctic freshwaters, with a low proportion of humic substances (Barker et al., 2013; Foreman et al., 2013). However, ongoing climate change may impact carbon fluxes in Antarctica, including DOC (Quesada and Velázquez, 2013).

The subarctic zone may experience intense browning due to acid recovery, increased temperatures and precipitation, and permafrost thawing, which promote the release of more colored but less efficiently processed DOM from soils (Monteith et al., 2007; Ekström et al., 2011; Finstad et al., 2016; Björnerås et al., 2017; Ma et al., 2019). Mzobe et al. (2018) showed that peatlands and secondarily forest productivity are key contributors of DOC in subarctic streams, but water remains less brown than in boreal zones (Lau et al., 2021). Boreal surface waters are affected by all drivers identified in Table 2, making them particularly susceptible to brownification.

3.2.2. Temperate regions

In the temperate area, DOC/DOM increase and composition change, as well as their drivers have been primarily studied in Europe and North America. In the UK, studies focused more on DOC concentration rather

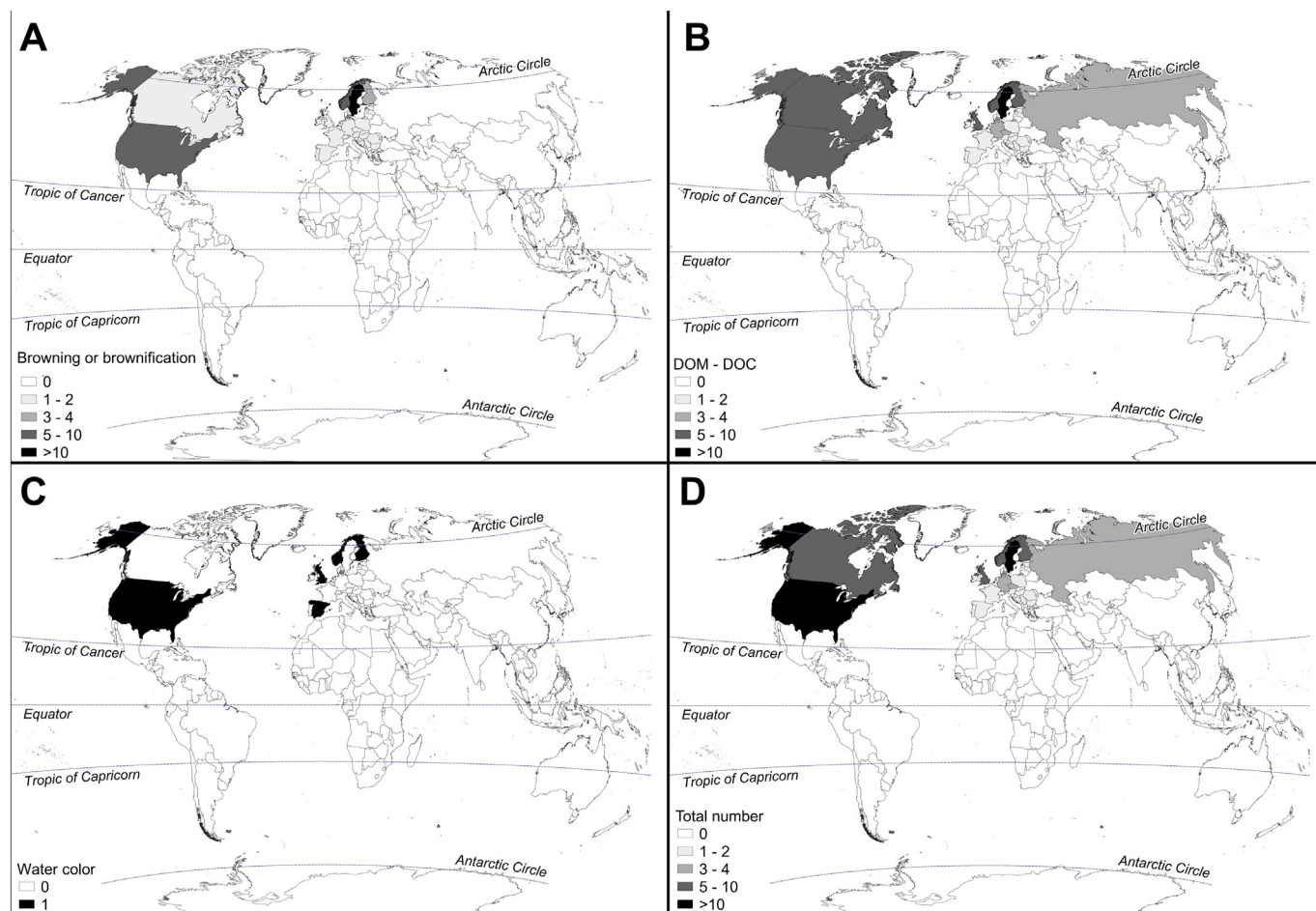


Fig. 2. Spatial extent of in situ studies on water browning processes cited in this review. A: articles demonstrating evidence of water browning or brownification (increase in absorbance, color units, or DOM/DOC content); B: articles highlighting an increase in DOM/DOC concentration with or without mentioning the term water browning (and synonyms); C: articles showing an increase in water color without mentioning the term water browning (and synonyms); D: total number of articles demonstrating browning processes combining A, B, C without duplicated articles. Reviews and controlled experiments were excluded.

than the browning phenomenon in itself (Fig. 2). DOC concentration has doubled in the Acid Waters Monitoring Network since the 1980s (Worrall et al., 2003; Evans et al., 2005), and has been linked to decreasing acid deposition (Davies et al., 2005; Evans et al., 2005). DOC trends were positively correlated to temperature, and negatively correlated to ionic strength (Evans et al., 2005). Rainfall patterns (wet-dry cycles) seem to influence DOC trends, but in a more variable way since rainfall varies intra- and inter-annually, while forestry practices are considered to play a minor role in the increase in DOC levels (Harriman et al., 2003; Evans et al., 2005). However, UK lakes may experience browning differently since the composition of DOM related to water color depends on catchment parameters, i.e. land use/land cover (Yates et al., 2019). It has been demonstrated that DOM originating from agricultural inputs is mainly of a low aromaticity and molecular weight; high aromaticity being associated with high water color (Fasching et al., 2014). As agriculture covers 72% of UK territory (UK Government, 2020), a change in DOM composition is likely to have concurrently happened with increased DOC concentration in waters, potentially leading to slow water browning in some catchment areas.

Czech Republic was exposed to high atmospheric pollution, which peaked in the 1980s and sharply declined in the 2000s. The change in acid deposition strongly influenced DOM concentration in the Malše River since 1969 (Hejzlar et al., 2003) and in 9 water bodies, streams and reservoirs (Oulehle and Hruška, 2009). Concurrently with changes in acid deposition, climatic (increasing temperature) and hydrologic conditions

(i.e. proportion of histosols, runoff), may have resulted in large amounts of DOM in surface waters due to an increased solubility, mobility and transport. A change toward more colored DOM may also be expected in response to acid recovery (Ekström et al., 2011).

In France, 30% of the lakes may be affected by organic matter enrichment (Sepp et al., 2018); several studies have investigated DOM parameters in French streams, but no studies focused on browning have been carried out. Humic substances generally dominated DOM composition between 2010 and 2013 in a north-eastern French river, and the highest values of the SUVA₂₅₄ (an index for aromaticity) could not be explained (Assaad et al., 2015). Few studies in France have investigated DOM quality in lakes and reservoirs, although humic substances are present in a higher proportion than in rivers (Martin-Mousset et al., 1997). Birgand and Novince (2004) observed a long-term (15–20 years) increase of DOM concentration in Breton streams (Western France). Climate fluctuations could explain the interannual variation, and the riparian zones appeared as a substantial contributor of DOM export to surface waters. Humic substances, DOC and Fe concentrations were strongly and positively correlated in the Penzé river. As several streams in the Brittany region have already experienced a rise in DOM concentration and exhibited a high proportion of humic substances (Birgand and Novince, 2004; Marie et al., 2015), water browning is likely to impact the local biodiversity and drinking quality since 85% of surface waters in Brittany are used for drinking purposes. Hence, there is a clear necessity to understand the factors governing the transfer of DOM to surface waters in France.

In the US, based on the US Environmental Protection Agency's National Lakes Assessment (NLA) data (1000+ lakes sampled in 2007 and 2012), Leech et al. (2018) showed that the proportion of "murky" lakes (experiencing both eutrophication and browning) increased by almost 12%, with suspected negative consequences for water quality and food web structure. This study called for more research to understand how the combined "greening" and "browning" of lakes affects ecological processes in the US.

In Canada, Meyer-Jacob et al. (2020) assessed whether DOC levels are still influenced by acid deposition in 75 lakes in the Greater Sudbury region that has been heavily affected by sulfur dioxide emissions from local metal smelting during the 20th century. They found that acid deposition has historically had a strong impact on lake-water DOC dynamics in this region, but that other drivers, such as changes in climate or vegetation cover, are becoming the dominant controls on changes in DOC concentration.

At a larger scale, comparisons between European countries have been done. Mattsson et al. (2009) showed that catchments with drained surfaces in France concentrated and exported less DOC compared to Danish and Finnish measurements, explaining that more factors promote the export of DOM into surface waters in boreal environments than in more temperate ones.

3.2.3. Tropical regions

In the tropical and subtropical regions, only one recent article directly mentioned water browning while studying harmful algal blooms (Hu et al., 2021); however, it does not appear in Fig. 2 as the study does not provide evidence of browning. The term "blackwater river" is, nevertheless, often used to describe a type of tropical brown river (Gandois et al., 2020; Zhang et al., 2020; Constantino et al., 2021). With the exception of blackwater rivers, natural tropical rivers have generally low DOC concentration compared to temperate rivers (Lewis et al., 2006).

Land-use and land cover changes (e.g., to pasture, crop production, urbanization) seem to be the main factors influencing DOM export, concentration, and changes in composition, especially in Brazil where agriculture and urbanization contribute the most because of low water treatment (Hudson et al., 2007; Gücker et al., 2016). In Rwanda, agricultural lands are not a substantial contributor of DOC transfer to streams (Rizinjirabake et al., 2019) compared to forest plantations. Many tropical regions have experienced clear-cutting and monoculture plantations. Clear-cutting of tropical riparian areas may have immediate effects on carbon fluxes and water color (Smolders et al., 2018). Indonesian oil palm plantations are often established by draining natural peatlands, with subsequent and potentially long-term effects on DOC leaching (Cook et al., 2018). Tropical peatlands are natural sources of large amounts of DOM: most blackwater rivers drain peatlands (Martin et al., 2018). Peatlands degradation by deforestation and drainage for agricultural exploitation may have resulted in an enhanced export of DOM and Fe to surface waters, especially in the wet season (Moore et al., 2011; Gandois et al., 2013; Zhang et al., 2020). The Siak blackriver in Sumatra, for example, drains heavily degraded peatlands and exhibits one of the highest DOC concentrations in the world (Rixen et al., 2008).

Spencer et al. (2010) showed that DOM concentration with more aromatic and colored molecules, increased in a tropical river with greater runoff, suggesting that hydrological conditions may play a similar role in waters of tropical, temperate and cold regions. In the context of climate change, the predicted increase of temperatures and precipitations could stimulate DOC soil production and export in tropical regions, leading to water browning (Moore and Dalva, 2001; Hawkins and Sutton, 2011).

4. Browning trends with global changes and remote sensing as an approach for global studies

Global changes, e.g., land cover/land-use changes and climate change, are expected to drive further browning, while having major impacts on biodiversity and societies. Land cover and land-use changes are one of the main drivers of changing color of surface waters. Sixty percent of land-use changes are associated with direct human activities and 40% with indirect

drivers such as climate change (Song et al., 2018). Waters are likely to become browner in tropical areas with deforestation, and in temperate areas with reforestation or afforestation, since these practices enhance DOM export to surface waters (Schelker et al., 2012; Kritzberg, 2017; Song et al., 2018; Škerlep et al., 2020). Global changes may deeply impact species distribution worldwide (Chen et al., 2011), which in turn will affect ecosystems community composition and functional diversity (Ochoa-Ochoa et al., 2012; Buisson et al., 2013; Pecl et al., 2017), but no studies have assessed the link with browning and potential feedbacks. Browning of waters has not been identified as a global change component yet (but see Freeman et al., 2020), but its strong interrelation with other global environmental changes needs immediate attention and further research to improve conservation and management strategies at all scales.

An array of remote sensing approaches can provide an inclusive view of water quality variability to help understanding the possible causes of variations at large scales (Boggs et al., 2001). Hence, the new availability of spectral and spatial resolutions for remote sensing data time series is opening up opportunities to monitor the impact of land-use and land cover changes on water quality at spatially explicit scales; remote sensing has thus high potential for evaluating control efforts to protect freshwater habitats (e.g., lakes, rivers, ponds, wetlands). Current monitoring data cannot provide a global picture of browning (Sepp et al., 2018). Nevertheless, several remote sensing analyses have focused on color, or DOC and DOM measurement parameters in recent years. The increase in colored DOM (CDOM) concentration can be detected in the blue and green region of the light spectrum (especially below ~500 nm). At high concentrations of CDOM, the absorbance of the red light spectrum can be significant. Hence, passive remote sensing has been investigated through a large number of sensors on various platforms to map this water quality parameter (Gholizadeh et al., 2016). The band ratio has been the most common algorithm used. Landsat 7 and 8 imageries can be reasonably used for the estimation of CDOM levels (R^2 up to 0.82 with Landsat 8 data) (Olmanson et al., 2016; Chen et al., 2020). Using the green to red band ratio (band 3 to band 4, B3/B4 ratio) from Sentinel-2 imagery, Toming et al. (2016) obtained good correlations with lake CDOM ($R^2 = 0.72$) and DOC ($R^2 = 0.92$) concentrations, but weaker ones with lake color ($R^2 = 0.52$). Additionally, lake color in the study did not exceed 30 mg Pt/L, while many lakes in the boreal and arctic regions may display color values twenty times higher (Taipale et al., 2008; Arvola et al., 2010; Vesterinen et al., 2016). Nevertheless, remote sensing of water color is progressing since it is considered as a useful indicator of water quality (Gardner et al., 2021).

Remote sensing may also be used to monitor drivers of water browning like forestry activities (Xulu et al., 2020) that may contribute to a large export of DOM to surface waters (Schelker et al., 2012). Several approaches could be combined at the catchment scale. For instance, in a study using the Normalized Difference Vegetation Index (NDVI) on forested areas in the western US, vegetation cover and several soil properties were identified as the key variables that explained water quality response across a broad range of conditions (Rust et al., 2019). In Sri Lanka, a study based on remote sensing provided empirical evidence of the contribution of healthy (high NDVI values) forest cover on the improvement of watershed water quality (Kumarasiri et al., 2021). The above ground biomass was the dominant carbon storage among the other carbon pools. The water quality parameters were not correlated with the soil erosion rates, which was possibly attributed to the mitigation effects of the healthy forest cover within the studied catchment. Time series of remote sensing data can also be used to quantify how forest disturbances vary in space and time, then to estimate related factors (e.g., proximity, intensity, and total areal extent of harvest) that influence water quality within a watershed. Regarding active remote sensing, recent technologies of growing interest such as LIDAR sensors offer accurate perspectives to estimate the role of forested wetlands in the carbon cycle, and understand how forest practices impact carbon storage at the landscape scale (Halabisky et al., 2020). Hence, remote sensing can be used to assess the color of surface waters worldwide, as well as the global causes and consequences of water browning.

5. Conclusion and future steps in research on browning

We identified five research actions to make significant steps forward in our knowledge of water browning:

- 1- *Assess browning ecological processes in other wetland types than lakes and rivers.* No study has addressed processes at the catchment scale, including networks of small and temporary wetlands with lakes and rivers. Their potential degradation due to browning may affect all levels in the landscapes.
- 2- *Evaluate the impact of browning on aquatic food webs at multiple scales.* The majority of studies overlooked macrophytes, invasive species, and the impact on the whole food web structure in different freshwater habitats. Multiple food web structure markers such as compound specific stable isotopes of amino acids or mercury would likely provide options to study food web processes in full browning gradient.
- 3- *Investigate the effects of browning on aquatic and terrestrial coupling.* There are many fluxes between the aquatic and terrestrial habitats, such as through beaver activity and pathogen emergence. There is a clear lack of knowledge on the effects of browning on water-dependent amphibians, waterbirds and mammals. The coupling of aquatic and terrestrial habitats will help to understand consequences on the transfer of energy through the food webs.
- 4- *Understand the water browning processes at the global scale.* Most of the research has focused on the boreal region in the Northern Hemisphere, but we highlighted the occurrence of water browning processes at a larger scale from the polar to the tropical regions. We note a clear lack of knowledge on polar, especially Antarctic, and tropical waters.
- 5- *Develop remote sensing methods to monitor the ecological consequences of water browning from catchment to global scales.* Passive remote sensing has been mainly used to monitor CDOM in freshwaters, but other promising approaches are emerging; that includes active remote sensing, and focus on landscape parameters and land use determinants related to water quality.

The reinforcement of water browning impacts water bodies through its interrelation with global environmental changes. There is a clear need for global studies to investigate the extent, underlying mechanisms, and ecological consequences of browning. Remote sensing has a crucial role to play in such future research.

CRedit authorship contribution statement

Clarisse C. Blanchet: Conceptualization, Investigation, Writing – Original Draft, Visualization, Project administration, Funding acquisition. **Céline Arzel:** Conceptualization, Resources, Writing – Review & Editing, Visualization, Supervision, Project administration, Funding acquisition. **Aurélié Davranche:** Conceptualization, Resources, Writing – Review & Editing, Visualization, Supervision, Funding acquisition. **Kimmo K. Kahilainen:** Conceptualization, Resources, Writing – Review & Editing, Supervision. **Jean Secondi:** Resources, Writing – Review & Editing. **Sami Taipale:** Resources, Writing – Review & Editing. **Henrik Lindberg:** Resources, Writing – Review & Editing. **John Loehr:** Writing – Review & Editing. **Sanni Manninen-Johansen:** Writing – Review & Editing. **Janne Sundell:** Writing – Review & Editing. **Mohamed Maanan:** Resources, Writing – Review & Editing. **Petri Nummi:** Project Leader, Conceptualization, Resources, Writing – Review & Editing, Supervision.

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 data

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