Brownification shapes the food web of aquatic invertebrates: a review

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Abstract

Brownification, a global phenomenon of increasing surface water colour to yellow-brown hues, has an array of effects on drinking water supply and aquatic biodiversity. Aquatic invertebrates, as indicators of aquatic ecosystem health and providers of ecosystem services, have received limited attention in the context of water browning. In this review, we explored the effects of brownification on aquatic invertebrate communities and species traits and discussed the interactions between aquatic invertebrates and organisms at different trophic levels. We synthesized current knowledge on both the beneficial and detrimental effects of brownification on aquatic invertebrates and identified knowledge gaps in current studies. The review highlights the importance of considering interactions between brownification and other abiotic and biotic factors in aquatic biodiversity conservation in the changing world.

Introduction

Brownification, also known as browning, is a global phenomenon that refers to an increase of surface water colour towards yellow-brown hues due to the shift of underwater light towards long wavelengths (Graneli, 2012; Luimstra et al., 2020). Brownification has been driven by the increase concentration of chemical substances, especially coloured dissolved organic carbon (DOC) (Freeman et al., 2001; Pace & Cole, 2002; Hongve et al., 2004; Arvola et al., 2016) and iron (Kritzberg & Ekström, 2012; Sarkkola et al., 2013; Hassan, 2020). The phenomenon has become a hot topic in environmental sciences in recent decades and has been intensively studied in the Northern Hemisphere, because brownification affects ecosystem services, such as drinking water supply and aquatic biodiversity (Anderson et al., 2023).

Climatic variables and land-use change have been recognised as the main drivers of brownification (Evans et al., 2005; Porcal et al., 2009; De Wit et al., 2016; Ritson et al., 2019; Lei et al., 2020; Škerlep et al., 2020; Klante et al., 2021; Zhang et al., 2022). For example, increased precipitation will enhance the mobilisation of organic carbon from soil into aquatic ecosystems (De Wit et al., 2016). Increased precipitation can reduce the rates of organic carbon decay in boreal freshwaters (Catalán et al., 2016). Also, the decreasing acid deposition in the past decades, as a result of the reversal of acidification, has led to a reduction of soil acidity (Evans et al., 2005; Oulehle et al., 2013) and ionic strength in soil solutions (De Wit et al., 2007; Haaland et al., 2010). Such changes in soil chemistry can consequentially lead to an increase of organic matter solubility (Monteith et al., 2007) and subsequently enhances the transport of coloured organic matter to surface waters (De Wit et al., 2007; Lawrence & Roy, 2021), thus increasing water colour.

Land-use change has been considered as another driver of browning, as current water colour is higher than before the peak acidification in many boreal water bodies (Meyer-Jacob et al., 2015; Kritzberg, 2017). For example, the transition from agriculture to modern forestry can accumulate more coloured organic carbon in soil, and forestry in boreal regions has often changed species composition from deciduous to coniferous trees (Rouvinen et al., 2002; Fredh et al., 2012; Kritzberg, 2017), making a large quantity of coloured organic carbon become available for export into aquatic ecosystems (Hansson et al., 2011; Kritzberg, 2017; Ritson et al., 2019; Lei et al., 2020; Škerlep et al., 2020). Urbanisation tends to darken water colour due to increased concentrations of DOC and Fe in streams and rivers, possibly due to sewage leaking and waste from industrial and residential areas (Hosen et al., 2014; Noacco et al., 2017; Zhang et al., 2022). Land-use change can have long-term effects on the organic carbon dynamics because the soil process is gradual (Meyer-Jacob et al., 2015), thus having a lag between land-use change and its influence on surface water colour.

Brownification can alter aquatic communities via different pathways (Heibo et al., 2005; Estlander et al., 2010; Jonsson et al., 2015). Aquatic invertebrates are important part of aquatic ecosystems and play vital roles in ecosystem functioning, such as nutrient cycling and food webs (Jackson & Fuereder, 2006; López-López & Sedeño-Díaz, 2015). They are sensitive to environmental changes, such as decreasing water quality, which may consequentially affect their organic matter decomposition efficiency (Xu et al., 2014; López-López & Sedeño-Díaz, 2015). Although aquatic invertebrates have been utilised as an indicator to assess the health of aquatic ecosystems (Reynoldson & Metcalfe-Smith, 1992; Birk et al., 2012; Jeppesen et al., 2011), they are still often ignored in aquatic conservation (Collier et al., 2016; Jeppesen et al., 2011). So far, limited knowledge has been synthesized regarding aquatic invertebrate conservation in the browning world.

The browning of surface water has a cascade of effects on food webs, which may decrease the stability and resilience of aquatic ecosystems. For example, the increasing water colour decreases light availability under the water surface, which leads to a reduction of primary production in some primary producers but an increase in others (Ekvall et al., 2013; Lebret et al., 2018; Feuchtmayr et al., 2019; Luimstra et al., 2020; Lyche Solheim et al., 2024; Urrutia-Cordero et al., 2017). The change in primary production can have consequential effects on the food availability of aquatic invertebrates. Cyanobacteria may produce high concentrations of toxins in browning waters (Urrutia-Cordero et al., 2016), which expose humans and other animals, including aquatic invertebrates, to even fatal health problems (Codd et al., 2005). Understanding the effects of brownification is important to making biodiversity conservation plans to deal with issues raised due to global change. This review aims at synthesizing current knowledge of how brownification has affected aquatic invertebrates and at bringing insights into future research on aquatic invertebrates in browning waters for biodiversity conservation.

Overview of the findings

We conducted a literature review by searching literature on Web of Science and Google Scholar with the keywords “(brownification OR browning) AND (water color OR water colour) AND (invertebrate* OR zooplankton)” written in English up until the end of April 2024, which returned 715 hits and 1290 hits, respectively. The hits included research papers in peer-reviewed journals and student degree theses. We read the title and the abstracts to decide the relevance of the hits. In total, we reviewed 73 research papers in the review. Aquatic invertebrates received more attention in the past decade, with 59 papers published between 2014 and 2023, whereas only 11 papers between 1996 and 2013 (Figure 1). The 73 papers studied aquatic ecosystems in 15 countries, one of which had an international comparison of the data collected in Canada and Finland. The Nordic countries contributed to approximately 52% of the research, whereas North America contributed to approximately 27%. Other European countries contributed to 12 papers, while South America contributed to 2 papers and China contributed 1 paper (Table 1, Figure 2). Freshwater ecosystems, especially boreal lakes, received most attention (Table 1), while only four papers investigated seawater in the field (Bandara et al., 2022; Soulié et al., 2022) and the mesocosms (Garnier et al., 2023).

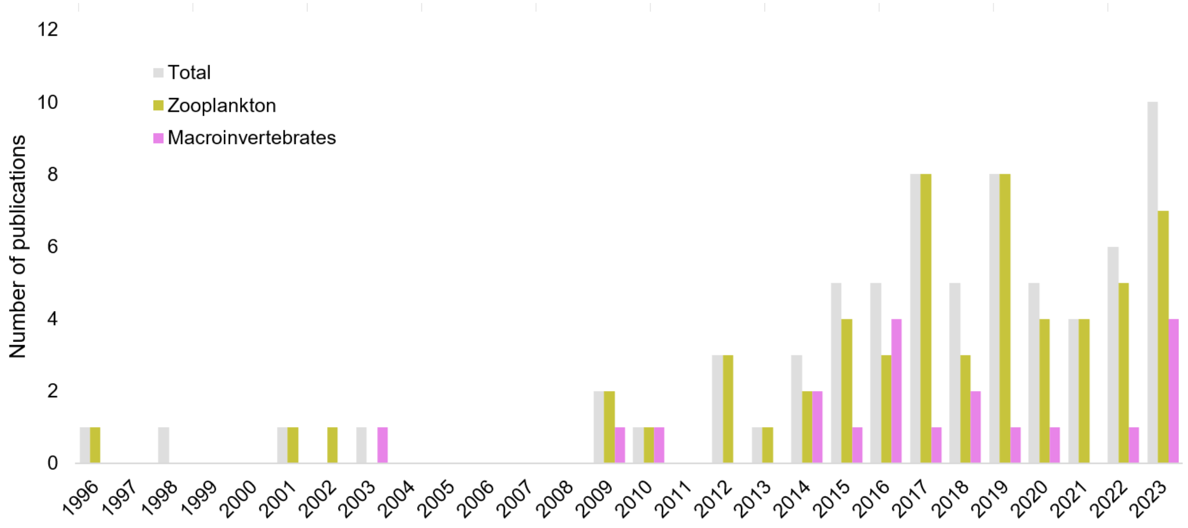

Figure 1 Aquatic invertebrates in browning waters started gaining attention in the past 10 years. Zooplankton has received more attention than macroinvertebrates in this topic. The grey bar stands for number of publications per year, the light green for papers that investigated zooplankton, the light purple for papers that investigated macroinvertebrates.

Zooplankton received more attention than other aquatic invertebrates: Fifty-seven papers included zooplankton either as focal taxa or prey of the focal taxa, while 23 papers included macroinvertebrates in the studies; 10 papers investigated both zooplankton and macroinvertebrates (Figure 2); one paper investigated an invasive alien macroinvertebrate species, the peach blossom jelly fish (*Craspedacusta sowerbii*), in browning waters and found that high DOC concentrations protected the invasive jellyfish from UVR and decreased its mortality (Caputo et al., 2018). This invasive jellyfish is a predator of other aquatic invertebrates, such as zooplankton (Spadinger & Maier, 1999). The survival rate of *C. sowerbii* facilitated by brownification may have consequentially harmful effects on aquatic invertebrate communities, especially in regions where *C. sowerbii* is an alien species.

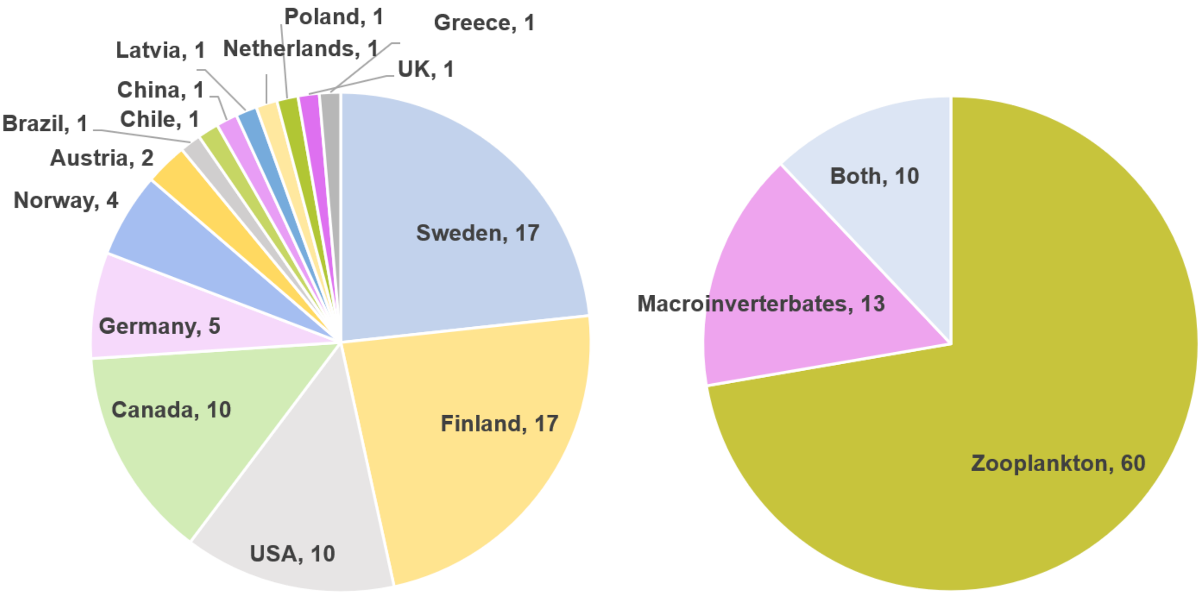

Figure 2 The locations (left) and the study taxa (right) of the reviewed publications. One paper included lakes from both Canada and Finland. 'Both' on the left included 10 studies on both zooplankton and macroinvertebrates.

We found contradictory results in the reviewed papers (Table 1). A few studies showed browning had no effects on zooplankton abundance (Karlsson et al., 2009; Rasconi et al., 2015; Zhang et al., 2015), biomass (Weidel et al., 2017; Robidoux et al., 2015; Vasconcelos et al., 2016; Hedström et al., 2017; Urrutia-Cordero et al., 2017; Leech et al., 2018; Estlander & Horppila, 2023), biovolume (Lebret et al., 2018), community (Clair et al., 2001; Robidoux et al., 2015; Mattila, 2020), and recruitment (Zhang et al., 2015), nor on macroinvertebrate species richness (Arzel et al., 2020), community structure (Koizumi et al., 2023), and biomass (Jonsson et al., 2015; Kelly et al., 2016; Hedström et al., 2017; Table 1).

However, most studies showed that brownification had various effects on aquatic invertebrates: Increasing water colour was found generally to decrease zooplankton abundance (Druvietis et al., 1998; Hansson et al., 2013; Tonin, 2019; Mattila, 2020; Pilla & Wiliamson, 2023) and biomass (Leach et al., 2019; Taipale et al., 2019). Increasing DOC concentrations was found to decrease the fecundity of some *Daphnia* spp. (Saebelfeld et al., 2017; Ktistaki et al., 2024) but increase the biomass, growth, and survival probability (Gall et al., 2017; Minguez et al., 2020; Koizumi et al., 2023). Water colour was also found to be a determinant of zooplankton communities, causing species trait shifts and community structure changes (Wissel et al., 2003; Lehtovaara et al., 2014; Van Dorst, 2020; Williamson et al., 2020; Shchapov et al., 2021; Gohil, 2022; Soulié et al., 2022; Lau et al., 2021), behavioural change (Wolf & Heuschele, 2018; Adamczuk, 2021), and timing of the peak (Nicolle et al., 2012). Zooplankton in clear lakes appeared more sensitive to brownification than those in brown lakes (Williamson et al., 2015). Brownification was also found to decrease macroinvertebrate abundance (Brothers et al., 2014; Arzel et al., 2020; Turunen & Aroviita, 2024), species richness (Brüsecke et al., 2023; Strandberg et al., 2023a), density (Estlander et al., 2010) and habitat use (Horppila et al.,2018), while some taxa, such as Chironomidae and Corixidae, became more abundant along the increasing water colour (Wissel et al., 2003; Feuchtmayr et al., 2019). Macroinvertebrates, however, are much less studied than zooplanktons (Figure 2).

The contradictory patterns in the publications may have resulted from two main reasons identified below. First, the studies were conducted with different study designs. For example, some studies were conducted in short-term manipulated mesocosms (e.g. 4 weeks, Gall et al., 2017), while some in long-term field surveys (e.g. 30 years, Pilla & Wiliamson, 2023). Some studies directly measured water colour, whereas some measured the concentrations of DOC as an indication of water colour (Table 1). Even within the studies applying similar measures, the gradients of water colour had different ranges. For example, no significant effects of increasing water colour on zooplankton along the DOC gradient of 1.2 – 4.8 mg/L were detected (Lebret et al., 2018), while zooplankton appeared to have thresholds of water colour that they can tolerate along the DOC gradient of 2 – 35 mg/L, and the body sizes of *Ceriodaphnia* sp. and *Diaphanosoma* sp. became smaller when water colour was above 12 mg/L (Mattila, 2020). As the study designs are usually different, the contradictory results in literature should be interpreted carefully.

Second, the effects of brownification can be species-specific. Within macroinvertebrates, some shredders, such as *Asellus aquaticus*, were found to respond positively to increasing water colour, while other shredders, such as *Ephemerella aroni*, responded negatively in Finnish rivers (Brüsecke et al., 2023). Within zooplankton, increasing water colour had positive effects on cladoceran biomass and recruitment, but no effects on copepods (Ekvall & Hansson, 2012; Koizumi et al., 2023). Even under Cladocera, some species, such as *Bosmina longirostris* and *Thermocyclops oithonoides*, positively responded to increasing water colour and were tolerant to brownification, while many species responded negatively to brownification (Lehtovaara et al., 2014). Such different responses of taxa or even species to brownification could have been an explanation for the different responses of invertebrate communities found in browning waters (Wissel et al., 2003; Williamson et al., 2020; Gohil, 2022; Brüsecke et al., 2023; Koizumi et al., 2023; Adamczuk, 2021).

Interestingly, one paper showed that aquatic invertebrates can induce brownification. The aquatic month larvae of *Paraponyx stratiotata* were found to induce brownification by feeding on submerged plants (Grutters et al., 2016). The study investigated its herbivory on seven native submerged plant species and four alien species and found that the larval herbivory increased water colour, possibly via increasing DOC and its subsequent breakdown into humic acid (Graneli, 2012). The herbivory-induced brownification was plant species-specific and not associated with the origin of a species; in addition, herbivory also induced phosphate release in water and changed water chemistry (Grutters et al., 2016). The study brings insights of aquatic invertebrates as inducers of brownification, instead of being passively affected by brownification.

Beneficial and harmful effects of brownification on aquatic invertebrates

Brownification has both positive and negative effects on aquatic invertebrates. Highly coloured water protects aquatic invertebrates from ultraviolet radiation (UVR), because DOC can absorb UVR (Wolf et al., 2017). The protection lowered mortality (Caputo et al., 2018) and changed behaviour and vertical distribution in aquatic invertebrates (Wolf & Heuschele, 2018; Pilla & Wiliamson, 2023). For example, *Daphnia magna*, a cladoceran species, swam more actively, with increasing explored area, swimming depth, and percent of swimming time along the DOC gradient, especially in the treatments with extra UV light (Wolf & Heuschele, 2018). The vertical distribution of *Daphnia* was found to be shallower possibly because browning lowered UV exposure (Pilla & Wiliamson, 2023). However, DOC can be photoactivated and release free radicals and reactive oxygen species (Richard et al., 2007), which induced higher DNA damage in zooplankton, such as *Daphnia* (Wolf et al., 2017). The protection effects of DOC may offset the adverse effects on invertebrates; thus, how the mutual effects of brownification and UVR affect invertebrates is not yet clear.

Similarly, brownification provides prey refuges to aquatic invertebrates to avoid predation, while potentially decreasing their feeding efficiency. For example, with fish cues, copepod activity became more frequent with increasing water colour (Santonja et al., 2017). With fish presence, cladoceran *Sida crystallina*, had more free-swimming individuals in brown lakes, while more individuals stayed on plants in clear lakes (Estlander et al., 2017). Such behavioural changes may have resulted from the lowered predation risk in browning waters, due to the decreased feeding efficiency of fish predators (Estlander et al., 2009; Estlander et al., 2012; Bartels et al., 2016; Hedström et al., 2017). However, some aquatic invertebrates are also predators and were found to have negative responses to increasing DOC (Brüsecke et al., 2023), possibly also due to decreased feeding efficiency in highly coloured waters. Thus, there can be trade-offs between predator avoidance and foraging in browning waters.

Aquatic invertebrates as primary consumers in browning water

Many papers studied aquatic invertebrates with other taxa in the aquatic food web, most of which focused on interactions between zooplankton and primary producers in browning waters, whereas little research investigated macroinvertebrates as consumers (Table 1, Figure 3). Brownification can affect aquatic invertebrates by altering primary production, as increasing DOC contents were found to reduce primary production of many taxa due to decreased light availability (Karlsson et al., 2009), inducing changes in phytoplankton community composition (Bandara et al., 2022; Soulié et al., 2022) and reducing the abundance and biomass of phytoplankton, such as diatoms and gold algae (Leech et al., 2021; Weidman et al., 2014; Hébert et al., 2023; Strandberg et al., 2023b; Soulié et al., 2022; Bandara et al., 2022), which are important food sources to aquatic invertebrates (Weidman et al., 2014; Bandara et al., 2022).

Decreasing quantity of primary producers can substantially affect primary consumer invertebrates, such as Ephemeroptera grazers (Turunen & Aroviita, 2024), in the food web.

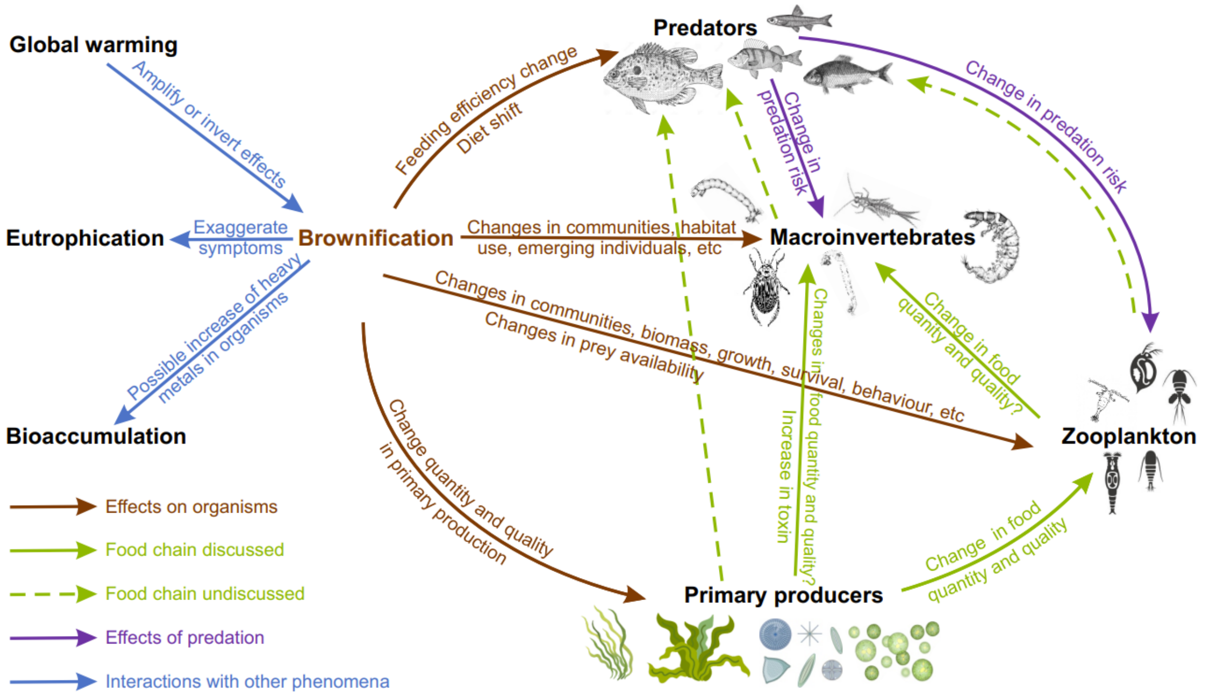

Figure 3 The main effects of brownification on aquatic invertebrates in the food web. The review mainly discusses the effects in the context of the food web. The effects with question marks indicate speculations based on literature. The dashed lines stand for predator-prey relationships undiscussed due to limited literature. Brownification interacts with other phenomena; global warming, eutrophication, and bioaccumulation are the three main themes identified from the reviewed papers.

The quality change of primary producers in browning water can also affect aquatic invertebrates. Some studies found that browning water increased phytoplankton biomass but associated with a decline in polyunsaturated fatty acids (PUFAs) in lake seston, such as eicosapentaenoic acid (EPA) and docosahexaenoic acid (DHA); PUFAs are essential fatty acids for the development and reproduction of consumers, including zooplankton and macroinvertebrates (Senar et al., 2019; Bandara et al., 2022; Strandberg et al., 2023a; Strandberg et al., 2023b; Lau et al., 2021). The PUFAs decline in lake seston was found to decrease PUFAs in zooplankton, such as copepods and cladocerans, but not in all studies (Lau et al., 2021; Senar et al., 2019; Nova et al., 2019). Meanwhile, the browning-induced DHA content decrease in phytoplankton may result in monounsaturated fat (MUFA) increase in zooplankton, which is less nutritious than PUFAs because of its low assimilation (Bandara et al., 2022). In both boreal and temperate lakes, via changing fatty acids of phytoplankton, brownification has led to increased reliance of zooplankton on a heterotrophic microbial pathway (Strandberg et al., 2023b). In laboratory experiments, brownification eliminated zooplankton reproduction and growth by diminishing their assimilation of high-quality algae (Taipale et al., 2019). These results suggest that brownification decreases not only food quantity but also quality for invertebrates.

A few studies reported that brownification had positive effects on heterotrophic bacteria (Rasconi et al., 2015) and cyanobacteria (Urrutia-Cordero et al., 2016; Senar et al., 2019; MacKeigan et al., 2023). Cyanobacteria biomass increase in browning waters was especially prominent when water temperature also increased (Urrutia-Cordero et al., 2016; MacKeigan et al., 2023). Cyanobacteria are known to produce toxins that are harmful to aquatic invertebrates (Bownik, 2016). The increase of toxic *Microcystis* was negatively associated with *Daphnia* biomass (Urrutia-Cordero et al., 2016). Yet, the pattern was not universal: in another study, the browning-induced total cyanobacteria biomass increase was positively associated with the biomass of zooplankton, such as daphnids and copepods (MacKeigan et al., 2023), which may have partially resulted from zooplankton choosing high-quality algal groups for food (Keva et al., 2023). The findings may have resulted from improved fatty acid quality via cyanobacteria being ingested by heterotrophic nanoflagellates, increasing food quality for zooplankton (Bec et al., 2006). There is eco-evolutionary dynamics between cyanobacteria and their grazers, affecting the toxin production (Ger et al., 2016), which may have consequential effects on nongrazer invertebrate communities. The browning-induced changes in food quantity and quality for primary consumers can have a cascade of effects on consumers at higher trophic levels.

Aquatic invertebrates with other roles in the food web

A few studies have investigated how brownification affects different functional groups, mainly in macroinvertebrates, the species richness of which appeared to decrease with increasing DOC concentration (Brüsecke et al., 2023). These macroinvertebrates play different functional roles in aquatic ecosystems. Macroinvertebrate grazers, such as *Baetis niger* and *Limnius volckmari*, responded negatively to the high water colour (Turunen & Aroviita, 2024). Water colour had positive and negative effects on shredders and gathers, respectively, but the effects were not always significant (Brüsecke et al., 2023; Turunen & Aroviita, 2024). Filter feeders seemed unaffected by water colour. However, some species within these functional groups, such as *Habrophlebia lauta* (collector-gatherer), *Protonemura meyeri* (shredder), and *Chimarra maginata* (filter feeder), were significantly affected by water colour (Turunen & Aroviita, 2024).

Macroinvertebrate predators appeared positively affected by water colour as a functional group, but not all species are tolerant to high water colour (Horppila et al., 2018; Liao, 2024; Turunen & Aroviita, 2024). For instance, Chaoboridae larvae density was higher in the brown lake than the clear lake; in the brown lake, chaoborids had a wider vertical distribution in water than in the clear lake (Horppila et al., 2018). Predaceous diving beetle (Dytiscidae) abundance was found to positively correlated with increasing water colour in urban ponds, although not every species benefitted from brown waters; for instance, *Hygrotus* spp. and *Hyphydrus ovatus* tended to occur in clear waters (Liao, 2024). The significant effects of water colour were also found on non-insect macroinvertebrate predators, such as *Erpobdella octoculata* (leech)

(Turunen & Aroviita, 2024). The effects of water colour on macroinvertebrate predators may be part of the cascade effects of brownification on primary producers and consumers.

Aquatic invertebrates as prey in the browning water

In some papers, aquatic invertebrates were studied as the prey of fish and predatory insects, such as Chaoboridae (Table 1). The presence or absence of fish tends to diverge the effects brownification on aquatic invertebrates. Among macroinvertebrates, brownification negatively affected chironomid biomass with fish presence, but not in the absence of fish (Garnier et al., 2023). With fish presence, chaoborid larvae were found to use habitats with low oxygen levels to avoid fish in waters with high DOC concentrations (Horppila et al., 2018). The negative effects of brownification on zooplankton abundance and biomass were stronger with fish than without fish (Hansson et al., 2013; Van Dorst, 2020). The effects of water colour have led to significant changes in invertebrate community compositions at different levels of predation risk (Van Dorst, 2020; Liao, 2024).

The mutual effects of brownification and predation on aquatic invertebrates, however, are not straightforward. For example, European perch (*Perca fluviatilis*) was found to shift its diet from zooplankton to macroinvertebrates due to limited vision in the darkening water (Estlander et al., 2012), but this was not found in roach (*Rutilus rutilus*) or insect predators, such as Chaoboridae larvae (Estlander et al., 2009; Estlander et al., 2012). However, perch diet vaguely shifted from macroinvertebrates to zooplankton in another study, whereas its eye-index increased with increasing DOC concentration in water (Bartels et al., 2016). In sticklebacks, mortality of overwintering fish increased in browning waters due to the decreased food search efficiency in a freshwater mesocosm in Sweden (Hedström et al., 2017), but no clear change in stickleback predation on zooplankton and macroinvertebrates was found in a mesocosm conducted in the UK (Feuchtmayr et al., 2019). Low light availability caused by brownification affected the black bass (*Micropterus*) and the sunfish (*Lepomis*) negatively but the minnow (*Pimephales*) positively regarding zooplankton consumption (Weidel et al., 2017). Also, the decline of zooplankton abundance due to brownification, in turn, was found to result in the reduced survival of some fish, such as gold shiner (*Notemigonus crysoleucas*) (Wissel et al., 2003). Therefore, brownification may have dynamic effects on predator-prey interactions in aquatic ecosystems.

Brownification may also affect terrestrial predators via aquatic invertebrates, especially aquatic insects that emerge as adults and enter food webs in terrestrial ecosystems through energy flow (Scharnweber et al., 2014; Xiang et al., 2017). Brownification was found to have no effects on the total dry biomass of emerging aquatic insects, with the decreased number of emerging individuals but increased dry biomass (Jonsson et al., 2015). Brownification changed the emergent insect community composition, as dry biomass per individual per trap was significantly higher in humic treatments than in clear water, indicating brownification led to community shift to large-sized insects, among which Chironomidae benefitted from brownification, whereas Trichoptera and Ephemeroptera did not (Jonsson et al., 2015). The changes in aquatic ecosystems have consequential impacts on terrestrial ecosystems via the movement of energy, nutrients, and materials, and vice versa (Soininen et al., 2015).

Interactions between brownification and other water physicochemical properties

Global warming. Water temperature was studied in the context of climate change (Ekvall & Hansson, 2012; Hansson et al., 2013;Jonsson et al., 2015; Rasconi et al., 2015; Zhang et al., 2015; Vasconcelos et al., 2016; Gall et al., 2017), more specifically global warming. It is unclear whether warming and browning have synergistic effects on aquatic invertebrates. In some studies, increased water temperature had stronger positive effects on the recruitment and abundance of zooplankton than brownification alone (Ekvall & Hansson, 2012; Nicolle et al., 2012), whereas zoobenthos biomass was affected only by warming but not brownification (Vasconcelos et al., 2016). In other studies, however, brownification plus warming seemed to have stronger effects than brownification or warming alone (Nicolle et al., 2012). For example, browning plus warming led to significantly higher *Daphnia* had higher growth in browning plus warm than browning alone (Gall et al., 2017) and aquatic insect community shifts to large-sized taxa (Jonsson et al., 2015). The synergistic effects of brownification and warming were also found to differ at different predation risk levels: with fish, browning plus warming had negative effects on zooplankton abundance; without fish, browning plus warming had positive effects. These results emphasize that the impacts on aquatic invertebrates can be even more complex when brownification interacts with climate change (Hansson et al., 2013).

Eutrophication. Nutrient contents are also studied with brownification, as its effects on primary producers can modify eutrophication symptoms (Deininger & Frigstad, 2019). Zooplankton communities were found to be determined by nutrient-colour status at the order-, genus-, or species-level (Leech et al., 2018; Shchapov et al., 2021). Brownification plus eutrophication had stronger positive effects on the total zooplankton biomass than brownification alone. More specifically, the effects were positive on rotifer and copepod biomass (Garnier et al., 2023; Leech et al., 2018), but not on chironomid biomass (Garnier et al., 2023) nor cladoceran biomass (Leech et al., 2018; Keva et al., 2023). Brownification or eutrophication had no negative effects on the transfer of essential PUFAs from phytoplankton to herbivorous cladocerans (Keva et al., 2023). These results suggest brownification may exaggerate eutrophication symptoms in certain taxa and modify food webs.

Bioaccumulation. Two papers found that bioaccumulation of methyl mercury was significantly higher in brown lakes than in clear lakes (Westcott & Kalff, 1996; Poste et al., 2019). DOC concentrations can affect heavy metal bioavailability and consequentially affect heavy metal bioaccumulation (French et al., 2014; Broadley et al., 2019). The correlation between DOC and heavy metal bioaccumulation can be nonlinear (French et al., 2014). The transfer of heavy metals from aquatic invertebrates to their predators is not restricted in aquatic ecosystems. When aquatic insects, such as Trichoptera and Ephemeroptera, emerge from larvae to adults, they become prominent prey to terrestrial predators, such as spiders and bats (Nummi et al., 2011; Chaves-Ulloa et al., 2016), transferring heavy metals to the terrestrial food web via bioaccumulation (Cristol et al., 2008; Chaves-Ulloa et al., 2016; Clarke et al., 2022). Brownification may exacerbate heavy metal bioaccumulation in organisms via the food web, which eventually threatens our own well-being (Sundseth et al., 2017).

Knowledge Gaps

How does zooplankton interact with macroinvertebrates in browning waters?

Zooplankton has been better studied than macroinvertebrates from different perspectives. Current research has investigated the effects of brownification on zooplankton assemblages and species traits, such as fecundity and survival (Minguez et al., 2020; Adamczuk, 2021), as well as nutrient contents (Lau et al., 2021; Senar et al., 2019). A few papers investigated how zooplankton abundance affects fish species traits (Karlsson et al., 2009; Van Dorst, 2020; Leech et al.,2021). Yet, there is lack of study regarding how zooplankton quantity and quality affect higher trophic levels within aquatic invertebrates in browning waters, and whether competition between zooplankton taxa differ in brown water from clear water. Future studies should build links between zooplankton and their non-fish predators.

Macroinvertebrates are understudied

In browning waters, macroinvertebrates are rather understudied. Most papers investigated macroinvertebrates as the prey of fish predators (Table 1), although a few papers focused on macroinvertebrate functional groups (Brüsecke et al., 2023; Liao, 2024; Turunen & Aroviita, 2024). There is generally lack of studies on the macroinvertebrates as consumers. Some macroinvertebrates are herbivores, such as Haliplidae and Hydrophilidae adults, and feed on green algae (Hickman, 1931; Hansen, 1987; Holmen, 1987; Inoda et al., 1994), the growth of which can be limited by brownification due to reduced light availability (Vasconcelos et al., 2016; Urrutia-Cordero et al., 2016; Choudhury et al., 2019). Diminished algal growth may eliminate the tolerance of macroinvertebrates that have narrow diet ranges and rely on certain phytoplankton. The quality and quantity of primary producers may affect other functional groups, such as shredders. Future studies should expand the interactions between primary producers and zooplankton to a wider range of taxa.

Many aquatic invertebrates, such as Odonata larvae and Dytiscidae, are predators, which consume other invertebrates in aquatic ecosystems. Macroinvertebrate predators usually play double roles as predators and as prey in aquatic ecosystems (Horppila et al., 2018). Brownification can decrease their predation efficiency and change their behaviour, as some macroinvertebrates utilise visual cues to detect prey and predators (Peckarsky, 1982; Åbjörnsson et al., 1997). In the presence of predators at a higher trophic level, macroinvertebrates have to alter their behaviour, such as reducing their activity, to avoid predators when the visual cues are limited (Åbjörnsson et al., 1997), which reduces foraging opportunities, especially under low food density (Formanowicz Jr et al., 1982;Formanowicz Jr, 1984; Pintar & Resetarits Jr, 2017). In addition, the availability of other prey refuges, such as macrophytes, can be reduced by brownification due to light penetration (Law et al., 2019; Borowiak et al., 2017; Choudhury et al., 2019; Liao et al., 2023; Liao et al.,2024). Some fish species, such as the common roach, may benefit because they prefer to feed in habitats with sparse vegetation (Persson & Crowder, 1998; Nurminen, 2003; Estlander et al., 2009; Estlander, et al., 2010). The predator-prey interactions with macroinvertebrates are generally understudied in browning waters. Current research cannot untangle the complex interactions in predator-prey dynamics, especially when prey refuges, such as macrophytes, are also affected by brownification. Future studies should apply both predator-centred and prey-centred approaches to investigate macroinvertebrate predators in browning waters.

How about other aquatic habitat types than lakes?

Lotic habitats. Only three papers investigated how brownification affected aquatic invertebrates in streams and rivers, and three papers studied aquatic invertebrates in browning brackish water (**Table 1**). Lotic waters, such as streams and rivers, have different hydrology than lakes, and they experience larger fluctuations and faster increases in water temperature than lakes and the sea (Ficke et al., 2007; Fenoglio et al.,2010). Thus, the interaction between warming and brownification on aquatic invertebrates can be different in lentic and lotic waters, especially in the context of climate change. Therefore, aquatic invertebrates in lotic habitats need more attention in research on brownification.

Marine habitats. Four papers studied aquatic invertebrates in browning marine habitats (Bandara et al., 2022; Soulié et al., 2022; Garnier et al., 2023) in the context of eutrophication. Eutrophication is known to enhance primary production in the sea (Andersen et al., 2017) and alter the food web via bottom-up effects, as well as top-down control (Soulié et al., 2022; Garnier et al., 2023); its symptoms can be amplified in browning water (Garnier et al., 2023). The Baltic Sea and the Norwegian Sea in the studies are important sea areas for fish production with high commercial values (MacKenzie et al., 2007). Thus, it is important to investigate how invertebrates in marine habitats are affected by brownification and its interactions with other issues for the production of omnivorous and insectivorous fish.

Beaver-engineered habitats. Except for lakes, there are many other types of freshwater ecosystems in boreal landscapes, such as beaver ponds, bogs, and vernal pools, which may also be affected by the change in water chemistry that leads to browning of surface water (Spitzer & Danks, 2006; Kivinen et al., 2020; Dixneuf et al., 2021). For example, beaver flooding is a natural way of water browning: when the beaver dams a lake or a creek, the flood water kills terrestrial plants on the shore, leading to high leaf-litter decomposition, which dramatically increases DOC concentration, especially during the first few years (Law et al., 2016; Johnston, 2017; Nummi, 1989; Nummi et al., 2018; Vehkaoja et al., 2015; McDowell & Naiman, 1986). During early beaver impoundment, beaver engineered ponds and lakes have higher abundance but not necessarily higher species richness of aquatic invertebrates – such as cladocerans, *Asellus*, chironomids, and dytiscids – than non-beaver engineered habitats (McDowell & Naiman, 1986; Law et al., 2016; Bush & Wissinger, 2016; Nummi et al., 2021; Washko et al., 2022; Schloemer et al., 2023). As clear lakes can be more sensitive to brownification than brown lakes (Williamson et al., 2015), it is interesting to investigate beaver-induced browning in lakes with different water colour.

Vernal pools. Vernal pools usually experience annual floods and hold abundant detritus, which may result in high DOC concentrations and increase water colour (Cable Rains et al., 2006; Capps et al., 2014; Hervé et al., 2020). The hydrology of vernal pools has also resulted in lower predation risk for aquatic invertebrates than in boreal lakes (Snodgrass & Meffe, 1998; Nummi et al., 2021). Fish predation in vernal pools is negligible due to their water cycles of filling and drying (Calhoun & DeMaynadier, 2007; Williams, 2012; Dixneuf et al., 2021), which makes fish unable to establish, even though individuals can disperse to vernal pools via temporary connection to nearby lakes or ponds (Nummi's personal observations). As aquatic invertebrates often respond to brownification differently in the presence or absence of fish (Estlander et al., 2017; Santonja et al., 2017), brownification may affect invertebrates differently in habitats with different levels of predation risk in the same landscape.

Table 1 Details of the 73 papers included in the review. The publications follow a chronological order.

Reviewed papers	Locations	Habitats	Water colour range	Study taxa	Role of Invertebrates in the papers	Main findings
Westcott & Kalff, 1996	Canada	Boreal lakes (24)	Water colour 3 – 39 mgPt/L in the clear lake, 68 – 231 mgPt/L in the brown lake	Zooplankton	Focal taxa	Methyl mercury levels in cladocerans were significantly higher in brown lakes than clear lakes.
Druvietis et al 1998	Latvia	Boreal lakes (24)	Water colour 130 – 260 ° Pt/Co scale; Humic substance 20 – 100 mg C/L	Bacterioplankton, phytoplankton, zooplankton	One of the focal taxa	Zooplankton abundance was positively correlated with humic substance concentration.
Clair et al 2001	Canada	Mesocosm in temperate lakes (2)	DOC 2 – 4 mg/L in the clear lake, 10 – 14 mg/L in the brown lake	Zooplankton	Focal taxa	1. No zooplankton community changes in the different treatments of UV radiation in the brown lake; 2. in clear water, copepods had increased reproduction, enhanced species diversity, and greater variablility in community structure.
Wissel et al., 2003	USA	Enclosures, lakes (2)	20PTU, 53PTU, Absorbance at 440nm	Fish, macroinvertebrates, zooplankton	Focal taxa	In highly coloured water, *Chaoborus* was more abundant and the zooplankton community shifted from small species to large species
Estlander et al., 2009	Finland	Boreal lakes (4)	Water colour 130 – 340 mgPt/L	Zooplankton	Focal taxa	1. In humic lakes, low water transparency protected cladocerans from fish predation, while the importance of the littoral zone as refuges decreased; 2. Chaoborid feeding efficiency was not affected by visibility.
Karlsson et al., 2009	Sweden	Boreal lakes (12)	DOC 1.5-16.8 mg/L	Zooplankton, benthos	Prey of the focal taxa	1. High DOC reduces algal primary production due to reduced light availability in lakes, which limits fish production; 2. DOC affected light irradiation, the decrease of which reduces benthic contribution to fish biomass.
Estlander et al., 2010	Finland	Boreal lakes (4)	Water colour 130 – 340 mgPt/L	Fish, macroinvertebrates, zooplankton	Prey of the focal taxa	Benthic macroinvertebrates density was higher in lakes with low water colour than in humic lakes; Trichoptera and Ephemeroptera were more abundant in clearer lakes than humic lakes.
Ekvall & Hansson, 2012	Sweden	Freshwater mesocosms	0.0087 – 0.0198, absorbance at 420nm	Zooplankton	Focal taxa	1. Brownification positively affected cladoceran recruitment and pelagic abundance, but did not affect copepods; 2. water colour had weaker effects than warming.
Estlander et al., 2012	Finland	Freshwater tanks	Water colour 50 – 340 mgPt/L	Fish, macroinvertebrates, zooplankton	Prey of the focal taxa	1. Dark water can eliminate the perch predation on zooplankton due to limited vision and force perch to feed on macroinvertebrates; 2. dark water did not affect roach feeding on

						invertebrates.
Nicolle et al 2012	Sweden	Freshwater mesocosm	TOC 26.3 mg/L, Fe 3 mg/L	Phytoplanktons, zooplankton	One of the focal taxa	1. Browning plus warming had stronger effects on zooplankton time than browning alone. 2. Browning plus warming benefitted cladocerans and calanoid copepods and resulted in top-down contral of algae.
Hansson et al., 2013	Sweden	Freshwater mesocosms	0.013-? absorbance at 420nm	Phytoplanktons, zooplankton	One of the focal taxa	1. The negative effects of brownification on zooplankton were stronger in the presence of fish than in the absence of fish, especially after massive roach (*Rutilus rutilus*) egg hatching; 2. no sign of mismatch between zooplankton and the phytoplankton resource.
Brothers et al., 2014	Germany	Boreal lake (1)	DOC (24.6 - 53 mg/L), iron (0.12 - 1.07/L)	Bacteria, macroinvertebrates	One of the focal taxa	Few macroinvertebrate individuals were found after the increase of DOC.
Lehtovaara et al., 2014	Finland	Boreal lake (1)	Water colour ca. 80 – 250 mgPt/L	Macroinvertebrates, zooplankton	Focal taxa	1. Water colour was a determinant of crustacean zooplantkon community; 2. Some species, e.g. *Bosmina longirostris* and *Thermocyclops oithonoides*, positively responded to the increasing water colour, while many species were negatively affected.
Weidman et al., 2014	Canada	Montane and alpine lakes (4)	DOC ca. 0.1 – 5.0 mg/L	Phytoplanktons, zooplankton	Consumer of the focal taxa	1. Higher water temperature and DOC concentrations separately reduced phytoplankton abundance; however, warming plus brownification increased phytoplanktons; 2. Warming simulated *Daphnia* while suppressed *Hesperodiaptomus*, but brownification did not affect zooplankton biomass.
Robidoux et al 2015	Canada	Field experiment with enclosures in a boreal lake	DOC 3.0 – 15.5 mg/L	Zooplankton	Focal taxa	Zooplankton biomass and community did not differ between clear and brown treatments. Zooplankton richness and Shannon-Wiener diversity were higher in the clear treatments than in the brown treatments.
Williamson et al 2015	USA	Temperate lakes (2)	DOC 1 – 2 mg/L in the clear lake, 5 – 7 mg/L in the brown lake	Zooplankton	Focal taxa	1. Clear-water lakes are more sensitive to brownification than brown lakes. 1. In the clear lake, the abundance of cladocerans and calanoid copepods declined, whereas the abundance of cyclopoid copepods and rotifer increased during brownifiation; 2. In the brown lake, only the calanoid copepods declined significantly during brownifiation.
Jonsson et al., 2015	Sweden	Freshwater mesocosms	DOC ca. 3.6 – 11.4 mg/L	Aquatic insects	Focal taxa	1. Warming or brownification did not affect total dry biomass of emerging aquatic insects; 2. Brownification alone led to higher dry biomass per individual per trap; 3. Browning with warming

						led to invertebrate community shift to large-sized taxa.
Rasconi et al., 2015	Austria	Freshwater mesocosms	DOC 1.5–14.5 μ g/L; 0 – ca. 0.025 absorbance at 420nm	Bacteria, phytoplanktons, zooplankton	Consumer of the focal taxa	Brownification, warming, and brownification + warming had positive effects on heterotrophic bacteria, but not on zooplankton abundance.
Zhang et al., 2015	Sweden	Freshwataer mesocosms	Unknown, doubling water colour in treatements	Zooplankton	Focal taxa	Brownification had negligible effects on zooplankton abundance and recruitment compared to elevated temperature, except for *Agronotholca* sp.
Kelly et al 2016	USA	Experiment in a temperate lake	DOC ca. 6 – 12.5 mg/L	Zooplankton, macroinvertebrates	Focal taxa	1. Chaoborus biomass did not vary significantly along DOC manipulation. 2. zooplankton density had a small increase with the increasing DOC concentration, which was due to significant increases in gross primary production and resource quality (lower seston carbon-to-phosphorus ratio; C:P). Temporal impacts of DOC on invertebrate communities can be different from spatial impact.
Bartels et al., 2016	Sweden	Boreal lakes (8)	DOC 3.6 – 34.3 mg/L	Fish, macroinvertebrates	Prey of the focal taxa	1. Perch eye-index increased with increasing DOC; 2. Perch diet vaguely shifted from macroinvertebrates to zooplankton.
Grutters et al., 2016	Netherlands	Freshwater mesocosms	Absorbance at 510nm, 0 – 0.022	Aquatic insects	Focal taxa	1. Herbivories by *Parapoynx stratiotata* larvae can induce brownification by increasing DOC in water and its subsequent breakdown into humic acids; 2. its herbivory on some plant species, e.g. *Myriophyllum spicatum*, leads to more intensive brownification than other species, e.g. *Ceratophyllum demersum*.
Urrutia-Cordero et al., 2016	Sweden	Freshwater mesocosms	absorbance at 420nm， details not shown	Phytoplanktons, zooplankton, fish	One of the focal taxa	Brownification with warming led to increase of toxic microcystis, which is harmful to zooplankton (*Daphnia* spp.)
Vasconcelos et al., 2016	Sweden	Freshwater mesocosms	Background attenuation 0.5 – 2.5/m	Zooplankton, benthos	Focal taxa	Zooplankton biomass was not affected by brownification or warming, whereas zoobenthos was affected by warming but not brownification.
Saebelfeld et al 2017	Germany	Lab experiment with deionised water	DOC 0, 15, 30 mg/L	Zooplankton	Focal taxa	1. DOC reduced the fucundity of *Daphnia magna* and longispina and increased mortality in *D. longistpina*. 2. In *D. magna*, antioxidant capacity and oxidative damanage increased and available energey reduced in the DOC treatments
Wolf et al 2017	Norway	Lab experiment with filtered	DOC 2.03, 5, 10, 20 mg/L	Zooplankton	Focal taxa	Increased DNA damange in DOC treatments due to reactive oxygen species production of photoactivated DOC.

		tap water				
Estlander et al., 2017	Finland	Boreal lakes (2)	Water colour 50 – 340 mgPt/L	Macroinvertebrates, zooplankton	Focal taxa	1. Water colour affected the diurnal attachment behaviour of *Sida crystallina*; humic lakes had more free-swimming individuals, while transparent lakes had more individuals fixed on plants; 2. In transparent lakes, the attached *S. crystallina* individuals were larger than free-swimming individuals.
Gall et al., 2017	Austria	Freshwater mesocosms	Absorbance at 420nm, 0.003-0.009	Zooplankton	Focal taxa	1. *Daphnia* growth was slightly higher in brownification treatment than the control and was significantly higher in treatment with both brownification and warming than other treatments; 2. Brownification treatment leads to a higher mortality of *Daphnia* than the control and the other treatments (warming, warming + brownification).
Hedström et al., 2017	Sweden	Freshwater mesocosms	DOC 1.06 – 22.5 mg/L	Fish, macroinvertebrates, zooplankton	Prey of the focal taxa	1. Brownification led to higher mortality of overwintering sticklebacks due to the decreased search efficiency of food; 2. zooplankton dry biomass and total macroinvertebrate dry biomass did not differ significantly between ambient and humic treatments.
Santonja et al., 2017	Germany	Freshwater lab aquaria	DOC from 0.1 mg/L to 19.3 mg/L (HumicFeed 0 mg/L to 50 mg/L)	Zooplankton	Focal taxa	With no fish cue, copepods jumped fewer times along the DOC gradient; with fish cue, copepods became more active and jumped more times along the DOC gradient.
Urrutia-Cordero et al., 2017	Sweden	Freshwater mesocosms	Absorbance at 420nm, ca. 0.008 – 0.032	Phytoplanktons, zooplankton	Consumer of the focal taxa	Browning and warming did not affect zooplankton biomass
Weidel et al., 2017	USA	Indoor tank	DOC 3 – 19 mg/L	Fish, macroinvertebrates, zooplankton	Prey of the focal taxa	Decreasing light availability had negative effects on zooplankton consumption of *Micropterus* and *Lepomis*, but positive effects on *Pimephales*.
Caputo et al., 2018	Chile	Lakes (3)	DOC 0.64 – 2.6 mg/L	Jellyfish	Focal taxa	Brownification decreased the mortality of an invasive jellyfish, because high DOC contents provided protection against the adverse UV radiation.
Horppila et al., 2018	Finland	Boreal lakes (2)	Water colour 50 – 340 μg L^{-1} Pt	Macroinvertebrates	Focal taxa	Brownification affected chaoboridae habitat use; in low DOC, chaoborids mainly used habitats with oxygen level too low for fish; in high DOC, chaoborids used habitats with higher oxygen.
Lebret et al., 2018	Sweden	Freshwater mesocosms	low (1.2mg/L DOC), medium (2.4mg/L), and high(4.8mg/L)	Bacteria, phytoplanktons, zooplankton	One of the focal taxa	Zooplankton biovolume was not significantly affected by water colour

Leech et al., 2018	USA	Boreal lakes (1000)	Ceteogories Blue≤20 PCU, TP <30µg/L; Green≤20PCU, TP>30µg/L; Brown >20PCU, TP≤30µg/L; Murky >20PCU, TP>30µg/L.	Zooplankton	Focal taxa	1. Zooplankton had the highest biomass in murky lakes, and no difference between blue lakes and brown lakes; 2. Zooplankton community composition was related to lake nutrient-colour status; 3. Brown lakes had lower zooplankton:phytoplankton biomass ratios than blue lakes.
Wolf & Heuschele, 2018	Norway	10 L bottles	DOM 2 – 20mg C/L	Zooplankton	Focal taxa	Increasing DOC buffers the detrimental effects of UVR on *Daphnia* swimming behaviour, possibly by shading.
Kankaala et al 2019	Finland	Boreal lakes (2)	Water colour median 100 – 200 mgPt/L	Zooplankton, fish, phytoplankton	One of the focal taxa	No change in total zooplankton abundance with the increasing water colour, but dominant zooplankton species was recorded in both copepods and cladocerans.
Leach et al 2019	USA	Temperate lakes (28)	DOC ca. 2.5 – 12.5 mg/L	Zooplankton	Focal taxa	1. Zooplankton biomass was negatively correlated with increasing DOC, mainly due to the decline of calanoid copepod biomass; 2. brownification affected zooplankton communities, with zooplankton shifting from dominant calanoid copepods to cladoceran grazers. 3. Rotifer biomass did not change during brownification, but Gastropus spp and Keratella spp. declined, while other rotifer groups did not have consistent increase in biomass. 4. Declines in calcium concomitant with browning play an important role in driving long - term declines in zooplankton biomass;
Nova et al 2019	Germany	Lab experiments	DOC 0, 15, 30, 60 mg/L	Zooplankton, phytoplankton	Focal taxa	1. Daphnid growth was affected by phytoplankton, but not by DOC concentrations. 2. Daphnid clutch size increased with DOC concentration. 3. Levels of some PUFAs, such as DHA in *Cryptomonas*, increased with DOC concentration.
Poste et al 2019	Norway	Boreal lakes (2)	TOC 2.6 mg/L in the clear lake, 8.1 mg/L in the brown lake	Zooplankton	Focal taxa	1. MeHg is higher in cladocerans and calanoid copepods in the brown lake than in the clear lake. 2. the brown lake had higher rotifier abundance than the clear lake. 3. Higher tOM results in higher MeHg concentrations in water and zooplankton; Increased tOM decreased the nutritional quality of zooplankton due to higher MeHg concentrations but lower concentrations of essential fatty acids.
Feuchtmayr et al., 2019	UK	Freshwater mesocosms	DOM 3.7 – 8.5 mg/L	Fish, macroinvertebrates, zooplankton	Focal taxa	1. Macroinvertebrate abundance, such as Corixidae abundance, increased in treatments with both low and high concentrations of organic matter, compared to the control; 2. stickleback predation

						on zooplankton and macroinvertebrates was not affected by organic matter contents.
Senar et al., 2019	Canada	Temperate lakes (29)	DOC from 2 mg/L to 15 mg/L	Bacteria, phytoplanktons, zooplankton	Focal taxa	Cladocera and Copepoda may have met their nutritional requirements by relying on alternative food sources (e.g. heterotrophic ciliates and flagellates), because increasing DOC led to increasing cyanobacteria biomass and phytoplankton biomass, but phytoplankton was associated with a decline in EPA and DHA contents in lake seston.
Taipale et al., 2019	Finland	Lab experiments with lake waters	DOC 5 – 28 mg/L	Phytoplanktons, zooplankton	Consumer of the focal taxa	Eutrophication and browning diminished assimilation of high-quality algae, limiting *Daphnia* biomass production.
Tonin, 2019	Canada	Boreal lakes (8)	DOC 3.5 – 9.2 mg/L	Fish, zooplankton	Prey of the focal taxa	Zooplankton biomass declined at high DOC concentrations, as zooplankton acquired proportionately more energy from low quality terrestrial sources.
Arzel et al., 2020 (Arzel, et al., 2020)	Finland	Boreal lakes (5)	Ca. 100 – 500 mgPt/L	Macroinvertebrates	Focal taxa	Macroinvertebrate abundance declined with increasing water colour, but not species richness.
Mattila, 2020	Finland	Boreal lakes (9)	Low DOC (<19 mg/L), moderate (10-20 mg/L), and high (>20 mg/L)	Zooplankton	Focal taxa	1. Zooplankton were most abundant with DOC concentrations around 20 mg/L in the studied lakes, but the community structure did not change significantly along the DOC gradient; 2. *Ceriodaphnia* sp. and *Diaphanosoma* sp. body length decreased along the DOC gradient (2 - 35mg/L), whereas *Bosmina* sp. body length increased along the gradient; 4. Zooplankton may have tolerant thresholds of water colour. E.g. Ceriodaphnia sp. and Diaphanosoma sp. were smaller above the threshold of 12 mg/L.
Minguez et al., 2020	Germany	Enclosures in a lake	Absorbance at 436 nm, water colour ca. 2.4 – 43.2 Pt/L	Zooplankton	Focal taxa	1. *Daphnia* had the highest survival probability when being kept in brown water, with mortality rate <20%, despite its origins; 2. *Daphnia* originated from brown water showed high reproductivity than those from clear water; 3. *Daphnia* was less abundant in the brown enclosures due to the limited phytoplankton growth caused by the reduced light availability; 4. *Daphnia* transferred from clear to brown water or vice versa adjusted their nucleic acid and protein contents.
Van Dorst, 2020	Sweden	Mesocosms, lakes	Absorbance at 420 nm, 0.7 – 22.2 m^{-1}	Fish, zooplankton	Prey of the focal taxa	Brownification had no effect on zooplankton biomass in the absence of fish; in the presence of fish, zooplankton community compositions were significantly different in clear waters and brown waters.

Williamson et al., 2020	USA	Temperate lakes (2)	DOC 0.9 – 6 mg C/L	Zooplankton	Focal taxa	Habitat-related changes had stronger effects on zooplankton community structure in clear-water lakes than in browning lakes.
Adamczuk 2021	Poland	Lab experiment	tDOM 0, 5, 10, 15, 20, 25, 50 mg/L	Zooplankton	Focal taxa	1. Species applies different strategies to deal with the gradient of tDOM: C. spahericus produced more asexual offspring in high concentrations of tDOM, no decrease in population; A. harpae mainly produced resting eggs in high tDOC, resulting in decreasing populations. 2. The impact of tDOC on cladoceran appeared negligible at the community level and should be careful in interpretation of the results.
Lau et al 2021	Sweden	Boreal lakes (33)	DOC 1.8 – 25.6 mg/L	Zooplankton	Focal taxa	1. Boreal lakes are warmer and browner than subarctic lakes. 2. The EPA, DHA, or EPA+DHA contents of Bosmina, cyclopoids, and copepods increased in lakes with higher DOC concentrations or aromaticity.
Leech et al 2021	USA	Lab experiments	Absorbance at 440nm, 1.5/m in natural lake water, light brown 1.6/m, moderate brown 5.7/m, dark brown 10.8/m	Fish larvae, bacteria, phytoplankton, zooplankton	Prey of the focal taxa	1. The total zooplankton density was negatively affected in moderate and dark brown treatments; 2. the fish larvae growth was negatively correlated with increasing water colour, despite the feeding rates were not affected by water colour.
Shchapov et al 2021	USA	Temperate lakes (14)	DOC 5.5 – 19.2 mg/L	Zooplankton	Focal taxa	1. Water colour affects zooplankton communities. 2. On average, green lakes had higher zooplankton density than brown lakes and blue lakes.
Bandara et al., 2022	Sweden	Baltic sea	Humic substance 8.0 – 19.9 µg/L	Phytoplantons, zooplankton	One of the focal taxa	1. Increasing coloured terrestrial organic matter in water altered the phytoplankton composition, which affected the zooplankton nutritional quality; 2. Brownification reduce the PUFA availability in seston and zooplankton, consequently impairing the overall pelagic food-web quality.
Gohil, 2022	Canada	Boreal lakes (87)	DOC 0.2 – 9.4 mg/L	Zooplankton	Focal taxa	DOC was a determinant of zooplankton community, because DOC attenuates light and can cause surface waters to warm.
Kesti et al., 2022	Finland	Boreal lakes (26)	DOC 2.8 – 18.7 mg/L	Macroinvertebrates	Focal taxa	1. Humic lakes had higher abundance of chironomids, but lower abundance of stoneflies and mayflies than clear-water lakes; 2. in humic lakes, the proportion and content of PUFAs of several taxa were lower than in clear-water lakes.
Soulié et al., 2022	Norway	Coastal water	HuminFeed®0, 2	Phytoplanktons, zooplankton	Consumer of the focal taxa	Brownification induced significant changes in phytoplankton and zooplankton community compositions; brownification favoured

			mg/L (2 mg/L corresponding to 0.8 mg/L DOC			appendicularian but disfavoured copepod *Acartia* sp.
Vargas et al., 2022	Brazil	Freshwater mesocosms	DOC 0, 50, 100 mg/L	Zooplankton	Focal taxa	Increased DOC decreased cladoceran emergence via light attenuation.
Estlander & Horppila 2023	Finland	Boreal lakes (27)	DOC 2.9 – 36.9 mg/L, Fe 0.1 – 3.6 mg/L	Zooplankton	Focal taxa	1. Herbivore species richness decreased with increasing DOC concentration, but omnivore richness increased. 2. The total zooplankton biomass was not correlated with DOC concentration. 3. Shannon diversity index of zooplankton decreased with increasing DOC concentration.
Hébert et al 2023	Canada	Field experiment in a temperate lake	DOC 2.99 – 4.72 mg/L	Zooplankton, phytoplankton, bacterioplankton	One of the focal taxa	DOM enrichment weakly increased zooplankton biomass. Copepods but not cladocerans seemed to be favoured by DOM enrichment.
Luan et al 2023	China	Temperate river (1)	DOC ca. 3 – 10 mg/L	Zooplankton	Focal taxa	DOC is a determinant of rotifer communties. Autochthonous and fresh DOM was positively associated with rotifer abundance and richness, and terrigenous humic-like substances were positively associated with rotifer diversity and evenness.
Brüsecke et al., 2023	Finland	Boreal streams (63)	DOC 3.6 – 27 mg/L	Macroinvertebrates	Focal taxa	1. Macroinvertebrate species richness decreases with increasing DOC, but taxa responded to DOC differently; 2. scrapers, gatherer-collectors, and predators exhibit negative responses to increasing DOC; 3. shredders exhibit no response to DOC; 3. *Asellus aquaticus*, Ceratopogonidae, *Nemoura* spp., *Leptophlebia* spp. positively response to DOC.
Garnier et al., 2023	Sweden	Seawater mesocosms	DOC 4.88, 7.07 mg C/L	Algae, fish, macroinvertebrates, zooplankton	One of the focal taxa	1. Zooplankton were not affected by the interactions between the presence of fish and the darkening water (brownification); 2. Chironomid biomass was the lowest in darkening water with fish, but darkening alone did not affect the chironomid biomass; 3. Nutrients (eutrophication) + darkening increased the zooplankton biomass dramatically, but not affect chironomid biomass.
Keva et al., 2023	Finland	Boreal lakes (23)	DOC 5 – 22 mg/L	Zooplankton	Focal taxa	Brownification had a positive relationship with linoleic acid (LA) and alpha-linolenic acid (ALA) content of herbivorous cladocerans, which are considered beneficial for the growth and reproduction success of primary consumers.
Koizumi et al., 2023	Sweden	Freshwater mesocosms	DOC 1.6 – 9.3 mg/L	Zooplankton, macroinvertebrates	Focal taxa	1. *Daphnia* biomass was positively affected by the increasing DOC, but not rotifers or copepods; 2. zoobenthos communities, which were dominated by chironomids, Oligochaeta, Trichoptera,

						and *Asellus* sp., had little response to brownification.
MacKeigan et al., 2023	Canada	Boreal lakes (664)	Water colour 0 – 369.5 mg Pt/L	Cyanobacteria, zooplankton	Consumer of the focal taxa	1. Total cyanobacteria biomass was positively affected by DOC; 2. total cyanobacteria biomass was positively related to zooplankton biomass, especially daphnid and cyclopoid copepod biomass.
Pilla & Williamson, 2023	USA	Temperate lake (1)	DOC 1 – 2 mg C/L	Zooplankton	Focal taxa	1. *Daphnia* populations decreased in abundance and shallowed in their vertical distribution in browning Lake Giles for the past 30 years; 2. *Daphnia* vertical distribution became shallower, possibly due to lower UV exposure near the surface caused by brownification.
Strandberg et al., 2023a	Canada, Finland	Boreal lakes (25, collectively 95)	Water colour 5 – 447 Pt mg/L	Macroinvertebrates	Focal taxa	1. Species richness of benthic macroinvertebrates decreased with increasing water colour; 2. PUFAs (polyunsaturated fatty acids) were unrelated to human-induced nutrient loading or increasing water colour.
Strandberg et al., 2023b	Finland	Boreal lakes (10), temperate lakes (29)	DOC 2.6 – 18.9 mg/L	Zooplankton	Focal taxa	1. Brownification led to increasing phytoplankton biomass and concentrations of eicosapentaenoic acid (EPA) and docosahexaenoic acid (DHA) in study lakes; 2. browning-induced phytoplankton biomass increase was associated with increased reliance of zooplankton on a heterotrophic microbial pathway; 3. phytoplanktons responded to browning similarly across regions, whereas zooplankton responses were highly taxa- and region-specific.
Ktistaki et al 2024	Greece	Mesocosm in Mediterranean sea	HumicFeed 0 and 2 mg/L	Zooplankton and other plantkon	One of the focal taxa	The abundance of copepods and their eggs were significantly lower in the humic treatment than the control
Liao 2024	Finland	Urban ponds (26)	Water colour 5 – 360 mgPt/L	Macroinvertebrates	Focal taxa	1. Dytiscid species richness and abundance increased along the water gradient in the presence of fish but not significantly change in the absence of fish. 2. Some species, such as *Dytiscus* spp., appeared tolerant to brownification, whereas some species, such as *Hygrotus* spp. and *Hyphydrus ovatus*, tended to occur in clear water.
Tuurunen & Aroviita 2024	Finland	Boreal streams (94)	Water colour 19 – 313 mgPt/L	Macroinvertebrates	Focal taxa	1. Water colour affected grazer abundance negatively, but predator abundance positively, and no effects on shredders, collector-gatherers, and filter feeders. 2. Water colour had negative effects on Ephemeroptera, Plecoptera, and Trichoptera

Conclusion

Anthropogenetic activities, such as land-use change, have led to browning surface waters, which has a cascade of impacts on the aquatic food web. Aquatic invertebrates started to gain attention in the past decade, with zooplankton being better studied than macroinvertebrates. Brownification has both beneficial and harmful effects on aquatic invertebrates, such as protecting invertebrates from UVR whereas causing DNA damage due to photoactivated DOC. Brownification can directly affect aquatic invertebrate species traits, such as fecundity, survival, and growth, and indirectly via its impacts on food quantity and quality. Brownification may affect the eco-evolution of zooplankton and primary producers. Yet, there is generally lack of links between macroinvertebrates and other aquatic organisms in the reviewed papers, despite having been studied as prey of fish. The effects of brownification on aquatic invertebrates are complex and may vary with abiotic factors, such as global warming and eutrophication, and biotic factors, such as predation risk and food quantity and quality. The effects of brownification on aquatic invertebrates can diverge at different taxonomic resolutions, thus careful interpretation is needed.

Based on the reviewed papers, we provide the following perspectives to be considered in future studies on brownification and aquatic invertebrates:

1. Longer gradients of water colour should be studied in experiments and field studies, to allow the detection of thresholds and patterns regarding how invertebrates respond to brownification;
2. More chemical components that affect water colour, such as iron and manganese, should be investigated, instead of only using humic substances to increase water colour in experiments;

3. The interactions between water colour and other water physicochemical properties, such as nutrient contents and turbidity, should be investigated in the field from the perspectives of aquatic invertebrate conservation;
4. Aquatic invertebrates in seawaters and lotic freshwaters, such as springs and rivers, should receive more attention in the research of brownification;
5. More lentic habitats, such as bogs, vernal pools, beaver ponds, than lakes should be investigated, to understand if and how habitat features, such as different levels of predation risk, diverge the effects of brownification on aquatic invertebrates in the field;
6. Long-term field studies are needed to monitor the effects of brownification on aquatic invertebrates, as short-term experiment results may not be applicable in the real world;
7. Aquatic invertebrates, especially macroinvertebrates that lack studies, should be studied to the species or genus level, as the effects of brownification on invertebrates can be species-specific, especially when invertebrates under the same family or order play very different ecological roles;
8. In food webs, aquatic invertebrates should be studied with both predator-centred and prey-centred approaches;
9. Some aquatic invertebrates should be investigated as inducers of water browning.

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