Chapter 29
Land and Freshwater Complex Interactions in Boreal Forests: A Neglected Topic in Forest Management

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Abstract Aquatic and terrestrial habitats are interdependent components of the boreal forest landscape involving multiple dynamic interactions; these are manifested particularly in riparian areas, which are key components in the forest landscape. However, this interdependence between aquatic and terrestrial habitats is not adequately accounted for in the current management of forest ecosystems. Here we review the impacts of land disturbances on the optical and physicochemical properties of water bodies, aquatic food web health, and the ecological functioning of these freshwaters. We also describe how freshwaters influence the adjacent terrestrial ecosystems. A better understanding of these dynamic biotic and abiotic interactions between land and freshwater of the boreal forest is a first step toward including these freshwaters in the sustainable management of the boreal forest.

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29.1 Introduction

The boreal forest, the world's largest land biome, is characterized by a high density and diversity of freshwater environments. These water bodies form a complex aquatic network that interacts dynamically with the surrounding terrestrial environment. However, scientists have traditionally kept to their respective areas of interest, and research in the respective fields of terrestrial and aquatic ecology has remained separate. Consequently, there is a knowledge gap in our understanding of the interactions between aquatic and terrestrial habitats as well as those processes specific to the aquatic–terrestrial ecotones (Hjältén et al., 2016). Nevertheless, environments such as the littoral zone in lakes and the shoreline area in forests are habitats rich in biological diversity and are sites where essential processes occur, e.g., the primary production of macrophytes and benthic algae or tree species associated with wet areas. Land–water interactions, comprising energy and matter fluxes, occur mainly in this ecotone (Fig. 29.1). The largest fluxes from land toward freshwater are the dissolved and particulate organic and inorganic matter carried by surface runoff, groundwater, and wind (Vander Zanden & Gratton, 2011). The freshwater to land fluxes are smaller in volume but greater in energy and are higher in nutritional quality. These fluxes follow animal movements, such as insect emergence or terrestrial predation on aquatic prey.

Both types of fluxes are intimately entangled, connecting the land and water environments in the boreal forest (Baxter et al., 2005); however, these habitats are commonly viewed as separate ecosystems and are thus managed by distinct environmental institutions or agencies. The aquatic habitats are therefore usually not directly included in sustainable forest management. This view may pose risks of underestimating the complexity of the structure and functioning of the forest and

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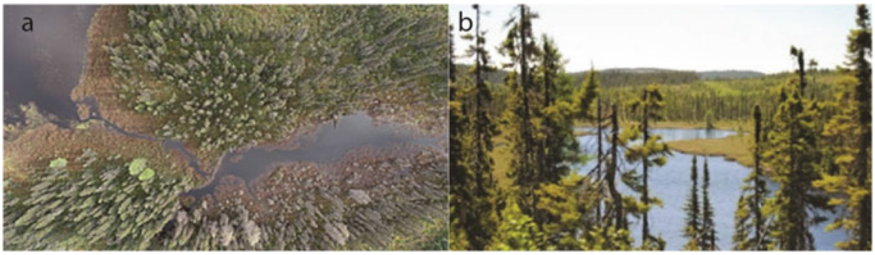

Fig. 29.1 **a** Connectivity between the aquatic and terrestrial habitats of the boreal forest; **b** forest harvesting in a lake watershed. *Photo credits* Miguel Montoro Girona and Janie Lavoie

hinder successful management (Gauthier et al., 2009; Messier et al., 2013). For an improved representation of reality, we highlight in this chapter that terrestrial and freshwater habitats are integral parts of the same boreal forest ecosystem, and, as such, we will no longer refer to terrestrial and aquatic ecosystems as separate entities.

One way to consider land–water interactions is by implementing riparian buffer strips, which are commonly included in forest management. Although the direct and indirect effects of these buffer strips on aquatic habitats have been studied extensively (Lidman et al., 2017a, b; Peterjohn & Correll, 1984), there remains an absence of information of the site-specific role of riparian forests, e.g., on different types of forest soil, with different slopes or different stand compositions (Kuglerová et al., 2014); this knowledge gap impedes the advancement of best practices in boreal forest management (Kuglerová et al., 2017). Furthermore, the effectiveness of riparian forests in moderating the impacts of harvesting on the terrestrial part of the boreal forest has rarely been tested. The construction of roads related to forestry practices and the type and timing of harvesting may affect how forestry machinery modifies stream habitats, both directly and indirectly, by increasing turbidity (Reiter et al., 2009). Extensive cutting may raise the water table and increase the amount of organic matter exported to aquatic habitats (Laudon et al., 2009; Sun et al., 2000). In addition, increases in the number of water pools in the tracks of the machines may increase mercury methylation and the related contamination of the landscape (de Wit et al., 2014; Sørensen et al., 2009). Fertilization, liming, and fire control may also affect the leaching of nutrients and other constituents into the water (Bisson et al., 1992; Degerman et al., 1995). This chapter therefore aims to describe the existing natural and anthropogenic interactions between the aquatic and terrestrial habitats of the boreal forest and highlight the importance of integrating the aquatic environments into the sustainable management of the forest. We demonstrate that revising the existing forest management paradigm, which currently considers land and freshwater habitats as isolated ecosystems, is essential to acknowledge the interdependence between these components and enhance forest management success.

29.2 The Browning of Boreal Freshwaters

A portion of the brown color of boreal lakes and rivers is caused by dissolved organic matter (DOM) leaching from the soil and litter of forests (Roulet & Moore, 2006). The DOM concentration, including the dissolved organic carbon (DOC) component, has increased in freshwaters during the last decades to shift the water color of boreal water bodies toward brown, a phenomenon called *browning* or *brownification* (Fig. 29.2; Lennon et al., 2013). The browning of freshwater is a serious concern for many ecosystem services, including drinking water supply (Haaland et al., 2010), as treatment of brown water rich in DOM is costly and may produce chlorinated carcinogenic compounds (Richardson et al., 2007). Whereas the extent and intensity of browning remain poorly studied at the global scale, the most dramatic changes in DOC concentrations ($>0.15\ \mathrm{mg{\cdot}L^{-1}{\cdot}yr^{-1}}$) have been reported in temperate and boreal regions (de Wit et al., 2016; Monteith et al., 2007).

Browning is associated with natural and anthropogenic changes in land cover as well as other factors that modify the amount and nature of organic matter exported from the watershed into freshwater habitats (Kritzberg, 2017). In boreal forests, increasing DOC concentrations in lakes is a direct consequence of forest harvesting. Harvesting raises the water table, thereby increasing the hydrological connectivity between shallow DOC-rich soils and the recipient freshwaters (Glaz et al., 2015). Organic matter export may also increase because of greater terrestrial primary production in the forest (Larsen et al., 2011), enhanced by increased atmospheric carbon dioxide levels (Campbell et al., 2017). Other factors include increased nitrogen deposition (Rowe et al., 2014), higher precipitation (Hongve et al.,

Fig. 29.2 Lake water with low (l*eft*) and high (*right*) concentrations of dissolved organic matter. *Photo credit* Guillaume Grosbois

2004), and greater export of iron, which can form stable, highly colored complexes with DOM (Weyhenmeyer et al., 2014). Several recent studies have attributed the DOC increase to recovery from atmospheric acid deposition, which enhances organic matter solubility and, therefore, the mobility of DOC from forest to aquatic environments (Meyer-Jacob et al., 2019). These researchers questioned whether the current browning of freshwaters reflected a re-browning to reach past levels of water color or whether this represented a new trend toward unprecedented browning (Meyer-Jacob et al., 2020). Both trends have been observed, and whereas re-browning is associated with regions having received moderate to high levels of acid deposition, higher than preindustrial DOC concentrations have been recorded in regions characterized by low levels of acid deposition (Meyer-Jacob et al., 2019). Thus, recovery from acidification is insufficient to explain browning in all lakes, and the trends in water color may be more related to changes in land use, e.g., from agriculture to modern forestry (Kritzberg, 2017).

An increase in DOM in freshwaters can drastically change the structure and functioning of inland waters having a darker water color by increasing the surface water temperature and modifying thermal stratification (Williamson et al., 2015). Although higher temperatures can potentially enhance algal production, browner waters also attenuate the penetration of photosynthetically active radiation and therefore diminish a water body's suitability for aquatic primary production (Creed et al., 2018). Increasing DOM in freshwater strongly affects microbial processes by shifting basal pelagic production from phytoplankton to bacteria (Jansson et al., 2000). Although the biodegradation coefficient per unit of DOM is reduced in brown lakes and rivers (Berggren & Al-Kharusi, 2020; Berggren et al., 2020), the absolute amount of organic carbon that is assimilated and metabolized by microorganisms increases with greater DOM concentrations (Lennon, 2004). This has consequences for higher trophic levels, affecting zooplankton production and fish survival and growth (Hedström et al., 2017; Taipale et al., 2018). Browning therefore radically alters the functioning and subsidies of aquatic food webs (Hayden et al., 2019).

In the near future, green (eutrophication) and brown (browning) lakes are expected to replace blue lakes in the boreal forest (Leech et al., 2018). The increase in DOM export in some regions is clear, particularly in northern ecosystems where higher temperatures and shorter winters will allow a greater water movement through litter and soil and thus increase DOM export to freshwaters (Laudon et al., 2012). These major changes in DOC could modify the overall C budget of the boreal forest, and future research must focus on this issue to better understand how these new conditions will influence the future C sinks and sources.

29.3 Nutrients in Freshwaters: Eutrophication and Oligotrophication

Lake and river environments depend strongly on nutrient export from their associated watersheds (Hynes, 1975). In boreal forests, nutrients are fixed via atmospheric deposition, N-fixation by cyanobacteria, or weathering, and a portion is exported to aquatic ecosystems through runoff (Hall, 2003). Nutrients are not only transported by freshwaters but are also physically, chemically, and biologically processed. One way of estimating these biotic contributions is to experimentally manipulate the watershed, for example by preventing acid rain (Hultberg & Skeffington, 1998) or harvesting the trees (Likens et al., 1970). During the Hubbard Brook Experiment, the cutting of all watershed vegetation demonstrated the key role of terrestrial vegetation in retaining nutrients within the watershed (Likens et al., 1970). Moreover, nutrient export to streams and lakes drastically increased after tree harvesting; this highlighted the terrestrial origin of most nutrients. Rivers and lakes are, therefore, highly dependent on watershed sources of nutrients. The Global Nutrient Export from Watersheds (NEWS) model estimated that, at the global scale, the export of dissolved inorganic nitrogen (N) and phosphorus (P) is dominated by anthropogenic sources, whereas 80% of the dissolved organic N and P is dominated by natural sources (Seitzinger et al., 2005). Bernhardt et al. (2003) also demonstrated that rivers react to major forest disturbances, reducing nitrogen concentrations downstream of the disturbance. Thus, aquatic environments are strongly dependent on the export of forest nutrients and are biogeochemically reactive habitats where algae and grazers/predators have a high capacity for assimilating and storing nutrients.

Increased exploitation of natural resources, e.g., forestry and mining, and associated infrastructure development in boreal regions has increased the leakage of carbon, nitrogen, and phosphorus from catchments into watercourses (Payette et al., 2001). This increase of biologically reactive dissolved inorganic nitrogen has been measured over large areas globally and has been found to affect nutrient ratios in freshwaters and lead to lake eutrophication (Hessen, 2013). Such an increase in nutrient inputs may shift an initial N-limitation to P-limitation for primary producers and consumers; this alteration causes major changes to the base of food webs in lakes (Elser et al., 2009, 2010) and rivers (Chen et al., 2013). Additionally, terrestrial organic matter is associated with DOM, nitrogen, and phosphorus (Aitkenhead-Peterson et al., 2003), and their respective inputs increase with browning (see Sect. 29.2). Many boreal freshwater ecosystems will experience greater nutrient inputs in the future; however, the effect on the functioning of food webs remains relatively unknown. Prepas et al. (2001) demonstrated that harvesting around the headwater lakes of Alberta's boreal plain increased total phosphorus concentration in the lakes, triggering an increase in cyanobacteria and cyanotoxins. Consequently, zooplankton biomass and abundance decreased in these boreal lakes impacted by forest harvesting. Given that N and P export to freshwaters is predicted to increase over the next decades, terrestrial–aquatic interactions must be accounted for in the future management of the boreal forest.

In already-nutrient-poor systems in many boreal regions of the world, e.g., Sweden, Canada, and Finland, lakes have experienced a substantial, long-term decline in total phosphorus concentrations ($2.1\% \cdot \mathrm{yr}^{-1}$ since the 1980s), reaching values close to the detection limit; this process is referred to as lake oligotrophication (Arvola et al., 2011; Eimers et al., 2009; Huser et al., 2018). These declines are linked to the recovery from acidification, the increased climate change–induced trapping of nutrients by plant roots (Elmendorf et al., 2012), changes in watershed processes related to soil properties (Gustafsson et al., 2012), or a combination thereof. Cyanobacterial blooms are often triggered by an excess of nutrients in lakes; however, they can also be enhanced by N-limitation, as cyanobacteria can fix environmental N and are therefore more competitive than other algae (Berman-Frank et al., 2007). Diehl et al. (2018) report that cyanobacteria make up more than 50% of the biomass in shallow, epilithic biofilms in northern Swedish lakes. Cyanobacteria-dominated communities in oligotrophic waters negatively impact lake food webs through a lower trophic transfer efficiency from primary producers to consumers (Brett & Muller-Navarra, 1997). Declining total phosphorus concentrations could therefore act in synchrony with increasing DOM and suppress aquatic productivity.

When harvesting a significant area of a watershed as part of a management strategy in boreal forests, it is essential to consider the effect on the already fragile balance of nutrients resulting from browning, eutrophication, or oligotrophication.

29.4 Metabolism in Freshwaters: Heterotrophy Versus Autotrophy

Inland waters process, store, and outgas most of the carbon (C) exported from land, thereby playing a significant role in the global C cycle (Battin et al., 2009; Raymond et al., 2013). These external carbon inputs can vary from being a primary energy source in freshwater metabolism (*heterotrophy*) to being less important relative to aquatic photosynthetic production (*autotrophy*). This reliance depends on many factors that determine the interactions between the aquatic and forest components of the boreal landscape, such as ecosystem size. For example, small streams connected to the landscape mainly emit terrestrially derived carbon dioxide (CO_2), whereas larger rivers mostly re-emit CO_2 previously fixed by aquatic primary producers (Hotchkiss et al., 2015). Inland waters are classified as net heterotrophic when metabolism based on external watershed inputs causes the CO_2 emissions from aquatic organisms, i.e., respiration R, to be greater than aquatic gross primary production (GPP). In contrast, waters are classified as net autotrophic when the metabolism is predominantly based on aquatic production and, therefore, R is less than GPP (Jansson et al., 2000). New inputs of organic matter from the boreal forest are also a source of nutrients to the water and may increase GPP even though they may not change the net ecosystem production (NEP, i.e., GPP–R), as it may also increase R (Cole et al., 2000). New inputs from forests, such as those following forest harvesting, thus affect the basal production of aquatic ecosystems, potentially increasing heterotrophic bacterial metabolism as well as photosynthetic production. Clapcott and Barmuta (2010) demonstrated that forest harvesting increases metabolism and organic matter processes in small headwater streams; however, it remains unclear whether this is the case in larger ecosystems (Klaus et al., 2018). The impact of forest harvesting on aquatic metabolism is, therefore, very difficult to predict because organic matter inputs from the watershed are susceptible to switching from an equilibrated ecosystem, i.e., R = GPP, toward net heterotrophy when bacterial metabolism is favored but also toward net autotrophy when the associated nutrients favor photosynthetic algal production.

Inland waters are classified in terms of their trophic state as eutrophic (very productive), mesotrophic (moderately productive), or oligotrophic (unproductive) environments. The impact of forest harvesting is expected to differ according to the trophic state of lakes and rivers. Extra watershed inputs of organic matter to eutrophic lakes may increase an already high GPP but still trigger a switch of an ecosystem from a sink to a source of greenhouse gases because of increased production and diffusion of methane (Grasset et al., 2020). Greater nutrient and organic matter inputs from the catchment can unbalance autotrophy versus heterotrophy processes and lead to an accumulation of organic matter in the sediments. The degradation of this extra t-OM under anoxic conditions in the sediments is likely to produce methane (Donis et al., 2017). Mesotrophic and oligotrophic lakes can alternate from autotrophic to heterotrophic states, in different seasons, from one year to another, or after meteorological events such as storms that uncouple R and GPP (Richardson et al., 2017; Vachon & del Giorgio, 2014; Vachon et al., 2017). Given that even within the same ecosystem, C from the forest and C synthesized by algae can be used differently by bacteria—forest C for biomass and algal C for respiration (Guillemette et al., 2016)—the impact of forest harvesting on aquatic bacterial communities is difficult to predict.

Limnologists often consider terrestrial DOM (t-DOM) to be homogeneous; in reality, however, t-DOM represents a mix of material of very different origins and differing states of degradation (Berggren et al., 2010b). It includes low molecular weight compounds, such as carboxylic acids, amino acids, and carbohydrates, which bacteria easily utilize and eventually transfer to higher trophic levels (Berggren et al., 2010a). Molecules are referred to as labile, semi-labile, or recalcitrant according to how easily they can be degraded by bacteria (Kragh & Sondergaard, 2004). The terrestrial share of DOM is composed of compounds that originate from terrestrial plant tissues, and soil microorganism communities often modify these compounds before entering inland waters (Solomon et al., 2015). Generally, t-DOM is composed of humic and fulvic acids that contain aromatic hydrocarbons, including phenols, carboxylic acids, quinones, and catechol, and a nonhumic fraction characterized by lipids, carbohydrates, polysaccharides, amino acids, proteins, waxes, and resins (McDonald et al., 2004). Among these compounds, low molecular weight carboxylic acids, amino acids, and carbohydrates can potentially support all bacterial production in boreal ecosystems (Berggren et al., 2010a). The remaining incoming terrestrial organic matter is highly concentrated in tannins and represents organic compounds not degraded by microbial fauna in the soil (Daniel, 2005). Degradation processes preferentially remove oxidized, aromatic compounds, whereas reduced, aliphatic, and N-containing compounds are either resistant to degradation or tightly cycled; they therefore persist in aquatic systems (Kellerman et al., 2015). The role of allochthonous carbon in aquatic ecosystems is closely related to bacterial abundance, biomass, and production (Azam et al., 1983; Roiha et al., 2012), as most DOM decomposition is undertaken by planktonic bacteria (Daniel, 2005; Wetzel, 1975). Depending on the quality of the organic carbon, bacterial productivity might change, whereas the quantity of the organic carbon appears to define community composition (Roiha et al., 2012). Glaz et al. (2015) demonstrated that, in contrast to DOM quantity, the nature of t-DOM in lakes affected by forest harvesting did not change. Therefore, forest harvesting triggers extra inputs of DOM into aquatic environments that can directly influence and foster bacterial communities and modify the entire-lake metabolism.

29.5 Allochthony in Boreal Aquatic Consumers

In aquatic habitats within forests, organic matter (OM) inputs from the adjoining terrestrial counterparts are *allochthonous*, whereas aquatic primary production is referred to as *autochthonous*. Terrestrial OM eventually enters the aquatic food webs, and its use by aquatic organisms for biomass production is referred to as *allochthony*. The significance of allochthony in supporting aquatic food webs has been shown recently for bacteria (Berggren et al., 2010a; Guillemette et al., 2016), zooplankton (Berggren et al., 2014; Grosbois et al., 2017a), invertebrates (Hayden et al., 2016), and fish (Glaz et al., 2012; Tanentzap et al., 2014).

Although all aquatic organisms may play a role in processing terrestrial OM directly or indirectly, zooplankton occupy a strategic position in aquatic food webs. Zooplankton can consume both autochthonous and allochthonous OM for biomass production and are key organisms responsible for transferring OM to higher trophic levels (Grosbois et al., 2020). Whereas earlier studies found significant trophic transfer of terrestrial particulate OM to zooplankton (Cole et al., 2006), recent studies demonstrate that this direct use of terrestrial particulate OM by pelagic food webs is rather limited (Mehner et al., 2016; Wenzel et al., 2012). However, the assimilation of terrestrial OM in aquatic food webs can follow different pathways and may begin at the lower tropic levels, i.e., through the microbial degradation of terrestrial OM. The terrestrial OM is then transferred to the trophic levels comprising ciliates, flagellates, or rotifers through their consumption of the microbes (Jansson et al., 2007; Masclaux et al., 2013). The allochthonous OM assimilated by these species is then consumed by larger zooplankton taxa that are, in turn, available for zooplanktivores, including numerous fish species, e.g., *Perca flavescens*, and invertebrates, e.g., *Chaoborus obscuripes* and *Leptodora kindtii* (Tanentzap et al., 2014). Thus, zooplankton can serve as indicators of allochthony in aquatic food webs and have been the focus of multiple studies of allochthony (Cole et al., 2011; Lee et al., 2013; Perga et al., 2006). Allochthony in zooplankton varies widely, from less than 5% (Francis et al., 2011) to 100% (Rautio et al., 2011). Although there remains some debate about the significance of the terrestrial OM contribution for zooplankton in different lake types, e.g., large clear-water lakes versus small humic lakes, it is now increasingly accepted that allochthony can often be very significant for many zooplankton taxa, especially in lakes that receive large terrestrial OM inputs, which limit light availability and aquatic primary production (Cole et al., 2011; Emery et al., 2015; Wilkinson et al., 2013).

The allochthony of benthic invertebrates in rivers and lakes has often been well defined because of the remarkable feeding adaptations of these taxa (grazers, filterers, shredders, and predators). Therefore, we can observe an allochthony gradient in these organisms, from the least allochthonous grazers to the most allochthonous shredders (Rasmussen, 2010). However, the diet of each feeding group can include a mix of food sources with organisms feeding mainly on autochthonous material and also assimilating allochthonous OM. For example, grazers can consume and assimilate terrestrial OM deposited on benthic algal mats, and filter-feeders can obtain suspended terrestrial OM. Inversely, animals feeding on allochthonous material may ingest autochthonous material, e.g., shredders can consume plant litter together with periphytic algae growing on the litter surface. The use of allochthonous or autochthonous OM by benthic invertebrates also depends on the riparian vegetation and the aquatic habitat size. The river continuum concept (RCC) (Vannote et al., 1980) describes a decreasing allochthony gradient from small forested headwater streams to large autochthonous rivers having minimal canopy cover. However, recent studies have also shown strong autochthony rather than allochthony in headwater streams (Lau et al., 2009a, b; Torres-Ruiz et al., 2007). Erdozain et al. (2019) demonstrated, contrary to RCC predictions, that allochthony in aquatic food webs is low in forest headwaters and increases with greater harvesting intensity and delivery of terrestrial OM. It is, therefore, very likely that silvicultural practices can strongly impact autochthony and allochthony in aquatic food webs.

Changes in the degree of allochthony in zooplankton, benthic invertebrate communities, or both will be reflected in their predators, e.g., fish. Moreover, detritivorous fish in reservoir ecosystems, such as gizzard shad (*Dorosoma cepedianum*), can ingest terrestrial detritus directly, accounting for about 35% of their biomass (Babler et al., 2011). Pelagic fish in a temperate lake had an estimated minimum allochthony of 44% in young bluegill (*Lepomis macrochirus*) and 43% in young yellow perch (*Perca flavescens*), whereas in older individuals, allochthony was 53% (Weidel et al., 2008). The quantification of fish allochthony can be complicated by the diet contribution from terrestrial insects, as fish can feed directly on terrestrial prey items that fall into the water. Neglecting to include the terrestrial prey will likely underestimate the terrestrial trophic support for fish. Allan et al. (2003) estimated that terrestrial and aquatic prey contributed equally to the diet of juvenile coho (*Oncorhynchus kisutch*) in Alaskan streams, and the fish ingested an average total of 12 mg of insect dry mass per day. Forest harvesting affects terrestrial invertebrate communities, such as red-listed beetles (Franc & Götmark, 2008), and, therefore, can strongly disturb the direct subsidy of terrestrial insects for fish growth.

29.6 Health of the Aquatic–Terrestrial Food Web

The health of food webs is largely determined by the nutritional quality of the available food resources. Terrestrial OM inputs comprise mainly biochemically recalcitrant lignocellulose and lack biomolecules such as polyunsaturated fatty acids (PUFA), which are essential for animal growth and reproduction (Schneider et al., 2016, 2017; Taipale et al., 2015). Because essential PUFA are mainly synthesized de novo by algae, their acquisition in aquatic food webs is negatively related to the consumers' degree of allochthony (Jardine et al., 2015; Lau et al., 2014). However, other studies have demonstrated that most aquatic biomass has a terrestrial origin in temperate and boreal lakes, illustrating the strong physical and hydrological connections to OM-rich catchments (Cole et al., 2011; Wilkinson et al., 2013). The effect of this substantial diet contribution of terrestrial OM on the health of aquatic consumers in the natural environment remains unknown; however, laboratory-based feeding experiments have shown lower survival, growth, and reproduction for benthic and pelagic invertebrates when they are fed only with terrestrial plant litter (Brett et al., 2009; Lau et al., 2013). Moreover, the survival of many zooplankton species in boreal lakes depends on the opportunity to accumulate PUFA from algae in autumn and under the lake ice at the beginning of winter (Grosbois et al., 2017b). Furthermore, algae sustain the production of benthic consumers and supply them the necessary PUFA in headwater streams despite the often dense riparian canopy cover over these streams (Lau et al., 2009a, b). Although many species of fungi degrade the detrital material of plant litter, few fungal species exist in aquatic environments to consume the lignified OM and make it accessible to consumers at higher trophic levels (however, see Masclaux et al. (2013) for pollen degradation by aquatic chytrids to access essential fatty acids). In forests, plant litter is degraded initially by microbial communities and then transported to aquatic habitats by runoff. This runoff carries only the "leftovers" of microbial degradation and hence the most recalcitrant molecules (Brett et al., 2017). Moreover, a large portion of terrestrial material can be deposited onto the anoxic bottom of lakes, greatly reducing or stopping its degradation, and lake metabolism becomes directed mainly toward methanogenesis (Schink, 1997).

Inputs of terrestrial DOM to freshwaters considerably affect the productivity of the entire ecosystem, thereby affecting the growth and reproduction of organisms. First, these inputs can diminish benthic and pelagic algal primary production, with the increases in t-DOM, i.e., the browning of waters, limiting light penetration through the water column (Fig. 29.3; Karlsson et al., 2009). Lower primary production in lakes and rivers will reduce the availability of essential molecules, e.g., PUFA, synthesized by algae and the transfer of these molecules to higher trophic levels (Strandberg et al., 2015). Kelly et al. (2014) showed that t-DOM concentrations are negatively correlated to zooplankton production. Karlsson et al. (2015) confirmed this observation, finding lower fish production in small boreal lakes with high t-DOM concentrations. Moreover, Grosbois et al. (2020) demonstrated that zooplankton production based on t-DOM (defined as the allochtrophy) in a boreal lake was lower, on average, throughout the year. Still, they remained in the same range as zooplankton production based on algae. Estimating secondary production in aquatic habitats is challenging, as traditional methods require identifying, counting, and measuring all individuals of a community during a long period and sampling at a high frequency (Runge & Roff, 2000). New methods to measure secondary production, such as the use of the chitobiase enzyme (Yebra et al., 2017), will help quantify the effects of terrestrial OM inputs on aquatic food webs and consumer production.

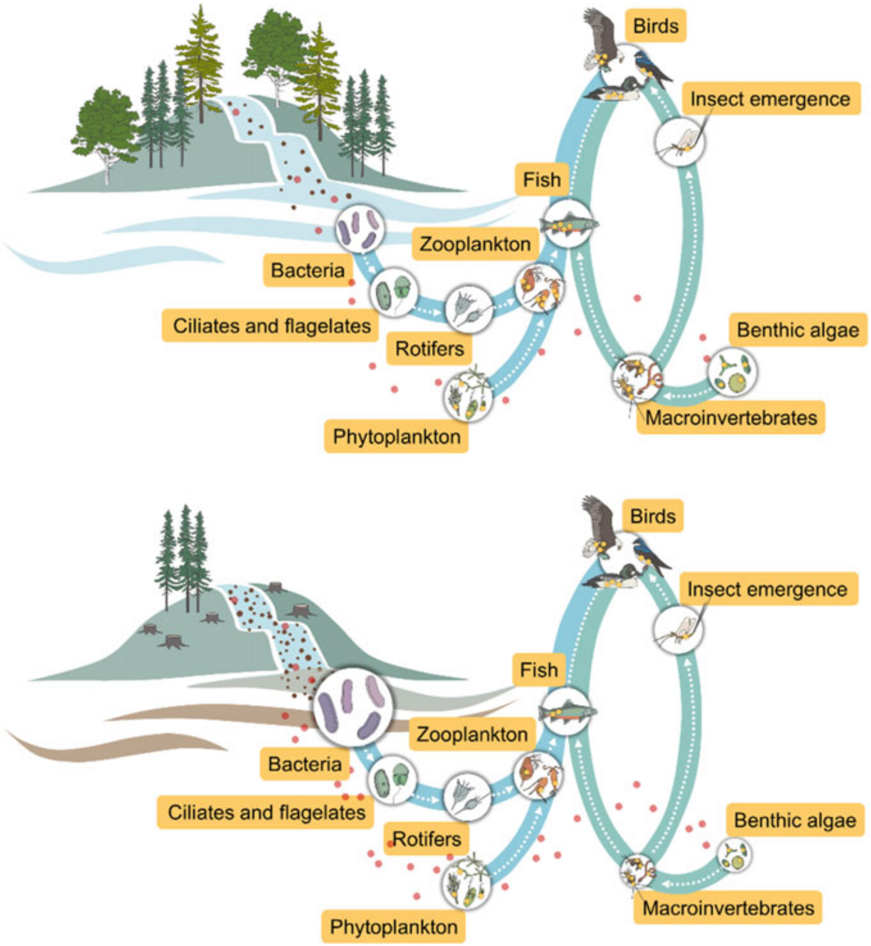

Fig. 29.3 Aquatic–terrestrial food web in an undisturbed (*top*) and a harvested watershed (*bottom*). Dissolved organic matter (*brown dots*) and nutrient inputs (*red dots*) to lakes increase with forest harvesting, leading to the browning of waters, increased bacterial metabolism, decreased light penetration into the water, and suppressed benthic primary and secondary production. Health consequences for terrestrial and aquatic organisms are expected with the altered transfer of essential fatty acids (*yellow dots*) within the aquatic–terrestrial food web

The concept of *one health* highlights that the health of one component of a system depends on that of the other components (Destoumieux-Garzón et al., 2018). This is particularly true for habitats interacting dynamically within the same landscape, such as observed in the boreal forest. Many terrestrial organisms depend on the aquatic environment to access important resources such as food and water for their survival, with some species, e.g., amphibians and insects, having life stages in water. Although subsidies from terrestrial to aquatic habitats are much higher in quantity, the aquatic subsidies to land are of higher nutritional quality (Martin-Creuzburg et al., 2017), energy density, and nutrient concentration; the result is a similar subsidy to animal carbon in both directions (Bartels et al., 2012). Most aquatic subsidies must go against gravity and therefore often rely on animal movement. One of the most observed examples is the emergence of insects from lakes or rivers; these insects eventually feed terrestrial insectivores (Fig. 29.3; Muehlbauer et al., 2014; Paetzold et al., 2005). Emerging aquatic insects are essential prey, as they have a high content of long-chain PUFA. Preliminary estimates of long-chain PUFA export to terrestrial ecosystems range from 0.1 to 672.2 mg dry weight$\cdot$m$^{-2}\cdot$yr^{-1} (Gladyshev et al., 2009). Dreyer et al. (2015) also estimated that the whole-lake emergence of aquatic insects in an Islandic lake (3.1–76.0 Mg$\cdot$yr^{-1}) had deposited 100 kg ha^{-1} yr^{-1} of insect biomass within 50 m of the lake shoreline, corresponding to 10 kg N$\cdot$ha^{-1} yr^{-1} and 1 kg of P ha^{-1} yr^{-1}. Fluxes from aquatic to terrestrial habitats are therefore potentially significant for many terrestrial animals. More studies are required to quantify the aquatic biomass export to terrestrial animals feeding on fish, e.g., bears, bald eagles, and herons, or on macrophytes, e.g., moose, although this type of export is more difficult to estimate.

Aquatic habitats also influence nutrient cycling in the forest landscape, with lotic waters transporting nutrients that are deposited outside of the river bed during flooding (Jacobson et al., 2000) and are made accessible to plant roots in the subsurface water, i.e., hyporheic zone (Pinay et al., 2009). Trees can therefore use aquatic nutrients for growth. In a boreal watershed in Alaska, about 25% of the foliar nitrogen of trees and shrubs was derived from salmon near the fish spawning sites (Helfield & Naiman, 2002). A greater understanding of the land–water interactions and the subsidies from aquatic to terrestrial habitats is essential for the sustainable management and maintaining the health of the forest ecosystem (Schindler & Smits, 2017).

Despite the general high quality of aquatic subsidies to the terrestrial food webs, anoxic zones may form in particular aquatic environments, e.g., ponds, wetlands, deep lake water, where bioavailable methylmercury is produced and bioaccumulates in aquatic food webs (Downs et al., 1998). Contaminants such as methylmercury can therefore be exported to terrestrial food webs with aquatic-feeding species (Cristol et al., 2008). However, this contamination of terrestrial food webs depends more on the complex trophic structure and interactions than on the aquatic prey contribution, such as through insect emergence or predation on fish (Schindler & Smits, 2017). For example, Bartrons et al. (2015) demonstrated that spiders feeding on contaminated aquatic midges had lower methylmercury concentrations than spiders feeding on terrestrial prey because the aquatic prey had a lower position in the food web than their terrestrial counterparts. The trophic position and food-chain length are stronger determinants of methylmercury contamination than trophic reliance on aquatic prey, as longer food chains enhance biomagnification. Furthermore, methylmercury production and accumulation in aquatic food webs can increase with more frequent and severe forest disturbances and climate change. For example, forest harvesting and fires increase the OM inputs in lakes and, therefore, the methylmercury contamination in zooplankton (Garcia & Carignan, 1999) and fish (Garcia & Carignan, 2000). Therefore, the production, assimilation, and export of contaminants is a complex process that depends on both aquatic and terrestrial components. This dependence highlights the need for considering the aquatic and terrestrial components as integral parts of the boreal forest ecosystem.

29.7 The Role and Impacts of Forest Disturbances on Aquatic Ecosystem Services

Aquatic environments provide an essential resource for humanity: freshwater. Freshwater is used for drinking water, watering crops, fisheries, and many important human activities; however, aquatic environments are highly sensitive to disturbances and management occurring on the adjacent forested land. The most well-known example of lake reaction is the temporal increase of lake turbidity after forest harvesting (Glaz et al., 2015) or the more permanent increase in cyanobacterial blooms caused by heightened nutrient inputs from residential areas or agricultural fields (Paerl & Otten, 2013). Thus, a greater consideration of interactions between terrestrial and aquatic environments is required to manage the forest ecosystem. In this respect, it is crucial to account for the role of both natural and anthropogenic forest disturbances and how changes to either of these disturbance regimes will affect aquatic environments. Natural disturbances that shape the structure and ecological functioning of the terrestrial component of the boreal forest have been well covered by Gauthier et al. (2009) and are already included in the sustainable management of boreal forests. Nonetheless, their effects on aquatic habitats have not been fully discussed, partly because of knowledge gaps, and it is crucial to consider possible effects in future management frameworks.

The effects of natural and anthropogenic disturbances, such as fire and forest harvesting, on freshwaters in the boreal forests have been studied previously (Carignan et al., 2000; Garcia & Carignan, 1999; Patoine et al., 2000; Pinel-Alloul et al., 1998). This research has shown that fires strongly affect the water biogeochemistry (Lamontagne et al., 2000; Olefeldt et al., 2013) through, for example, the increase of additional inputs such as phosphorus, which can be directly related to the proportion of burned areas (Carignan et al., 2000). Recently burned watersheds and their associated organic inputs into the surrounding freshwaters can increase lake metabolism and, therefore, the liberation of carbon through aquatic respiration (Marchand et al., 2009). Carignan et al. (2000) proposed a simple model to estimate the impact of fires on lakes on the basis of the burned watershed area divided by the lake's area or volume. Although the effects of fire on lake biogeochemistry have been addressed in these studies, research into the impact on food web functioning and ecology is almost nonexistent. Planas et al. (2000), however, demonstrated that fires modify the biomass and composition of algal communities. Moreover, Patoine et al. (2000) showed that zooplankton biomass is affected after a forest fire, albeit for only a few years, before returning to a normal level; this pattern suggests a high resilience capacity for lakes.

Both forest harvesting and fires can physically disturb aquatic ecosystems, as the removal of forest biomass by burning or harvesting increases a water body's exposure to wind (Montoro Girona et al., 2019; Scully et al., 2000). However, the impacts of forest harvesting on aquatic habitats often differ from that of fires, causing water tables and streamflow to fluctuate more if harvesting is carried out on unfrozen soil (Veny, 1986). Forest harvesting also affects water physicochemical properties by increasing dissolved organic carbon (DOC), algal biomass, and total nitrogen (Steedman, 2000). The concentration of DOC increases significantly one year after logging without changing its characteristics and usually decreases and returns to normal levels one to two years later (Glaz et al., 2015). The additional nutrients and DOC inputs may positively impact juvenile fish growth via an increased primary production in the lake and reduced prey visibility in browner waters (Leclerc et al., 2011). However, these effects depend on the relative increase of nutrients versus DOC because the growth rate and abundance of fish are negatively affected by DOC (Benoît et al., 2016). An important aspect to consider in the sustainable management of forests is that forest harvesting increases methylmercury bioaccumulation in zooplankton and fish via the mercury and methylmercury loadings associated with t-DOM inputs from land to aquatic systems (Garcia & Carignan, 2000; Wu et al., 2018). The effect can be mitigated by an associated higher nutrient input that alters food web structure and productivity (de Wit et al., 2014). To our knowledge, the impact of disturbances other than fire and harvesting, such as insect outbreaks or windthrows, on freshwater ecology has yet to be appropriately studied in the boreal forest, highlighting the need for more research to better understand the possible effects of disturbance on aquatic ecosystems.

It is of utmost importance to consider the potential impacts of forestry on aquatic habitats in future sustainable forest management guidelines because of the role of aquatic habitats in the boreal region in providing important ecosystem services. The consequences of not taking potential impacts into account include browner and more nutrient-rich water caused by anthropogenic, e.g., forest harvesting, or natural disturbances, e.g., fires, affecting drinking water supplies, commercial fishing, and recreational activities (Kritzberg et al., 2020). The browning of waters is associated with a higher concentration of aromatic molecules, which are more difficult to degrade by aquatic microbes (Koehler et al., 2012). Brown waters containing greater amounts of dissolved organic molecules require more treatment with chemical precipitation using $FeCl_3$, $AlCl_3$, or $Al_2(SO_4)_3$, which increases water treatment costs and the risks to human health (Kritzberg et al., 2020). Fisheries are susceptible to forestry practices because logging alters water properties, diminishes fish growth, and increases methylmercury in aquatic food webs. Sportfishing is an important activity in the economy and culture of boreal countries, generating in Canada, in 2018 alone, $3.5 billion CDN in income and supporting 58,000 jobs (Conference Board of Canada, 2019). Finally, many water-associated recreational activities, such as boating, kayaking, and swimming, are potentially impacted by logging. Brown lake water having a high DOC concentration is not considered a high-quality environment for water sports, and the increased nutrients in water may cause cyanobacterial blooms and liberate toxins harmful to humans. It is therefore essential to include considerations of freshwater ecology in the management of the boreal forest to achieve sustainable management goals.

Over the last decades, several tools and approaches have been developed in various parts of the boreal biome to minimize the impact of forestry practices on aquatic habitats, including riparian buffer strips, partial cutting (Fig. 29.4), and continuous cover forestry. Riparian buffer strips have served as the main silvicultural tool to preserve aquatic habitats from harvesting activities. The riparian strip is a physical barrier of vegetation and trees between uplands and rivers or lakes. This vegetation prevents or diminishes the input of organic and inorganic materials into the adjacent freshwater by reducing erosion and runoff (Kuglerová et al., 2014). Riparian strips also represent a refuge habitat for numerous groups of species and are used as a corridor to improve the connectivity across boreal landscapes (Barton et al., 1985; Machtans et al., 1996). Nonetheless, riparian strips are very vulnerable to wind exposure; therefore, their width and configuration must be modified in accordance with the topographic and forest stand conditions to guarantee their viability over the long term (Ruel et al., 2001). Partial cutting, where between 30 and 70% of the forest cover is logged, is also used as an intermediate disturbance to reduce the negative effects of logging on adjacent freshwaters (Montoro Girona et al., 2017, 2018; Moussaoui et al., 2020). One aspect that has been little studied is tree species composition and tree diversity around freshwaters and their role and impact on the

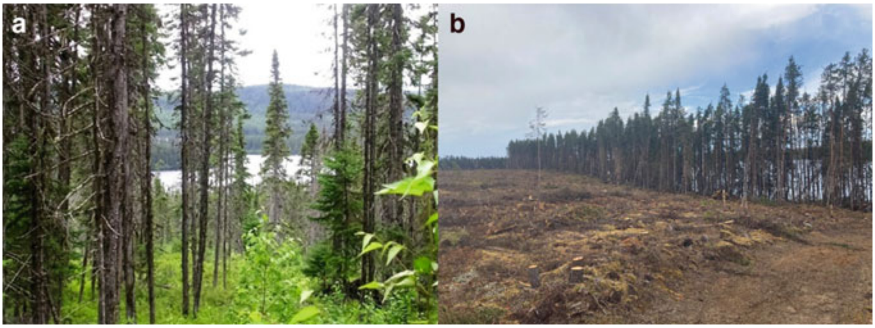

Fig. 29.4 **a** Partial cutting on the North Shore as part of the MISA experiment, Québec, Canada; **b** Forest buffers in a landscape in Abitibi-Témiscamingue, Québec, Canada. *Photo credits* **a** Miguel Montoro Girona, **b** Guillaume Grosbois

aquatic ecology. However, recent studies have suggested that species composition and diversity could play an important role (Kärnä et al., 2019; López-Rojo et al., 2019).

29.8 Conclusions

As boreal stands lie within a watershed, all natural and anthropogenic disturbances on the land within the watershed also influence the associated aquatic environments. Nonetheless, aquatic environments have been overlooked when assessing current silvicultural practices in boreal forests. In the sustainable management of the boreal forest, forestry operations emulate natural disturbances to reduce harvesting effects on forests. This approach also reduces the impact on freshwaters, as aquatic environments also experience the effects of natural disturbances on land, despite being largely untouched directly by anthropogenic disturbances. However, there remains a lack of information about the consequences of both natural and anthropogenic disturbances on aquatic environments. In this chapter, we have described the main effects of terrestrial changes to the watershed on aquatic habitats and how these changes in turn affect the forest. The complex interconnectivity between aquatic and terrestrial habitats should ultimately be included in the sustainable management of the boreal forest to preserve the health of the boreal biome. A healthy boreal biome will be crucial in mitigating climate change and managing the increased intensity and frequency of natural disturbances likely to heighten the vulnerability of freshwaters.

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