1 Streams and riparian forests depend on each other: a review with a special focus on

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8 **Highlights**

- The two-way dependency of streams and their riparian forests is reviewed
- We focus on biodiversity and ecosystem functions, including microbial processes
- Land use and climate change effects on riparian and stream ecosystems are discussed
- Potential management and protection practices are overviewed
- Future research questions are drawn together

14 Abstract

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In this review, we draw together the research on the two-way connection of streams and their riparian forests of the boreal zone from ecological points of view. Although the knowledge about stream-riparian interactions has increased considerably recently, in practice, riparian zones are still mainly seen as buffers for nutrient and sediment loading. However, recent research has shown that riparian forests disproportionately foster regional biodiversity and maintain stream ecosystem functions and diversity. On the other hand, streams contribute to riparian diversity and ecosystem functions. Microbes are key drivers of global biochemical cycles, and they also interact with plants and animals. The knowledge on microbial communities and understanding of processes they drive has considerably increased due to recent development in microbial profiling methods. However, microbes have been largely neglected in former reviews. Thus, this overview has a special focus on the role of microorganisms in controlling

stream-riparian interaction. We also review the land-use pressures that are threatening biodiversity and ecosystem processes of riparian zones in forested landscapes. In addition, we review the possible effects of climate change on stream-riparian interactions. Finally, we outline the research gaps that call for future research.

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Keywords: stream-riparian interface, ecosystem functions, biodiversity, riparian vegetation, reciprocal subsidies, microbial processes, flooding, forest management, nature protection, sediment and nutrient retention, decomposition, endophytes

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1. Introduction

Understanding the tight interlinkage between boreal streams and their riparian forests is necessary in order to preserve or improve the biodiversity of surface waters. The interaction needs to be acknowledged to manage forests in an ecologically sustainable manner near streams. Streams are sources of rivers (Vannote et al. 1980), thereby providing services to rivers by contributing to water quality and providing energy resources and enabling spawning grounds for fish (Freeman et al. 2007, Wipfli et al. 2007, Gomi et al. 2002, Wipfli & Gregovich 2002). Although small in size, streams contribute considerably to regional species pool and may act as reservoirs for river and lake organisms (Besemer et al. 2013, Clarke et al. 2008, Meyer et al. 2007). Riparian forests are transition zones which connect streams to upland forests (Naiman et al. 2005). Given that their occurrence is limited to near-stream locations, the area of riparian forests is small compared to that of upland forests. However, they have a disproportionate influence in maintaining biodiversity and ecosystem processes. First, streams are closely associated with their riparian forests, and the two ecosystems depend on each other hydrologically and ecologically. This is especially true for small headwater streams that rely on riparianbased energy sources. Second, riparian forests often have distinct assemblages of plants and invertebrates, which differ in their composition from upland forest assemblages, increasing regional

biodiversity (Kuglerová et al. 2014a, Selonen et al. 2011, Rykken et al. 2007a, Sabo et al. 2005). In addition, streams and their riparian zones serve as dispersal routes and corridors for many terrestrial and aquatic taxa, being integral parts of the landscape in augmenting organisms' movements between sites (Ament et al. 2014, Tonkin et al. 2018).

The interest in stream-riparian interactions in forested landscapes dates back to 1970's when it was realized that forest management based on clear-cutting severely impacted surface waters and forest soil (e.g. Brown 1973). Although the knowledge about stream-riparian interactions has increased, and the multiple ecosystem services provided by riparian forests are now being acknowledged by scientists, forest managers still mainly see riparian zones as buffers for nutrient and sediment loading. Riparian forests of small streams are not included in international directives and we still lack common protocols for their management. The use of stream riparian areas in some countries is restricted by national acts, yet there is huge variation among nations on how and to what extent riparian forests are considered in legislation (Ring et al. 2017, Lee et al. 2004). Because legislation acknowledges only a small proportion of riparian sites as conservation units, if any, the protection of streamside forests depends heavily on land owners' will. Some countries (e.g. Finland) offer a monetary incentive for the land owner for leaving a predefined stripe of a near-natural riparian forest uncut to enhance the protection of woodland key habitats (Timonen et al. 2010). In addition, forest certificates guide riparian forest management of small streams and even define the width of buffers, but also these buffers vary a lot among countries (Piirainen et al. 2017).

The close interactions between streams and riparian forests make the two inseparable. In this overview, we aim to highlight the two-way connection of streams and their riparian forests from an ecological point of view. We focus on the boreal zone, although many aspects apply also to temperate streams. By "streams" we mean fluvial channels with up to 100 km² catchment area and which have permanent water-flow. We assumed that a catchment of 100 km² would equal approximately to stream orders 1 to

3 (Strahler 1957). We refer to orders 1-2 as headwaters and to order 3 as mid-sized streams. These approximately resemble stream mean width under 2.5 and 7.5 meters, respectively (Downing et al. 2012). Some variation, however, may exist in stream order and width depending on regional features (such as the presence of headwater lakes). Large streams from order 4 onward are not considered in this review. Research on stream-riparian interactions has mostly focused on exchange of nutrients and material from land to streams and vice versa. In this overview, we include other processes and aspects of diversity that are important in shaping stream-riparian interactions, such as those including microbes and environmental forces. Although microbial community structure and processes largely drive the diversity and functioning of higher organisms, former reviews about streams or riparian interface have largely neglected the microbial point of view (e.g. Richardson 2019, Wohl 2017, Richardson & Danehy 2017, Hjältén et al. 2016). Particularly, a holistic understanding of the drivers of microbial community dynamics and the relationship between biodiversity and functioning of microbes is lacking (e.g. Ledesma et al. 2018). We aim to draw together the main points of stream-forest association and underline the importance of protecting streams and their riparian forests and maintaining the linkage between the two. We further describe in more detail the drivers of riparian biodiversity and how it is affected by anthropogenic pressures. Finally, we draw together the main aspects that should guide riparian management and protection and define future research needs.

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2. Ecosystem services provided by riparian forest to streams

In the boreal zone, riparian forest floor is often peat dominated, but the thickness of the peat layer varies due to climate and small-scale environmental variation. Peat layer thickness and vegetation affect the processes on the riparian forest that are the drivers of ecosystem services provided by riparian zones to streams. Sediment, organic matter, nutrient (Pinay et al. 1992) and metal (Lidman et al. 2014) retention capacity of riparian zone depends on soil type, vegetation, topography and hydrology of the riparian area. Streams are hydrologically connected by three-dimensional water flux: within the channels (longitudinally), between riparian zones and channels (laterally) and between surface water

and groundwater (vertically; hyporheic flow), all of which affect the fluxes of material in to stream network. In this review, we focus on describing fluxes across the lateral dimension. Riparian zones are situated on low elevation areas in the end of terrestrial hydrological flow paths. They receive and process considerable amounts of water, organic matter (OM), organic carbon (OC), nutrients and elements from the catchment, thus, they are considered as hotspots for biochemical processes (McClain et al. 2003). Microbes are key drivers of biochemical cycles metabolizing elements and organic compounds, which may be stored into plant biomass and bulk soil or carried to the stream channel.

2.1 Sediment retention and erosion prevention by riparian zone

Sedimentation is caused by bank erosion or transportation of sediments from riparian or upland forest.

Sedimentation may reduce the survival of stream organisms and alter community composition

(Tolkkinen et al. 2016), biodiversity (Annala et al. 2014, Izagirre et al. 2009) and productivity (Annala et al. 2014, Cardinale et al. 2002, Parkhill & Gulliver 2002). Roots of plants in the riparian zone stabilize the ground and thus prevent erosion. In forests, natural sedimentation of stream beds is usually low compared to that of less vegetated landscapes, although streams with riparian zones that have thin peat layer can also be sandy in the boreal zone. Further, drought or spring snow melt may significantly increase bank erosion (Wood & Armitage 1999, Naiman 1982).

2.2 Organic matter and carbon retention capacity of riparian zone

On a global scale, carbon processing rates in the riparian forests and streams are determined by temperature and precipitation (Tiegs et al. 2019). The hydrology of the riparian zone has a key role in determining the flux of OM and associated OC to the stream (Fiebig et al. 1990). OM may leach to a stream due to land use near the stream or in the catchment. High loads of OM my cause brownification of waters, which may further impair invertebrate diversity (Astorga et al. 2011), microbial community composition and functions (Wagner et al. 2015), and fish abundance (Hedström et al. 2017) locally or at

downstream reaches. Therefore, the OM retention capacity of riparian soil, i.e. the capacity to prevent organic substances draining to the stream, is an important ecosystem service needed to maintain stream functioning and biodiversity in a natural state.

OM retention capacity is maintained by vegetation forming OM traps together with soil microbes and invertebrates decomposing OM into simple particles, which eventually forms soil. Decomposition rate is controlled by soil moisture and temperature (Coûteaux et al. 1995, Singh and Gupta 1977), soil texture (van Deen & Kuikman 1990) and litter quality (Coûteaux et al. 1995). Fungi are often considered as the dominant decomposers on land, especially in acid soils and soils experiencing frequent drying-wetting dynamics (Bapiri et al. 2010, Yuste et al. 2011), while bacteria may overtake decomposition in circumneutral-alkaline and arid soils (Rousk et al. 2010). However, this pattern is not self-evident (see a review by Strickland & Rousk 2010). In riparian forests lower soil carbon:nitrogen (C:N) ratio may give competitive advantage to decomposer bacteria over fungi (Högberg et al. 2007, Fierer et al. 2009, Brockett et al. 2012), although this likely depends on the overall nutritional status of the habitat (Kyaschenko et al. 2017b). In addition to environmental factors, soil fungal community composition has been identified as an important controlling factor of OM storage in humic soil (Kyaschenko et al. 2017a).

The net balance of C along a stream network depends on terrestrial C gains, biological consumption of C, and inorganic processes such as outgassing of CO² (Dawson et al. 2004). Because groundwater table is shallow near headwater streams, these small streams likely receive terrestrial OC from riparian zone via subsurface pathways rather than from upland sites (Mei et al. 2012). However, upland sites may be principal sources of OC for headwater streams with adjacent hillslopes and those that have shallow bedrock near the channel (Gannon et al. 2015). The amount of OM fluxes may also depend on catchment type as shown by a long-term study from northern Sweden, where fluxes of terrestrial OM at baseflow were positively correlated with the proportion of wetlands in the catchment (Laudon et al. 2011). Increased discharge, due to for example heavy rain events, may further increase the flux of

riparian OC to streams (Lambert et al. 2011). Differences exist also in inorganic C sources of low and high order streams. Headwater streams may receive most of their inorganic carbon, namely CO₂, from the riparian zone, where it is formed by soil respiration (Winterdahl et al. 2016). Higher order streams, in turn, more likely gain inorganic C from in-stream processes, where DOC is turned into CO₂ in aquatic mineralization processes (Moody et al. 2013).

2.3 Riparian-based organic matter in streams

In streams, benthic microbial communities (Kreutzweiser & Capell 2003) together with benthic invertebrates may utilize OM effectively, controlling the flux and concentration of terrestrial OM and OC further downstream (Dawson et al. 2001). Terrestrial OM is important for the biodiversity and ecosystem functions of streams. As implicated by the River Continuum Concept (Vannote et al. 1980), headwater stream invertebrate communities usually depend on allochthonous energy resources (Cummins et al. 1989), which end up to the stream as dissolved and particulate organic matter (DOM and POM, respectively). Main source of coarse POM (CPOM) from riparian forest is leaf litter, but also pieces of other plants and terrestrial invertebrates enter the stream. Benthic invertebrate shredders are the main macroscopic consumers of leaf litter in streams (Cummins et al. 1989, Hieber & Gessner 2002). The major product of decomposition is fine POM (FPOM), which is then carried downstream where it is further consumed by microbes and invertebrates (Webster et al. 1999).

In addition to shredders, microbes, especially hyphomycete fungi, are important consumers of leaf litter in streams (Hieber & Gessner 2002, Gessner et al. 1999, Bärlocher 1992). Microbial processing is thought to be an essential phase of litter decomposition, because it is assumed to make leaves more palatable for invertebrate consumption due to changes in leaf matrix composition (Graça 2011, Rossi 1985). On the other hand, microbes can be seen as potential competitors for shredders as they use same the energy resource (Gessner et al. 1999).

Moreover, endophytic fungi, which colonize living leaves before abscission, may contribute to litter decomposition on land (Voříšková & Baldrian 2013, Koide et al. 2005) and in streams (Koivusaari et al. 2019, Wolfe et al. 2019, Mustonen et al. 2016, LeRoy et al. 2011). This may also hold true for endophytic bacteria, because they too can carry glycoside hydrolases genes, which encode enzymes required for decomposition of OM (Berlemont & Martiny 2016). The contribution of hyphomycete fungi to litter decomposition in streams may depend on hydrological factors. Mustonen et al. (2016) showed that endophytes were the main decomposers of stream litter in slow-flow experimental outdoor channels. Similarly, Wolfe et al. (2019) found litter infected by the endophyte *Rhytisma* decay faster than lesion-free litter in a third-order stream in a mixed conifer and hardwood forest. On the other hand, endophytes have ability to slow down decomposition rates on land (Omacini et al. 2004) and in streams (LeRoy et al. 2011) depending on endophyte identity and/or stream flow velocity. There are various possible ways how endophytes may control litter decomposition (e.g. by inhibiting other microbes), yet the underlying mechanisms are not currently well understood.

Decomposing biota primarily control decomposition rates, but their efficiency is codetermined by environmental factors such as litter quality (Cornut et al. 2015, Ferreira & Chauvet 2011a, Leroy & Marks 2006), trophic state of the stream (Ferreira et al. 2015, Ferreira & Chauvet 2011b), water chemistry (Mykrä et al. 2019, Tolkkinen et al. 2015, Suberkropp & Chauvet 1995) and temperature (Martínez et al. 2014, Ferreira & Chauvet 2011a, 2011b). Riparian diversity may affect leaf breakdown rates in streams because litter species composition and quality influences leaf processing rates (Fernandes et al. 2012, Schindler & Gessner 2009, Swan & Palmer 2006, Swan & Palmer 2004). This impact can be mediated through changes in invertebrate (Leroy & Marks 2006) and microbial (Fernandes et al. 2013) diversity or due to differences in riparian forest composition (Kominoski et al. 2011).

2.4 Metal retention capacity of riparian zone and toxicity of metals

Drainage of OC and elements to streams are often related, because many elements have high affinity with organic compounds (Lair et al. 2007, Mierle & Ingram 1991). Peat soils may prevent the fluxes of trace metals to streams more effectively than mineral soils (Lidman et al. 2014). Stream water chemistry determines bioavailability and toxicity of metals to organisms. In general, the more acidic and softer (lower concentration of calcium and magnesium) the water is, the lower concentrations of metals are needed to produce toxic effects on organisms (Paquin et al. 2000). Dissolved and particulate OC (DOC and POC, respectively) bind metals decreasing their bioavailability. Thus, in humic streams, organisms may not be as prone to toxic effects as in streams acidified due to, for example, acid sulfate soils or sulfate-rich bedrock. The latter can also decrease water pH more than OC. Ultimately, whether metals produce toxic effect on organisms or not, depends on organisms` sensitivity to metals. Metal contamination due to land-use changes may affect aquatic communities (Tolkkinen et al. 2016) and food-webs (Hogsden & Harding 2012).

Trace metals, draining from upland or flushing with flood, may accumulate on riparian zone, potentially making the riparian soil toxic for some plants. On the other hand, high affinity of metals with OM may decreases their bioavailability in the riparian zone (Lidman et al. 2017). Some plants, with the help of microbial symbionts, have the ability to accumulate metals in their shoots, thus avoiding toxic effects (Khan et al. 2000). Further, mychorrizal fungi, which form symbiotic relationships with their host plant, have ability to either inhibit (Hildebrandt et al. 2007) or exacerbate (Killham & Firestone 1983) toxicity of metal-polluted soil on the host plant. An example of such metal-tolerant fungus is *Suillus* Gray, 1821 from order Boleatus, a common genus in Northern Hemisphere, which contribute to the survival of their host trees (Pinaceae) on metalliferous soils (Colpaert et al. 2011). Forest soil bacterial communities may be able to adapt to metal pollution, presumably via changes in community composition (Pennanen 2001), yet their functional activity may decrease despite adaptation (Frey et al. 2006). However, relatively little is known how changes in microbial communities affect their processes.

2.5 Nutrient retention capacity of riparian zone

Because of their position between stream and upland sites, riparian zones play a major role in chemical processing (Ledesma et al. 2013) and controlling stream nutrient status and pH. Because riparian soil in boreal forests is usually rich in OM, it also tends to accumulate nutrients and trace metals. However, as the riparian zone can be a source of OM for streams, especially for small streams, it may be a source of those nutrients that tend to bind with OM (Lidman et al. 2017). The input of alkaline elements may prevent stream from acidification.

Vegetation and microbes are the primary consumers of soil nitrogen (N) and phosphorous (P), which are the main nutrients controlling ecosystem productivity in terrestrial and freshwater ecosystems (Aerts & Chapin III 1999). Denitrification, is often higher near river channels compared to upland forests (Hill et al. 2000, see also a review by Hill 1996), because the anerobic conditions in the wet ground enable the reduction of nitrate to nitrite and, eventually, to gaseous N forms (Tiedje 1988). Hill (1996) suggests that in watersheds with low drainage of nutrients, riparian forests may act as a nutrient source or sink to the stream depending on the potential redox conditions. In watersheds with relatively high nutrient drainage, riparian zone may act as a nutrient sink (Mulholland 1992).

Hedin et al. (1998) identified narrow near-stream zone as functionally the most important location for denitrification in riparian zone despite low DOC levels. This may be a consequence of, for example, unexceptionally high root mass in the soil. In their review of microbial "hotspots" and "hot moments" Kuzyakov & Blagodatskaya (2015) go further to microscale and point out that soil microbial activity is highly heterogenous in space and time. In hotspots, such as rhizosphere and detritusphere, microbial activity can be two to 20 times higher than in the bulk soil (Blagodatskaya et al. 2009, Blagodatskaya et al. 2014). Also, seasonal variation may affect the effectiveness of riparian forest to retain nutrients (Pinay et al. 1993), thus studies conducted at different seasons may produce highly variable results.

BOX 1. Microbial community profiling with molecular methods

Microbial communities can be extensively studied with modern molecular methods, so-called 'omics' (see Franzosa et al. 2015 and Knight et al. 2018). In this review we will concentrate on nucleic acid-based methods, i.e. marker gene, metagenome and metatranscriptome sequencing, which can be used for **taxonomic and functional microbial community profiling** answering questions: "who is there?" (using genomic DNA as a template), "who is active?" (ribosomal RNA; rRNA) and "what are they doing?" (messenger RNA; mRNA). Taxonomic studies are usually based on DNA, while functional genomics include both functional potentials (DNA-based metagenomics) and functional activities (RNA-based metatranscriptomics).

Shotgun and amplicon-based marker gene, metagenomic and metatranscriptomic sequencing studies involve extraction of total DNA and/or RNA from the community samples. In RNA-based studies, this is generally followed by mRNA enrichment to remove rRNA (which is around 80% of total RNA) and synthesis of RNA to complementary DNA (cDNA).

Typically, amplicon sequencing is based on single gene such as the bacterial 16S and fungal ITS or 18S rRNA gene region, which is amplified in PCR with specific primers. Shotgun sequencing instead gives millions of random genomic fragments from a studied microbial community that can be assembled into longer sequence reads (contigs). Acquired amplicon and shotgun sequence reads are then matched to reference databases and used for downstream analyses.

Challenges in molecular methods: In amplicon-based marker gene analysis, selecting primers that target all the taxa of interest is a challenge, while in shotgun-based studies the challenge is building contigs from complex environmental samples. In both, amplicon and shotgun-based methods, very short sequence reads may not be reliably matched. Still, the biggest problem with the 'omics' is the incomplete databases suffering from the missing reference species and functional genes, as for example 30-50% of the encoded proteins by any given genome are still unknown or incorrectly annotated, especially for taxa found from less well-studied environments. The problem may be even larger with the methods relying on whole genome reference databases or in pathway-reconstruction depending on species-specific databases.

Recommendations for the future: Combining different 'omic-methods' (including also proteomics and metabolomics) gives enhanced and more reliable results, e.g. by covering some of the weaknesses of the others. These 'multi-omics' studies can be used to acquire a more profound biological understanding and can be used to support new hypotheses. Also, combining traditional cultivation and modern molecular methods could provide new insights into life of microorganisms. However, microbiome studies with molecular methods acquire a careful planning all the way from the study setup, sampling, choosing the most appropriate 'omic-methods' (e.g. primer selection and sequencing platforms) to bioinformatics and statistical analyses.

2.6 Riparian control on stream microbial diversity

Although the development of molecular methods (Box 1) have made microbial profiling much easier, faster and cheaper than before, our knowledge on freshwater bacteria (Zwart et al. 2002) and fungi (Grossart et al. 2006) is still rather scarce compared to that of some other biotic groups, for example, benthic invertebrates. Especially microbial studies linking the aquatic and terrestrial ecosystems are lacking. However, there is evidence that the type of soil-originating DOM can affect aquatic microbial productivity (Berggren et al. 2009), which may be mediated through shifts in bacterial community compositions (Judd et al. 2006). Possibly also aquatic fungi are affected, but they have not been studied in this regard. DOM from the riparian soil originates mostly from plants (Wang et al. 2014). As OM quality and quantity depend on the quality (identity) and quantity of terrestrial plants, riparian vegetation potentially has a strong control of aquatic microbial communities. In addition, genetic variation affects the variability of phenotypic traits in plants having ecosystem-level effects (Hughes et al. 2008). For example, genetic variation can be realized as effects on community structure, species interactions, recovery from disturbance, primary production and decomposition (Hughes et al. 2008, Whitham et al. 2006), and can be detected also in streams (LeRoy et al. 2006).

Microorganisms originating from land can contribute significantly to richness, and possibly composition, of microbial communities in aquatic ecosystems, especially in streams, which are highly connected to land (Ruiz-Conzales et al. 2015). The relationship between riparian and stream microbial communities is, however, still poorly understood. Plant species (Carney & Matson 2006, Marchner et al. 2001, Borga et al. 1994) and soil properties, such as pH (Moon et al. 2016), can select for certain microbes in terrestrial habitats, and this may also hold true for aquatic environments. For example, certain terrestrial plants can favor fungi over bacteria (Bardgett & Walker 2004), which in turn may play a role in structuring aquatic microbial communities.

2.7 Terrestrial invertebrates in stream food-webs

The amounts of terrestrial invertebrates entering the stream are determined by riparian tree composition, especially to the amounts of deciduous trees in riparian forest. Deciduous forests support significantly greater fluxes of invertebrates from land to stream compared to coniferous forests (Inoue et al. 2013, Wipfli 1997). Terrestrial prey input is relevant for stream fish and predatory invertebrates, as they may depend nutritionally on terrestrial subsidies. Food consumed by stream fish may comprise 30-90% of terrestrial invertebrates (Inoue et al. 2013, Wipfli 1997), with a positive feedback on their growth (Gustafsson 2011). The effect may cascade further down the food-web due to predatory-release of aquatic invertebrates. For example, Nakano et al. (1999) experimentally prevented terrestrial invertebrate fluxes to stream, which shifted fish to feed on aquatic grazers, consequently leading to increased periphyton production. England and Rosemond (2004) showed that even a small reduction in riparian forest tree cover may significantly alter the food-web of aquatic consumers that are dependent on terrestrial subsidies.

2.8 Physical effects of riparian forest to stream

Riparian forests affect stream biodiversity and functions also physically. Because headwater streams are narrow, they are more shaded than rivers due to more closed canopy cover. Riparian trees thus have a great control on stream water temperature (Richardson & Danehy 2007, Moore et al. 2005). Also, groundwater input from hyporheic zone or the upland forest cools down stream water (Boulton & Hancock 2006). Canopy cover may affect stream diversity by controlling primary production (Mosisch et al. 2008, Hawkins et al. 1982, Murphy et al. 1981), water temperature (Moore et al. 2005) and litter input (Melody & Richardson 2004, Wallace et al 1997). The proximity of trees near streams enable falling of branches and trunks in to the channel. In-stream deadwood originating from riparian forests contributes to decomposition efficiency by trapping and accumulating leaves on the stream bed (Flores et al. 2011), thus extending the retention time of leaves in the stream. Accumulation of leaf litter to the

stream bottom may be particularly relevant in northern streams, where ice sheet and snow in the riparian zone prevent fluxes from land to water during winter.

3. Riparian forest diversity depends on the stream

Streams can shape riparian diversity by forming a disturbance regime on the riparian zone, by assisting the dispersal of riparian species and by offering subsidies for riparian food-web. Also, groundwater affects riparian diversity and although it is not strictly a mechanism caused by the stream, it is characteristic for stream riparian zones due to their low topographic position in the catchment. We first explain, why riparian diversity differs from that of upland forest and then describe in more detail the mechanisms by which the stream affects riparian diversity. Finally, we discuss the effects of the stream on riparian microbiome.

3.1 An overview of riparian diversity

Riparian zones may support more species than the upland landscapes. Studies have shown riparian habitats to be important at least for bird (Bennet et al. 2014, Mosley et al. 2006, Whitaker & Montevecchi 1999, Darveau et al. 1995) and plant (Pollock et al. 1998, Kuglerova et al. 2014a) diversity and dispersal. Even if riparian species richness does not exceed that of upland sites, the biotic communities differ in their composition (Sabo et al. 2005). Riparian zones support species that either prefer or withstand moist conditions, thereby increasing regional species richness (Kuglerová et al. 2014a, Selonen et al. 2011, Dynesius et al. 2009, Rykken et al. 2007a, Zinko et al. 2005). Soil can be moist due to groundwater input from upland sites or shallow groundwater table near the stream, or due to inundation by flooding waters. While the role of groundwater is usually more evident in headwater streams, flooding is more important in medium sized streams. In both cases, soil moisture tends to increase near-stream biodiversity, because different species inhabit wetted ground compare to drier sites. The mechanism is different, though. The proximity of groundwater wets the ground year-round

and increases pH and N availability (Kuglerová et al. 2014a), thus favoring some species of bryophytes and vascular plants over others. Flooding, on the other hand, causes disturbance and temporal inundation offering habitat for moisture dependent or resistant species that may be poor competitors in more stable conditions. While upland forest may consist of only one to few tree species, riparian zones of typically support a high species richness of trees, especially deciduous ones, which tend to form a zonation from reach to upper forest (Ward et al. 2002), especially in medium-sized streams.

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3.2 Effects of stream flooding and ice on riparian forest

Stream flooding shapes riparian diversity by creating a disturbance regime in the riparian zone. Climate, stream channel morphology, bank slope, groundwater discharge, and proximity of lakes determine the extent of stream flooding, which is typical for medium-sized (and bigger) streams. Precipitation and seasonal shifts in temperature affect the magnitude and duration of floods and the formation and melting of ice and snow. The effect of floods and ice on riparian zone is significantly different in a Vshaped stream valley with steep bank slopes compared to U-shaped valley with only moderate slope. Flooding can be an important, even fundamental, mediating factor of the diversity of riparian vegetation (Garssen et al. 2015, Lind & Nilsson 2015). As initially hypothesized by Connell (1978), intermediate disturbances should maintain highest biodiversity by promoting competitive release. In theory, intermediate flooding should thus create space for stress-tolerant species with low-competitive abilities and for pioneer species (Lind et al. 2014b). Accordingly, some field studies have found species richness to peak at intermediate flooding (Pollock et al. 1998, Townsend et al. 1997). However, local conditions, especially site productivity, determine the response of communities to disturbances, and thus environmental gradients should be considered when evaluating disturbance effects on diversity (Huston 2014). Furthermore, the scale at which diversity effect is evaluated should be considered carefully, because positive diversity effects at intermediate levels of flooding may be detectable more readily on large (hectares) than on small (square meters) scale (Pollock et al 1998). Due to flooding, riparian ecosystems are often highly variable in space and time. Because of frequent disturbances, riparian

communities can be considered highly resilient to natural perturbations, but it does not automatically make them resistant or resilient to anthropogenic disturbances, which are usually fundamentally different from natural ones.

In the northern hemisphere, ice is an important factor mediating riparian diversity (Lind et al. 2014a, Lind et al. 2014b, Engström et al. 2011). About 60% of the major river basins north of the equator experience ice processes during winter (Allard et al. 2011). Thus, the ecological importance of ice cannot be neglected. In small boreal streams, the formation of anchor ice promotes flooding (Beltaos 2008), which in turn can increase riparian vegetation diversity. While detrimental to individual plants, ice creates space for early successional species by ripping off vegetation during ice melt; thus, its effect is similar to that of flooding.

3.3 Stream as a dispersal corridor for riparian species

Species richness and assemblage composition in a given stream or riparian location is determined by the sum of environmental preferences, dispersal ability and other traits of the species (Tonkin et al. 2018, Heino et al. 2015, Leyer and Pross 2009, Hérault and Honnay 2005). Stream channel is an important dispersal corridor for passive dispersal of plants and their seeds (Kuglerová et al. 2015, Nilsson et al. 2010). Some studies suggest that seeds of riparian plants are more often adapted to floating than upper-forest species (Johansson et al. 1996, Lopez 2001), which implies that their dispersal success may be dependent on the transport capacity of the stream (Merritt & Wohl 2002, Jansson et al. 2000). The potential for transporting seeds and vegetative parts varies among streams due to differences in channel morphology and vegetation cover (van Leeuwen et al. 2014, Riis and Sand-Jensen 2006), magnitude of discharge (Nilsson et al. 2010) and water level (van Leeuwen et al. 2014). Jansson et al. (2005) and Merrit et al. (2010) showed in their studies in Swedish rivers that dispersal by water significantly increased the diversity of riparian plant species. However, hydrochory may be more important for the occurrence of species in larger streams compared to the smallest headwater streams

(Kuglerová et al. 2015), presumably because headwater populations do not have source populations upstream, and because they must rely on dispersal modes other than hydrochory. Water dispersal may be also relevant for other riparian organisms (e.g. fungi) as shown by a recent study (LeBrun et al. 2018).

3.4 Subsidies from stream to riparian forest

While terrestrial-to-aquatic subsidies concern mainly the flux of detritus, emerging aquatic insects dominate subsidies from water to riparian zone (Bartels et al. 2012). Insects emerging from the streams are consumed by riparian insectivores, and they are also a nutrient source for riparian plants and microorganisms (Dryer et al. 2005). Although benthic production of streams exceeds that of lakes, streams and rivers can support significantly lower fluxes of prey to land compared to ponds and lakes (Gratton & Vander Zanden 2009). That said many studies have shown that bottom-up effects initiated by aquatic prey can have major impacts on riparian ecosystems, contributing 25 to 100% of energy sources to spiders, lizards, birds and bats (Baxter et al. 2005). However, most studies are from the temperate zone, and it would thus be beneficial to gain more knowledge from the boreal zone.

3.5 Stream effects on riparian microbiome and related processes

Literature about the effects of stream hydrology and ecology on microbial process rates in the riparian zone is scarce, and riparian zones are widely variable regarding to, for example, moisture and nutrient status, which makes generalization difficult. However, biochemical processes in the riparian zone may be more stable than in the upland forest due to closeness of a permanent stream and associated relatively stable microclimate conditions, although we did not find any studies related on the subject. On the other hand, changing hydrology due to land-use change can have unpredictable effects on riparian processes, which may become detectable only in the long term (e.g. Bardgett et al. 2001). Further research is needed on how protecting stream flooding regimes, groundwater discharge and natural vegetation could contribute to the maintenance of biochemical processes in the riparian zone.

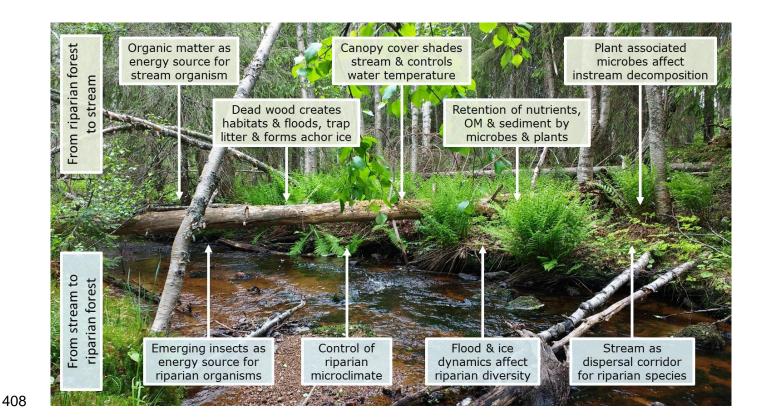


Figure 1. Main reciprocal effects in a stream and its riparian forest. Boxes with arrows indicate the direction of the effect, either from the riparian forest to the stream (light green boxes) or from the stream to the riparian forest (light blue boxes).

4. Human impact on riparian and stream ecosystems

Extensive land use and modification of stream channels have led to dramatic decline of natural riparian habitats (Richardson et al. 2007). Multiple pressures due to land management are threatening biodiversity and ecosystem processes in riparian zones. These pressures include forestry, drainage ditching, agriculture, grazing and invasion by alien species. Land use has been identified as the most influential pressure affecting biodiversity (Sala et al. 2000). Streams may be the most sensitive aquatic ecosystems towards human impact, given their topographically low position in the catchment (Richardson 2019). Channelization and damming of streams and rivers can affect freshwater and riparian zone diversity. Anthropogenic land use near streams can change riparian microclimate conditions and enable invasion by alien species, which translate into changes in species composition and may

subsequently affect ecosystem functions. If ecosystem functions are changed, it is possible that the consequences accumulate downstream and extend into riparian forest.

4.1 Effects of riparian land use on stream and riparian diversity and ecosystem functions

In this review, we only consider forestry-associated land use effect, and thus urban and agricultural impacts are beyond our consideration, for example. Forestry associated impacts include physical and chemical modification of streams and riparian forests, potentially leading to changes in biotic communities, and eventually to depauperate ecosystem functions.

4.1.1 Stream warming

Removing mature trees from riparian zone predisposes streams to warming directly and through warming of exposed spring waters (Kreutzweiser et al. 2009, Brown & Krygier 1970). Possible warming of the stream water depends on the site characters and the weather conditions following the time of logging. Headwater streams that rely on direct input of groundwater may not be as prone to warming (Mellina et al. 2002) as larger streams. On the other hand, wider streams are naturally less shaded than narrow ones, thus the temperature of headwater streams may be more susceptible to forest harvesting compared to higher order streams. The recovery from possible warming following forest harvesting varies a lot among streams and can take up to ten years (Moore et al. 2005). Warming may change the structure of stream communities (Piggott et al. 2015, Ryan & Ryan 2006, Quinn et al. 2004) and eventually the function of the stream. For example, increasing solar radiation accelerates primary production (Kiffney et al. 2004, Boothroyd et al. 2004, Feminella et al. 1989) and decomposition (Ferreira & Canhoto 2015, Ylla et al. 2014, Ferreira & Chauvet 2011), and can result in eutrophication and emission of CO₂ from streams (Acuña et al. 2008).

4.1.2 Stream water chemistry

Stream water quality is compromised in forest harvesting, because extensive cutting and site preparation often increase stream DOC levels in headwaters (Schelker et al. 2012). Clear-cutting leads to rapid increase in spring snow melting and runoff potentially increasing nutrient, element and sediment flow to streams (Schelker et al. 2013). In addition, drainage of even-aged peatland forests is a common practice in northern countries. It lowers the groundwater table enhancing tree growth, but at the same time it causes nutrients, suspended solids and sediment load to streams (Nieminen et al. 2017, Stenberg et al. 2015, Marttila & Kløve 2010) leading to depauperate biotic communities due to simplification of habitat structures (Vuori et al. 1998, Vuori & Joensuu 1996), brownification (Hayden et al. 2019, Haaland et al. 2010, Evans et al. 2005) and eutrophication (Hayden et al. 2019, Marttila et al. 2018).

Furthermore, ditch network maintenance poses similar threats to streams as new ditches (Nieminen et al. 2018a, Joensuu et al. 2002).

4.1.3 Aquatic diversity and functions

Removing trees, especially deciduous ones, from the riparian zone decreases the input of leaf litter and wood to the stream, which means less energy sources for decomposers, less traps for leaf retention and less variable habitat for microbes, algae, plants and invertebrates. These may lead to a decline in diversity, abundance and/or biomass of decomposer communities (Johnson et al. 2003, Wallace et al. 1997). Community changes may further decrease ecosystem stability (see the discussion in Bengtsson et al. 2000 and Cardinale et al. 2012) and lead to impaired stream functions, for example, decreased decomposition. In-stream decomposition can be extremely sensitive to land use in the riparian forest (Lecerf & Richardson 2010), but also upland land use changes can be detectable in such processes (Kreutzweiser et al. 2008a). On the other hand, clear-cutting near a stream can increase in-stream decomposition rate with a time lag if it leads to increased deciduous tree abundance in the riparian zone, increased nutrient load to the stream and/or increased mechanical fragmentation of litter due to higher sediment loads (Benfield et al. 2001, McKie & Malmqvist 2008).

Because riparian plant diversity affects stream microbes (Judd et al. 2006), any change in riparian vegetation – species composition, biomass, age structure and/or species ratio of riparian trees – may change stream assemblage compositions and functions through bottom-up effects on the food-web (Bartels et al. 2012, Inoue et al. 2013, Kominoski & Rosemond 2012, Kominoski et al. 2011, Sweeney et al. 2004).

4.1.4 Dispersal of aquatic species with terrestrial adult stages

Catchment-scale vegetation loss may also limit stream-organism dispersal, especially for species that have terrestrial adult stages (Smith et al. 2009), although there is no firm evidence of such from forested catchments. Headwater streams are situated at the top of the river network and suitable source populations are not always found upstream, thus populations may rely on dispersal via land or from source populations downstream (Tonkin et al. 2018). Their colonization success depends on their dispersal abilities and on distance between suitable habitats (Sarremejane et al. 2017). Particularly, the dispersal of caddisflies, stoneflies and mayflies is mostly dependent on adult flying stages (Bunn & Hughes 1997); hence forest habitat fragmentation may impact their population dynamics. Especially populations depending on nearby source populations and dispersal over-land, may be in jeopardy if dispersal is restricted due to land use changes (Heino et al. 2017).

4.1.5 Riparian diversity

In theory, riparian organisms may be more adapted to disturbances than upland-dwelling ones, and they may be more effective in re-colonization and re-establishment, because they can more readily take advantage of water-assisted dispersal (Johansson et al. 1996, Lopez 2001). This is especially the case if suitable source populations exist upstream. However, if species disappear after anthropogenic disturbance, they may not be able to recolonize denuded locations (Dynesius et al. 2009). For example, species depending on old-growth forest may not have suitable source populations in nearby areas.

Moreover, riparian vegetation removal may be too severe disturbance to overcome, because it reduces suitable habitat for riparian and semi-aquatic species. For example, riparian vegetation loss is a threat to web-spinning spider abundance and diversity because it reduces habitat for web sites (Laeser et al. 2005).

Tree removal in or near the riparian forest leads to drying of microclimate due to exposure to sun and wind (Oldén et al. 2019). Such changes in microclimatic conditions may affect especially species that are specialized to occur in moist riparian habitats, yet this likely depends on species` ecology and site characters. Species attracted to convex surfaces (e.g. logs, stumps or boulders) can have high mortality in uncut buffers due to edge effect caused by clear-cutting (Oldén et al. 2019, Hylander et al. 2005). On the other hand, some riparian organism groups may be more tolerant toward disturbance at sites with rough ground, which have concave surfaces (e.g. stony sites). Species attracted to concave surfaces may be unaffected by edge effect, because of the ability of the uneven ground to maintain moist conditions (Dynesius et al. 2009, Hylander et al. 2005, Hylander et al. 2004). However, in other cases species of concave surfaces have decreased due to logging (Oldén et al. 2019). If soil tillage is practiced in the riparian forest, the potentially beneficial effect of concave forest floor is lost.

4.1.6 Riparian microbes and microbial processes

Forest harvesting, especially clear-cutting, may affect microorganisms via changes in nutrient availability, microclimate conditions and root dynamics. Although most research has been conducted in upland forest rather than in the riparian zone, here-in we assume, that the microbial processes are pretty much similar in upland and riparian forests, if the differences in environmental conditions (such as soil moisture and microclimate) are considered. Logging impacts on soil nutrient cycling and flux to streams depends on soil type, site conditions, catchment hydrology, post-logging weather patterns, and type and season of harvesting (Kreutzweiser 2008b). Often soil N, P and possibly potassium (K) are increased after harvesting, because of decreased/ceased tree root nutrient uptake, increased erosion

and leaching, and increased mineralization and nitrification rates (Hynes & Germida 2013). However, removing logging residual may lead to negative effects on soil productivity and decrease in soil nutrient pools compared with stem-only harvesting and decrease decomposition (Thiffault et al. 2011). Also, clear-cutting effects on microbial dynamics vary among sites. While microbial biomass may not be directly affected by forest harvesting (Taylor et al. 1999), it may decrease due to reduced litter input and changes in microclimate (Hassett & Zak 2005) and soil moisture (Taylor et al. 1999) following clear-cut harvest. Furthermore, microbial community composition may change after harvesting (Hynes & Germida 2013, Lazaruk et al. 2005, Hagerman et al. 1999). Presumably fungi are more sensitive to forest harvesting than bacteria (Bååth et al. 1999), because the changes in root dynamics affect rootassociated (mycorrhizal) fungi (Kyashcenko et al. 2017b, Bååth 1980). This contradicts to natural disturbances, such as wildfires, which usually act above ground rather having little or no effect underground (Jonsson et al. 1999). Moreover, wildfire and forest harvesting have distinct impact on soil chemical composition, which potentially induces differing microorganismal responses (Thiffault et al. 2008). However, as Hynes & Germida (2013) point out, changes in microbial composition, or even biomass, do not necessarily resemble changed microbial functions - rather it may reflect ability of the community to adjust to changed conditions and keep up functions.

Harvesting-induced changes in soil moisture can affect microbiota. Soil moisture can either decrease or increase due to forest harvesting depending on the hydrological connectivity of the stream and the catchment (Smerdon et al. 2009). Typically, boreal streams are in the receiving end of groundwater flow path, and thus groundwater table more likely rises near the stream reach rather than decreases.

Groundwater level tends to rise due to removal of trees, which absorb water from the ground. This may make the soil more wet in places, where groundwater table is shallow, for example, near streams, especially headwaters. When the forest begins to regenerate, groundwater table may decrease back or close to basic level (Smerdon et al. 2009). Site preparation for a new tree generation can override harvesting effects on groundwater level. Full-cutting in peatlands may be accompanied with drainage

ditching, which is intended to lower the groundwater level, and thus soil may not get wetter. In addition, removing shading trees leads to drying of microclimate (e.g. Oldén et al. 2019) including topsoil. Thus, the effect of forestry practices on microbial communities and processes may be very different depending on which soil profile is being considered. Disentangling the effects of forestry-related changes in the soil is difficult, because tree harvesting affects simultaneously so many phenomena, which potentially induce changes to microbial biomass, composition and/or processes.

These include, for example, soil moisture and chemistry, soil bulk density, organic matter content and fine root biomass. Also, the effect on soil properties may vary depending on the harvesting method (e.g. partial-cut harvesting, green tree retention patches and strip-cut corridors; Lindo & Visser 2003).

4.2 Management of riparian forests and protection of streams

Streams and riparian forests are important areas for biodiversity and ecosystem processes, and at the same time they are sensitive to land-use changes needing special attention in management. We now discuss potential ways to protect streams and riparia from harmful effects of forestry. We use the terms "protection" and "preservation" interchangeably to mean the protection of near-natural habitats and species (but not necessarily to restrict all human use of the habitat). By "conservation" we mean ecologically sustainable use of nature and natural resources.

Riparian communities are highly dependent on the microclimatic conditions of near-stream forest (Pollock et al. 1998, Kuglerová et al. 2014a). Higher resilience of riparian compared to upland communities can occur if flooding and groundwater discharge maintain moist conditions (Dynesius et al. 2009). Promoting flooding by adding wood and boulders in the stream (Turunen et al. 2017) or by allowing colonization by beaver (Pollock et al. 2014) could mitigate harmful effects of catchment landuse, at least in given locations. However, if flooding significantly increases nutrient input to the riparian forest, it may pose a threat to riparian diversity (Lamers et al. 2006). This could happen if, for example,

nutrients from a heavily ditched catchment drain to the stream and are flushed on to the riparia by floods. To our knowledge this is a novel idea and we are no aware of any research studying this aspect of flooding. Also, due to their disturbance regime, riparian habitats may be easily invaded by alien species (Catford & Jansson 2014, Richardson et al. 2007, Planty-Tabacchi et al. 1996).

There are only few means of reducing harmful effects of ditch maintenance (Nieminen et al. 2018a). Integration of drainage with biodiversity conservation (Lõhmus et al. 2015), and a site-specific evaluation of the real need for ditch maintenance coupled with careful planning (Hasselquist et al. 2018), should be the primary approaches to avoid unnecessary disturbance to waters. In addition, considering continuous cover forestry in peatland sites (Nieminen et al. 2018b) and near streams could be a way to overcome the problem that ditches pose. Leaving trees and/or the shrub layer on the riparian zone mitigates heating of the stream (Mellina et al. 2002, Brosofske et al. 1997), although in some cases even partial harvesting of riparian trees may result in significant warming of water (Moore et al. 2005). Other potential management practices reducing the need for ditches include, for example, gap canopy harvesting and strip felling (see also Kuglerová et al. 2017).

If intensive land management is practiced in the watershed, a buffer is usually needed to prevent nutrient and sediments draining to stream. No ground-disturbance should be practiced on the buffer, but partial tree-harvesting may be allowed. Riparian forests have been acknowledged as effective nutrient sinks in agricultural watersheds (Lowrance et al. 1984, Peterjohn & Corell 1984), and at the same time they are able to maintain stream biodiversity (Turunen et al. 2019). They also have a great stream protection potential with forestry-associated land fertilization (Vowell & Frydenborg 2004). In order to function effectively, the buffer needs to be wide enough. Today, riparian researches recommend varying-width buffers (Kuglerová et al. 2017, Richardson et al. 2017). This is because riparian forest itself is varying width, if it is defined by its most important characters: microclimate and soil moisture. Also, the nutrient and sediment retention capacity of riparian forest is site specific

depending on soil characters and topography (Gundersen et al. 2010). However, in practice buffers are still usually designed as fixed-width. This is probably because fixed-width buffers were formerly the center of research (e.g. Pinay et al. 1993) and management tend to change slowly, and because fixed-widths are easier to design and implement compared to varying-width buffers. Nature-caring forest management would benefit from considering new ways of implementing riparian buffers.

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Buffers can also be used for biodiversity protection, but it is essential to define what the protection is targeted for (see Gundersen et al. 2010 and references therein). While relatively narrow buffer strip may (or may not; Vuori & Joensuu 1996) protect the stream from sedimentation, few rows of trees unlikely provide effective protection for natural values on the riparian zone. Furthermore, forestryassociated ground disturbance can affect aquatic food webs despite buffers (Erdozain et al. 2019). If the aim is to develop a dispersal corridor, then the buffer zone should be long and continuous, but not necessarily wide (see Gundersen 2010). The width of effective dispersal corridor depends on the target species: in general, the larger the target species is the wider the buffer should be. If the aim is to protect moisture-dependent species or certain habitat types, the buffer zones should be set wide enough where the targeted conditions prevail. This can be achieved by incorporating variable width buffers with wider buffers left where specific natural values occur and narrower buffers elsewhere (Kuglerová et al. 2014b). In general, however, wider buffer strips are usually better than narrow ones from the ecological point of view (Sweeney et al. 2004). The exception to this rule may be sites that have changed significantly because of former land-use practices, for example, riparian forest, which have become sprucemonocultures. Such sites may benefit from partial harvesting or management that emulates natural disturbances on the riparian forest (Sibley et al. 2012), because making space for other species can foster biodiversity and direct the plant communities towards more natural-like assemblages.

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Leaving riparian forests uncut may benefit most forest species because they can use riparian zones as refuges from clear-cutting and as dispersal corridors. Preserving natural riparian forests can also benefit

stream biodiversity and red-listed aquatic species (Suurkuukka et al. 2014). Particularly, protecting natural riparian and stream habitats could secure aquatic, semi-aquatic and terrestrial insects whose abundance has declined dramatically in the past decades (e.g. Hallman et al. 2017). In addition, preserving the functional diversity of the microbial community may sustain long-term timber and soil production, and diversity of plants, by retaining the capacity of symbiotic fungi and decomposing microbes. It is not clear, though, whether refugees cause unintended pressures on riparian buffers, for example due to increased rate of herbivory. Introduction of small herbivorous mammals, for example, may cause changes in the vegetation community composition and affect nutrition dynamics in riparian forest (Sirotnak & Huntly 2000).

Intermediate disturbances may increase functional diversity in the riparian forest (Biswas & Mallik 2010). It has been suggested that selective logging could be practiced on riparian buffers to emulate natural disturbances (Kuglerová et al. 2017). However, because clear-cutting itself is such a big disturbance that fundamentally differs from natural disturbances (Bergeron et al. 1999), more research and careful landscape-level planning is needed before any additional disturbance can be recommended. Overall, protection should not aim to increase local biodiversity, but rather the natural-like habitats and associated species. For example, harvesting riparian trees increases light availability and temperature, decreases near-ground air humidity and creates open space. Such environmental changes are likely to initiate community changes by allowing the establishment of pioneer species and species adapted to more open forest and concurrently losing species adapted to moist and/or shadow habitats. Especially communities colonizing moist parts of riparian forest are at risk (Oldén et al. 2019, Kuglerová et al. 2014b). While partial logging may promote local biodiversity, at the same time, it can decrease or increase beta diversity (Anderson et al. 2011) among sites, depending on the identity and number of winners and losers. Regional (gamma) diversity will decrease if species specialized to riparian habitats are lost. Considering the intensity of current forestry, gaps (clear-cuts) are well established in forests. It is the old-growth forest and associated species that need protection, that is, species typically found in

undisturbed natural forests, for example those associated to dead wood, but at the same time forest management needs to consider species of all successional stages (Spence 2001). However, it is not clear how different management practices affect rare or endangered species, which most urgently need protection.

The impact of selective logging on diversity depends on the width of the buffer, because the edge effect causes additional warming and drying of riparian microclimate (Oldén et al. 2019, Steward & Mallik 2006). Thus, some logging might be allowed in buffers, that are wide-enough to overcome the edge effect, without jeopardizing natural values. In boreal forests, a 30-45 m buffer without selective logging on both sides of the stream is needed to prevent changes in microclimate (air humidity, temperature) and moss communities in riparian forest that are considered hotspots of diversity (Oldén et al. 2019, Selonen et al. 2013, Rykken et al. 2007a, Steward & Mallik 2006). Similarly, a >30 m forested buffer is needed in between the stream and the clear-cut to prevent the stream from significant warming and biological changes (Sweeney & Newbold 2014). Continuous cover forestry near streams could be one way to dodge the issue of wide buffers. Currently, there is no research on how combining continuous cover forestry and selective logging in riparian forest affects riparian or stream populations and communities.

As much as riparian forests need protection, it is not an easy task if the forest must be deployed for timber production at the same time. In most forests, riparian habitats cannot be wholly preserved without any economic losses to forest owners. Therefore, effective and extensive riparian protection requires that the forest owners understand the value of biodiversity and riparian ecosystem services. However, even awareness of natural values may not be enough, because forest owners may have a conflict of interest, for example, among biodiversity, climate change mitigation and economic values (Eriksson & Klapwijk 2019, Norlund & Westin 2011) and because the demand of forest products forces to more extensive logging. On the other hand, sustainable forestry makes sense not only from

ecological, but also from economical point of view (Balmford et al. 2002). Thus, efforts should be put into finding a sustainable compromise between biodiversity protection and forestry. This can be achieved by targeting additional protection to biodiversity hotspots, such as riparian forests, while guaranteeing large enough forest areas for preserving overall biodiversity.

Especially nature prioritizing forest management would benefit from further research, but also economic gains from tree harvest and other ecosystem services depend on nature-caring forestry. It is important to maintain diversity of both micro- and macroorganisms at a level that enables communities to reject perturbations and adjust to changing conditions, that is, maintain the resilience potential of communities. For example, extensive clear-cutting has a negative effect on ectomycorrhizal fungal abundance (Kyashcenko et al. 2017b) and diversity (Lazaruk et al. 2005, Hagerman et al. 1999), decomposition (Ussiri and Johnson 2007), and the community of decomposing microbes through changes in organic carbon pool (Bååth et al. 1995) and vegetation (De Graaff et al. 2010). Thus, in the long run, alternative forest management practices (e.g. Lazaruk et al. 2005, Hagerman et al. 1999) could be beneficial for the maintenance of biodiversity and ecosystem services in riparian forests.

4.3 Climate change effects on stream and riparian ecosystem processes

Mitigation of climate change on rivers and their watersheds is a challenge that calls for optimized management practices. Climate change models predict increasing mean annual temperatures, more frequent drought and extreme rainfall events, decreasing water table levels, and in the boreal zone elongated thawed time and more frequent freezing-thawing cycles (Pachauri et al. 2014). Overall, wet areas become wetter and dry areas drier (Dore 2005). Streamflow dynamics may change, for example, it is predicted to increase in the winter and decrease in the summer in the northern hemisphere (Fortsieri et al. 2013, Stahl et al. 2010, Wilson et al. 2010, Zhang et al. 2001). It is likely that biotic communities and processes on streams and riparian areas will be affected due to changes in hydrology and environmental factors related to warming (Heino et al. 2009).

Nilsson et al. (2013) reviewed climate change effects on riparian vegetation on the boreal zone. Shortly, they conclude that decreased area of moist riparian zone due to increased summer-time drought and smaller spring floods may decrease local species richness. It is worth noting, that climate change can increase hydrological drought (van Loon 2015) due to increased evaporation, even if meteorological drought does not increase (an Lanen et al. 2013, Wong et al. 2013, Wong & Beldring 2011). The rate of formation and melting of ice in boreal streams has accelerated during recent decades and as the climate keeps warming the ice formation will become rarer (Tolonen et al. 2019). Increased ice dynamics may promote the formation of more species rich communities. Dead wood in streams creates similar flooding effects (Turunen et al. 2017) as ice (Prowse & Beltaos 2002) and, on the other hand, wood enhances the formation of anchor ice (Lind & Nilsson 2015). Promoting the amounts of dead wood could thus keep up the ice-like dynamics in streams under climate change. The dispersal of invasive species to higher latitudes will increase with climate warming, which poses further thread to native plant communities (Nilsson et al. 2013).

Microbes play a key role in immobilizing C from atmosphere to soil and biomass. Thus, understanding drivers of microbial processes are essential for climate change mitigation. Because water drains from upland area to riparian zones, their soils receive and process remarkable proportion of C and N from the drainage area, and they can be considered hotspots of C and N cycling and transformation (Vidon et al. 2010). Accelerated freezing-thawing, increased thawed time, and a decrease in water table and/or frozen soil depth may affect C (Groffman et al. 2001) and N (Groffman et al. 2001, Mitchell et al. 1996, Goodroad & Keeney 1984) cycling. Although decomposition relates to soil temperature on a local scale (Kirschbaum 2006), increased decomposition rates at higher temperatures and at increased freezing-thawing dynamics seems to relate to changes in soil moisture and substrate quality rather than warming per se (Giardina & Ryan 2000). Changes in decomposition rates occur through changes in microbial community composition (Haei et al. 2011, Nielsen et al. 2011, Zogg et al. 1997). Decomposition

efficiency may be related, for example, to the differences in the C processing or growth efficiency of the microbial species (Zogg et al. 1997).

There is the possibility that climate change will cause a positive feedback that would increase the emissions of greenhouse gases from riparian soils (Davidson & Janssens 2006) and drying stream beds (Shumilova et al. 2019). When soils dry and then become rewetted, there is a burst of decomposition, mineralization and release of inorganic N and CO₂ (Jarvis et al. 2007). Also, decreased snow cover can change C and N cycling, for example increase the fluxes of N₂O from forests (Groffman et al 2006). Given the extent of streams and their riparian areas and the fact that a relatively modest change in soil C stocks are assumed to have major consequences for atmospheric CO₂ concentrations and climate change (Nielsen et al. 2011), changes in the decomposition of riparian areas can have major consequences on C cycling. Further, N-cycling is predominantly determined by soil condition (Brenzinger et al. 2017), and significant emissions of N₂O from the soil due to climate change induced changes in microbial communities and/or their functions (Chen et al. 2015, Baggs 2011) would further enhance climate warming.

Global change is modifying microbial composition and functional potential in soil ecosystems (Amend et al. 2016). Based on the hypotheses of Wallenstein and Hall (2012) microbial communities are better able to adapt to changing temperature and precipitation condition in regions and habitats that naturally experience relatively rapid temporal temperature and moisture variation. In line with this theory, aquatic microbial communities would be less capable adapting to climate change than terrestrial communities, because temperature changes are typically more subtle in aquatic than in terrestrial habitats. Following this reasoning, biological communities in high latitudes would be more conservative towards climate change impacts than those at temperate regions. This is because natural temperature changes during a year are more pronounced in high compared to low latitudes. However, this is only theoretic, and the actual realization of climate change impacts on biotic communities can be

unpredictable. Furthermore, adaptation at the community level does not mean that processes do not change. In fact, adaptation of microbial communities to changing climate can have major impacts on biochemical processes (Wallenstein & Hall 2012).

According to Ferreira & Chauvet (2011a) water temperature is the major environmental factor controlling the structure of aquatic hyphomycete communities. Increase in water temperature due to climate change may thus affect species composition of and decomposition by aquatic hyphomycetes (Ferreira & Chauvet 2011b). Bacteria may be affected similarly. Reason may be the fact that microbial processes are driven by enzymes (Berlemont & Martiny 2016), the performance of which depends on temperature or that biomass production increases with temperature in both stream fungi and bacteria (Suberkropp & Weyers 1996). Significant changes may be detectable only after a substantial stream warming (e.g. 10 °C). On the other hand, warming may interact with increased nutrient loads (due to climate change or land use) exacerbating the effects on microbial communities and processes (Ferreira & Chauvet 2011b). Climate induced increase in flood dynamics also may increase the export of detrital material downstream. Thus, only little material may be left for decomposer consumption, which may lead to food depletion especially for invertebrate shredders (Buzby & Perry 2000).

Due to their high diversity, microbes can be expected to have higher functional redundancy compared to most other biotic groups (but see Mayfield et al. 2010). However, their communities consist of high proportions of rare species, which may make microbial processes vulnerable to climate or land use change because rare species can disproportionally increase functional diversity (Jousset et al. 2017, Mouillot et al. 2013). If low temperatures become less important in constraining decomposition, others, such as soil moisture and substrate quality, will become more important (Giardina & Ryan 2000). Therefore, prioritizing the protection efforts on maintaining natural hydrological conditions and riparian vegetation would benefit mitigation of climate change effects on streams and riparian zone microbial related processes.

5. Future research

In the world of increasing anthropogenic impacts, we need to evaluate the state of habitats and to point out the pressures threatening biodiversity and ecosystem functions of streams and riparian forests. In order to be able to mitigate the harmful effects on ecosystems, research should focus on comparing "what is there" to "what should there be". This means, that the reference sites should represent the natural state of the studied ecosystem as well as possible. As the footprint of anthropogenic actions can be nowadays seen everywhere on the Earth, researchers must define what is "a pristine enough" reference site to cover their study questions. For example, in Finland, almost all forests have been clearcut at some point of history, and even if not recently clear-cut (e.g. 100 years), they often have been partially harvested and/or their drainage basin has been ditched. Furthermore, climate crisis is now affecting all ecosystems around the world, thus we must accept that our new "reference" is forced under anthropogenic pressure. From conservation point of view, "what should there be" may also refer to future conditions rather than the past. Should we aim to protect the species and habitats as they have occurred before human interventions or should we conserve and restore for the future (Choi et al. 2008)? If the latter is the aim, long-term ecological studies ("knowledge of the past") may be needed to set future conservation goals (Willis et al. 2007).

Furthermore, headwater streams are often highly variable, and soil and forest types differ according to the geographical and topographical position. Thus, it can be difficult to control for among stream variation in statistical tests and interpretation of results. Studies focusing on biodiversity are needed to detect the effects of land management along riparian corridors and streams. Both qualitative and quantitative criteria should be used to evaluate biodiversity. Including multiple biological groups may enhance the detection of responses that can be seen in some organism groups but not the others (Mykrä et al. 2017, Annala et al. 2014, Williams et al. 2014). In addition, beta diversity should be included in biodiversity studies, but with a caution because habitat fragmentation or degradation may

lead to increased beta diversity (Mykrä et al. 2017, Hawkins et al. 2015). We now draw together main gaps in knowledge on riparian ecosystems that call for future research (Table 1.).

The interaction between terrestrial and aquatic microbiome is poorly understood. Deep understanding of circulation of energy and substances requires detailed knowledge of the interaction of different microbial processes. The role of endophytic fungi and bacteria on decomposition in streams should be studied more carefully. For example, the functional potential of decomposer microbes, including prokaryotes and eukaryotes, and the impact of interactions between fungi and bacteria on decomposition deserve further attention. Research would benefit from studying fungi and bacteria simultaneously, because responses may be detectable in one group but not the other and interaction between fungi and bacteria likely affect their functioning but are poorly understood. Environmental filtering strongly determines microbial community composition, and co-occurrence patterns among microbial groups are weak (Mykrä et al. 2017, Williams et al. 2014), which further emphasizes the importance of including multiple biological groups in studies. Furthermore, some microbial groups, such as archaea and fungi (e.g. Horner-Devine et al. 2007), are underrepresented in ecological studies and the relationship between riparian and stream microbial communities is still imperfectly understood. Simultaneous research on aquatic and terrestrial communities is necessary to understand the diversity and functioning of and the linkage between streams and riparian forests.

Riparian forests often contribute to OM cycling (McClain et al. 2003) and storage (Sutfin et al. 2016, Hazlett et al. 2015, Jaramillo et al. 2003) relatively more than upland forest. Further research is needed on how preserving stream flooding regimes, groundwater discharge and natural vegetation contribute on maintaining OM cycling on riparian zone. Also, most brownification studies are from lakes, and effects of brownification on lotic waters should thus be studied. As drainage ditching is a common practice in peatland-dominated forests, a question rises whether nutrient loads due to intensive drainage ditching at an upstream site can impact riparian diversity at downstream sites, if floods pass

nutrients to riparian forest. Furthermore, as the studies on the sensitivity of riparian zones towards disturbances are scarce and inconsistent, more research is needed to clarify the sensitivity of riparian zones to human disturbance and their importance as dispersal corridors (Gundersen et al. 2010).

The effect of habitat-specific microbial communities on OM decomposition and nutrient cycling deserves further studying. Especially fungi are an understudied group. Different fungal guilds have differing functional potential, which can be studied with novel sequencing techniques and applying analysis tools such as FUNGuild (Nguyen et al. 2016; and correspondingly PICRUSt2 for bacteria, Douglas et al. 2019; see Box 1.). For example, ectomycorrhizal fungi may compete for N with free-living decomposer microbes decreasing C cycling rate (Averill & Hawkes 2016) and increasing soil C storage (Averill et al. 2014, Orwin et al. 2011). Also, fungi have greater potential for stocking C in their biomass than bacteria (Godbold et al. 2006) and they are considered the main decomposers in aquatic ecosystems (Fabian et al. 2017). Functional potential (DNA-based) and activity (RNA-based) of streamriparian microbiome can be studied, for example, with metatranscriptomics and metagenomics, respectively (see Box 1.). However, if the aim is to study the active fraction of microbiome, relic DNA should be taken into consideration when planning the sampling and analyses. Relic DNA, which can exist in high amounts in soil (Fierer et al. 2017, Carini et al. 2016), can obscure the detection of active vs. inactive microbes. Thus, it should be removed from the samples or optionally RNA-based methods can be used instead or together with DNA-based methods.

Preserving shading vegetation in the riparian zone could be one way to prevent warming of surface waters by maintaining shading trees and shrubs near streams and around groundwater discharge spots.

Almost every permanent stream is somewhat dependent on groundwater hydrologically (Boulton & Hancock 2006), but groundwater discharge is also important for riparian diversity (Jansson et al. 2007, Zinko et al. 2005). However, the role of groundwater in mitigating harmful effects of forest harvesting, climate change and their interactions call for further research (Dwire et al. 2018).

While the importance of riparian forest to species diversity of many organism groups is relatively well established, there are many biological groups uncovered. What is the meaning of riparian zones to mammals, reptiles, frogs, insects, mollusks, fungi, bacteria and others and how does forest management affect them? The implementation of forest buffers is still a question of debate: how should they be planned and what management practices can or cannot be conducted in or near them if the aim is to protect the riparian ecosystem as well as the stream? It is not clear how riparian zones respond to different kinds of anthropogenic pressures, interactions of stressors, and which aspects of biological diversity are most sensitive or resistant towards disturbances. And further, how sensitive are different kinds of riparian zones to anthropogenic pressures and what kind of protection do they need?

Addressing these questions would further help the development of better forest management practices that consider simultaneously the protection of the streams and their riparian forests.

Table 1. Future research needs concerning streams and their riparian forests, and the interaction of the two.

Ecosystem	Subject	Specific research question/approach
	Ecosystem functions	Role of endophytic micro-organisms in aquatic decomposition and underlying mechanisms Symbiosis of differing microorganism groups in aquatic decomposition
Streams		Symbiosis of differing microorganism groups in aquatic decomposition
	Ecosystem	
	functions and	Effects of brownification
	diversity	
		Reciprocal exploration of aquatic and terrestrial communities: e.g. to what
Stream-	Diversity and	extent does terrestrial microbial diversity drive the diversity and ecosystem
riparian	ecosystem	functions of streams and vice versa?
linkage	functions	Variation in beta diversity and community composition
		Importance of functional and phylogenetic diversity
	Diversity	Combined effect of drainage ditching and flooding on riparian diversity
		Sensitivity to human induced disturbance
		Sensitivity of headwater riparian forests to invasions by alien species
		Effect of forest management practices (buffer widths, selective logging on
		upland and riparian forests, continuous cover forestry)
		Importance for regional diversity (especially for groups other than birds and
		plants)
Riparian forest		Contribution of flooding on carbon cycling
	Face systems	Contribution of groundwater discharge on carbon cycling
	Ecosystem functions	Contribution of natural vs. non-natural vegetation on carbon cycling
		The stability of biochemical processes in the riparian zone compared to upland
		forest
	Other ecological	
	relevance	Meaning of headwater riparian forests as dispersal corridors

Declaration of Competing Interest

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

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