OULU 2018
A 708

ACTA UNIVERSITATIS OULUENSIS

Jarno Turunen

RESPONSES OF BIODIVERSITY AND ECOSYSTEM FUNCTIONS TO LAND USE DISTURBANCES AND RESTORATION IN BOREAL STREAM ECOSYSTEMS

UNIVERSITY OF OULU GRADUATE SCHOOL;
UNIVERSITY OF OULU,
FACULTY OF SCIENCE;
FINNISH ENVIRONMENT INSTITUTE

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Academic dissertation to be presented with the assent of the Doctoral Training Committee of Technology and Natural Sciences of the University of Oulu for public defence in the Wetteri auditorium (IT115), Linnanmaa, on 9 February 2018, at 12 noon

UNIVERSITY OF OULU, OULU 2018

Acta Univ. Oul. A 708, 2018

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ISBN 978-952-62-1781-9 (Paperback)
ISBN 978-952-62-1782-6 (PDF)

ISSN 0355-3191 (Printed)
ISSN 1796-220X (Online)

Cover Design
Raimo Ahonen

JUVENES PRINT
TAMPERE 2018

Turunen, Jarno, Responses of biodiversity and ecosystem functions to land use disturbances and restoration in boreal stream ecosystems.
University of Oulu Graduate School; University of Oulu, Faculty of Science; Finnish Environment Institute
Acta Univ. Oul. A 708, 2018
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Abstract

Streams and rivers have been extensively altered by humans. Channelization and land use have changed stream habitats and water quality with adverse effects on biota and ecosystem functions. Impacted streams have been targets for restoration, but there is considerable lack of understanding how streams should be restored in an ecologically effective way. In this doctoral thesis, I studied the impacts of channelization (for timber floating) and agricultural diffuse pollution on stream biota. I also studied the effectiveness of restorations of forestry impacted streams stressed by excessive sand sedimentation from catchment drainage. Finally, I also studied the effects of mosses, fine sediment and enhanced dispersal on stream macroinvertebrate communities and ecosystem functions. I found that channelization did not have effect on diatom, macrophyte, macroinvertebrate and fish assemblages, whereas diffuse pollution had strong effects, with no interactions between the two stressors. I showed that excessive sedimentation from forest drainage was harmful for stream biota but had no effect on leaf decomposition and algal accrual rate. Restoration with boulders reduced sand cover and was more beneficial for in-stream biodiversity, whereas restoration with wood tended to increase hydrological retention of stream channels, thereby altering riparian plant assemblages toward more natural composition. In a mesocosm experiment, I found mosses to have a strong impact on macroinvertebrate communities and ecosystem functions. Mosses increased organic matter retention and reduced algal accrual rate and leaf decomposition. The effect of mosses on macroinvertebrates was stronger than that of sand sedimentation, and mosses mitigated some of the negative effects of sand. Extensive dispersal had a distinct imprint on invertebrate community composition but did not blur the effect of mosses and sand on communities, suggesting strong local-scale environmental control of composition. My thesis emphasizes that priority in stream restoration should be in the mitigation of diffuse pollution rather than restoration of channel morphology, especially in streams where channel alteration has been fairly modest, as in the case of timber floating. Addition of both boulders and large wood likely yields the best biodiversity response in the restoration of forestry impacted streams. Mosses are a key component of boreal lotic ecosystems; therefore, the recovery of mosses may be a prerequisite for the full recovery of biodiversity and ecosystem integrity of boreal streams.

Keywords: algal production, benthic macroinvertebrates, bryophytes, channelization, diffuse pollution, dispersal, hydromorphology, leaf decomposition, microbes, nutrients, sedimentation, stream restoration

Turunen, Jarno, Boreaalisten virtavesien biodiversiteetin ja ekosysteemin toimintojen vasteet maankäytöstä johtuviin muutoksiin ja kunnostukseen.
Oulun yliopiston tutkijakoulu; Oulun yliopisto, Luonnontieteellinen tiedekunta; Suomen ympäristökeskus
Acta Univ. Oul. A 708, 2018
Oulun yliopisto, PL 8000, 90014 Oulun yliopisto

Tiivistelmä

Ihmisen toiminta on laajasti muokannut virtavesiä. Uomien kanavointi ja maankäyttö ovat muuttaneet virtavesien elinympäristöjä ja veden laatua, millä on ollut haitallisia vaikutuksia virtavesien luonnon monimuotoisuuteen ja ekosysteemin toimintaan. Huonokuntoisia virtavesiä on kunnostettu paljon, mutta ymmärrys siitä, kuinka virtavesiä tulisi kunnostaa parhaan ekologisen lopputuloksen saavuttamiseksi, on edelleen vajaata. Tutkin tässä väitöskirjassa uittoperkausten ja maatalouden hajakuormituksen merkitystä ja yhteisvaikutusta virtavesien eliöyhteisöihin. Tutkin myös kunnostusten vaikutusta hiekasta kärsivissä metsätalouden muokkaamissa puroissa, sekä vesisammalten, hiekan ja eliöiden levittäytymisen merkitystä purojen pohjaeläinyhteisöjen ja ekosysteemin toimintojen muovautumisessa. Havaitsin, että uoman perkauksilla ei ollut vaikutusta virtavesien eliöyhteisöihin, mutta hajakuormituksen vaikutus oli voimakas. Perkauksella ja hajakuormituksella ei ollut yhteisvaikutuksia eliöyhteisöihin. Osoitin, että metsäojituksista aiheutuva ylimääräinen hiekan sedimentaatio on haitallista virtavesien eliöille, mutta sillä ei ollut vaikutusta lehtikarikkeen hajotukseen tai päällyslevien tuotantoon. Kunnostukset joissa käytettiin kiveä vähensivät hiekan peittävyyttä ja olivat hyödyllisempiä uoman eliöstölle kuin kunnostukset, joissa tehtiin puurakennelmia. Puukunnostukset kuitenkin lisäsivät uoman vedenpidätyskykyä ja siten muokkasivat rantavyöhykkeen kasvillisuutta luonnontilaisemmaksi. Havaitsin, että vesisammalilla on voimakas vaikutus pohjaeläinyhteisöjen koostumukseen. Sammalet vaikuttivat ekosysteemin toimintoihin lisäämällä eloperäisen aineksen pidättymistä ja vähentämällä lehtikarikkeen hajotusta ja päällyslevien tuotantoa. Sammalten vaikutus pohjaeläimiin oli voimakkaampi kuin hiekan, ja sammalet kykenivät jopa lieventämään joitakin hiekan negatiivisia vaikutuksia. Eliöiden levittäytymisellä oli selvä vaikutus yhteisöjen koostumukseen, mutta se ei hävittänyt hiekan ja sammalen vaikutusta, mikä viittaa korkeaan ympäristötekijöiden merkitykseen yhteisöjen rakentumisessa. Tutkielmani korostaa, että maatalousjokien tilan parantamisessa hajakuormituksen hallinta tulisi olla ensisijainen kunnostustavoite uoman rakenteen kunnostamisen sijaan. Metsätalouden vaikutuksista kärsivissä puroissa kivi- ja puumateriaalin käyttö samanaikaisesti tuottaa luultavimmin laajimman vaikutuksen purojen monimuotoisuuteen. Sammalilla on merkittävä vaikutus muiden eliöiden yhteisökoostumukseen ja ekosysteemin toimintoihin, joten sammalten palautuminen on tärkeä kunnostustavoite virtavesissä, joissa on luonnostaan paljon sammalkasvustoa.

Asiasanat: hajakuormitus, hydromorfologia, lajien levittäytyminen, lehtikarikkeen hajotus, levän tuotanto, mikrobit, pohjaeläimet, ravinteet, sammalet, sedimentaatio, virtavesikunnostukset

Mummolle

Acknowledgements

This work could not have been done without the help of many great people. First of all, I would like to thank my main supervisor, Jukka Aroviita. I thank you for believing in me and ultimately hiring me to work in this project and carry it to the end. The project has been something that I truly found interesting and meaningful to work with. In retrospect, I feel that during these years we have made substantial contributions to the understanding of ecology in boreal streams. The co-operation between us has always been easy and you have had the time and good advice in the moments when I needed it the most. The discussions with you were very fruitful and your intelligence always put the work in good direction. Secondly, I want to thank my second supervisor Timo Muotka. As a highly experienced scientist, your deep knowledge of ecological theory and command of scientific writing substantially improved the structure of the manuscripts. I thank you for the countless hours that you have spent to improve my writings.

I'm deeply grateful to SYKE for providing me full time work contracts for the whole period of my PhD research and the great facilities and equipment to conduct this work. Nothing was certainly missing. I know that I was in a privileged position to do this work. Not many PhD students have the same working conditions and *financial* security that I had. I also want to thank all the people that I have worked with in the SYKE Oulu office. You are the best. The spirit and the atmosphere in the office has always been fun and relaxed and it has been great to work with all of you. Many of you have become friends on and off work. I especially want to thank my office room mate Tiina Laamanen. We have shared the room ever since I started working in SYKE. When we first met, I immediately noticed that you are something different. The level of enthusiasm and excitement that you could find in anything, whether it was the bacteria, DNA sequencing and analyses, BenthoTorch™ or the function VLOOKUP (PHAKU) in excel, has made an impression on me. I do not know how many times you have helped me to find and fill documents related to SYKE's bureaucracy. I thank you for the DNA sequencing work and that you tolerated me even in the bad days when I was not in the mood.

I thank all the coauthors that contributed to the manuscripts. Especially Heikki Mykrä, Pauliina Louhi and Hannu Marttila, whom I closely worked with. I also thank Heikki for good company during our fly fishing trips. All kinds of funny and not so funny things have happened during these trips but we are still alive and in good health! The fact that you are an old school fly fisherman and in real-world touch with the streams has resulted in many inspiring discussions related to stream ecology. I thank Pauliina for her excellent humor and intellectual discussions during our field trips. I think we connected well in our views and opinions related to salmonid conservation or stream restoration. I thank you for all your guidance and work in statistical analyses and I hope we will work together for many years to come.

I want to thank all the other current and former aquatic ecology -orientated PhD students in the University of Oulu (Kaisa Huttunen, Kaisa-Riikka Mustonen, Kaisa Lehosmaa, Romain Sarremejane, Mari Tolkkinen, Heli Suurkuukka, Musawenkosi Mlambo), LUKE (Maare Marttila) and SYKE (Mira Grönroos, Mikko Tolkkinen, Annika Vilmi, Katri Tolonen, Kirsti Leinonen, Mariana Rocha) for friendship, help, collaboration and sharing the ups and downs of the PhD work. Thank you Mira Niemelä and Emmi Putkonen for your contributions to my thesis as masters' students. I appreciate and thank Professor Peter Haase and Dr. Jonathan Tonkin for the comments and pre-examination of this thesis.

I thank the Academy of Finland, EU funded REFORM-project and Maa- ja vesitekniikan tuki ry for funding my research.

Last but not least I want to thank my parents, twin brother, relatives and friends for support and activities outside of work. My parents have always had the love and support for me whatever my choices in life have been. I wish my grandmother would have seen this. You always knew it. The little "matomaisteri" has become a doctor.

30.8.2017 Jarno Turunen

List of original articles

This thesis is based on the following publications which are referred throughout the text by their Roman numerals:

I Turunen J, Muotka T, Vuori K-M, Karjalainen SM, Rääpysjärvi J, Sutela T & Aroviita J (2016). Disentangling the responses of boreal stream assemblages to low stressor levels of diffuse pollution and altered channel morphology. Science of the Total Environment 544: 954–962.

II Turunen J, Aroviita J, Marttila H, Louhi P, Laamanen T, Tolkkinen M, Luhta P-L, Kløve B & Muotka T (2017). Differential responses by stream and riparian biodiversity to restoration of forestry-impacted streams. Journal of Applied Ecology 54: 1505–1514.

III Turunen J, Louhi P, Mykrä H, Aroviita J, Putkonen E, Huusko A & Muotka T (2017). Habitat structure controls community assembly and stream ecosystem functioning under extensive dispersal and anthropogenic disturbance. Manuscript.

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1 Introduction

The last 200 years have been a period of daunting human impact on Earth (Crutzen, 2002). The size (7.5 billion in 2017) and growth of human population places tremendous pressure on the use of natural resources. Energy, infrastructure, food and secondary production demands are the main drivers of global warming, habitat loss, over harvesting and environmental pollution. Together, these human pressures are causing global change and reduction of biodiversity and functioning of ecosystems (Dirzo *et al.,* 2014). It has been estimated that the current extinction rate is at least 100 times higher than the natural background rate (Ceballos *et al.* 2015), and the population sizes of many present species have collapsed (Ceballos, Ehrlich, & Dirzo, 2017). The evident reasons for these devastating trends are unsustainable use of natural resources and introduction of exotic species (Sala *et al.,* 2000; Butchart *et al.,* 2010).

Among different ecosystem types, freshwater systems and their biodiversity are especially heavily impacted by humans (Dudgeon *et al.,* 2006; WWF 2016). Particularly, streams and rivers have been altered extensively (Malmqvist & Rundle, 2002), due partly to the long history of human dependence on river channels. Rivers have been channelized for navigation and flood protection, used as a sewage routes and dammed for energy production and water withdrawal. It has been suggested that 65% of global river discharge and associated aquatic habitats are under moderate-to-high threat (Vörösmarty *et al.,* 2010). Stream ecosystems are sensitive to land use because the effects of human activities in their catchments are readily seen in the small water volume of streams. The major impacts of land use (agriculture, forestry, and urbanization) on stream habitats are changes in discharge patterns, increased soil erosion and sediment supply, and increased nutrient and other pollutant concentrations in water (Waters, 1995; Paul & Meyer, 2001; Allan, 2004).

The key land-use induced stressors to stream ecosystems are excessive nutrient pollution and sedimentation due to fertilizer use and catchment erosion (Allan, 2004). Agricultural streams often have elevated water temperature, phosphorus, nitrate, and suspended sediment concentrations which are the major constituents of agricultural diffuse pollution in streams (Ekholm *et al.,* 2000, Sponseller, Benfield, & Valett, 2001; Buck, Niyogi, & Townsend 2004). These physical and chemical changes in the stream habitat commonly cause changes in biodiversity and ecosystem functioning (e.g. Greenwood, Harding, Niyogi, & McIntosh, 2012; Tolkkinen *et al.,* 2013, Rosemond *et al.,* 2015). In addition to diffuse pollution, streams are often channelized for navigation, flood protection and, especially in boreal regions, for timber transportation (Malmqvist & Rundle, 2002, Nilsson *et al.,* 2005). Because these habitat changes frequently co-occur, understanding their relative importance and combined effects on stream ecosystems is of high relevance for effective resource management.

Together with agriculture, forestry practices are a major land use causing erosion and excessive stream sedimentation (Waters, 1995, Allan, 2004). Deforestation by clear-cutting and construction of forest roads commonly increase sediment load to streams (Vuori & Joensuu, 1996, Sutherland, Meyer, & Gardiner, 2002; Dearing & Jones, 2003; Hassan *et al.,* 2005). Tree removal reduces interception, transpiration and roots' stabilizing effect on soil, which all increase the proneness to sediment erosion and flushing of fine sediments to receiving streams (Hassan *et al.,* 2005). Unpaved forest roads readily erode and adjacent road ditches can carry large quantities of fine sediments to streams (Kreutzweiser & Capell, 2001; Kreutzweiser, Capell, & Good, 2005). In certain regions, construction of ditch networks to drain naturally wet forests has been a common practice (Paavilainen & Päivänen, 1995). In Finland, for example, over half (55%) of the peatlands have been drained to enhance forest growth (Turunen, 2008). The ditches can be very prone to erosion, and as the ditches often drain directly into a stream channel, they can carry a lot of sediment to receiving streams (Vuori & Joensuu, 1996; Vuori, Joensuu, Latvala, Jutila, & Ahvonen, 1998).

Sedimentation is considered to be one of the most severe land-use related stressors to stream biota (Matthaei, Piggot, & Townsend, 2010; Wagenhoff, Townsend, & Matthaei, 2012). Excess sediments fill the interstitial spaces of coarser substrates and thus reduce habitat availability for crevice-dwelling invertebrates, impair salmonid spawning success, and scour periphytic algae (Kemp, Sear, Collins, Naden, & Jones, 2011; Jones, Duerdoth, Collins, Naden, & Sear, 2014; Mustonen *et al.,* 2016). Instability of fine-grained substrate hinders establishment of aquatic plants and sedentary invertebrates. Sedimentation can interfere with stream ecosystem processes, such as decomposition of leaf litter (Lecerf & Richardson, 2010; Louhi, Richardson, & Muotka, 2017). Considering the pervasiveness of fine sediments as a stressor (Waters, 1995) and the potential future increase of sedimentation in streams due to climate change (Poff, Brinson, & Day, 2002), there is clearly a need to further our understanding of its effects on stream ecosystems.

Streams affected by anthropogenic stressors are obvious targets for restoration. Restoration often focuses on increasing the physical habitat heterogeneity to improve the ecological state of degraded streams (Palmer, Menninger, & Bernhardt, 2010; Sundermann *et al.,* 2011). The rationale behind this is that habitat heterogeneity generally correlates positively with species diversity (Benton, Vickery, & Wilson, 2003; Tews *et al.,* 2004), and this relationship has also been detected in streams (Beisel, Usseglio-Polatera, & Moreteau 2000; Brown, 2003; Pedersen, Kristensen, & Friberg, 2014). This has led to the perhaps naïve assumption that by restoring the natural complexity of physical habitat, biodiversity will eventually become indistinguishable from that in unaltered systems ('Field of Dreams' principle) (Palmer, Ambrose, & Poff, 1997; Hilderbrand, Watts, & Randle, 2005).

Despite extensive restoration efforts (Bernhardt *et al.,* 2005), the ecological responses to habitat restoration have been highly variable, from low effects (Lepori, Palm, Brännäs, & Malmqvist, 2005; Palmer *et al.,* 2010; Louhi *et al.,* 2011; Stranko, Hilderbrand, & Palmer, 2011) to at least partial success (Jähnig, Brunzel, Gacek, Lorenz, & Hering, 2009; Whiteway, Biron, Zimmermann, Venter, & Grant, 2010; Lorenz, Korte, Sundermann, Januscke, & Haase, 2012). Often suggested explanations for the lack of positive responses are that (i) restoration has been conducted at an inappropriate scale, (ii) it has treated the symptoms rather than the actual causes for the deteriorated conditions, and (iii) restoration has used too narrow a range of measures ('one technique fits everywhere') (Bond & Lake, 2003; Hilderbrand *et al.,* 2005; Palmer *et al.,* 2010). Clearly, in at least some instances, other factors, such as poor catchment management and associated stressors, might be more critical than the loss of habitat heterogeneity per se (Palmer *et al.,* 2010; Stranko *et al.,* 2011; Sundermann *et al.,* 2011). Whether increased variability of habitat structure has a noticeable effect on stream communities and ecosystem functions can largely depend on the extent of dispersal in a metacommunity (Venail *et al.,* 2008; Brown & Swan, 2010; Tornwall, Swan, Brown, 2017). Recently, some studies have applied metacommunity theory to explain variable restoration outcomes. Generally, these studies have highlighted that dispersal and connectivity of source populations to restored sites may be crucial for the ecological success of stream restoration (Tonkin, Stoll, Sundermann, & Haase, 2014; Winking, Lorenz, Sures, & Hering, 2014). In this respect, restoration of habitat heterogeneity might not produce the desired restoration outcome if communities are dispersal limited. On the other hand, increased habitat heterogeneity might not produce the desired community structure if the restored site is under extensive dispersal and thus not strongly structured by environmental factors (i. e. mass effects) (Leibold, *et al.* 2004, Tornwall *et al.,* 2017). Thus, more isolated communities could be more responsive to habitat manipulations (Brown & Swan, 2010; Brown & Swan, 2017; Tornwall *et al.,* 2017).

Mosses are an important habitat component structuring boreal stream communities, and they may also affect ecosystem functions such as organic matter retention. Their recovery may therefore be a prerequisite of the full recovery of stream ecosystems after restoration (Muotka & Syrjänen, 2007; Louhi *et al.,* 2011; Koljonen, Louhi, Mäki-Petäys, Huusko, & Muotka, 2012). The presence of mosses can also reduce the temporal variation of macroinvertebrate communities (Huttunen *et al.,* 2017), suggesting a refugial effect during harsh environmental conditions. However, the interactive effects of mosses with anthropogenic stressors, such as excessive sedimentation, are poorly understood.

2 Aims of the thesis

The overall objective of this thesis was to study factors that are important for successful management, conservation and restoration of boreal stream biodiversity and ecosystem functions. The subprojects gave insight to several aspects of high importance to stream restoration. In the first study (I), the aim was to disentangle the response of stream communities to channelization and agricultural diffuse pollution to explore the relative importance and combined effects of these stressors on stream communities. In the second subproject (II), the aim was to study the effectiveness of boulder and wood based stream restoration methods in mitigating excessive sedimentation impacts on stream habitat, communities and ecosystem functions in forestry impacted streams. In the third paper (III), the aim was to experimentally study the effects of stream mosses, fine sediments and enhanced dispersal on stream communities and ecosystem functions. The emphasis in the third paper was to get understanding on dispersal and environmental factors in structuring macroinvertebrates communities and how the presence of moss and fine sediments interact and influence community structure and ecosystem functions.

In the following sections, I summarize the main study approaches and findings of the original articles of this thesis. Further details are given in the original articles.

3 Materials & Methods

3.1 Study area

The relative importance and interactive effects of stream channelization and agricultural diffuse pollution (I) were studied in 91 streams located in hemiboreal, south boreal and midboreal ecoregions in southern and central Finland (60–65 °N and 21–31°E). Streams in the area are typically slightly acidic and colored by dissolved organic carbon due mostly to acidic bedrocks and large peatland areas. The main anthropogenic pressures to the streams are diffuse pollution, due to agricultural and forestry land use, and modification of channel conditions mainly for the historical needs of timber transport. We selected the sites from the national monitoring network to represent the least impacted sites ('reference' sites, sensu Stoddard, Larsen, Hawkins, Johnson, & Norris, 2006) and sites impacted by agriculture and/or alteration of channel morphology.

The effectiveness of different stream restoration methods in the restoration of forestry impacted and sediment degraded streams (II) was studied in the headwaters of River Iijoki basin (area 14 191 km2), northern Finland, where the main anthropogenic stressor is excessive inorganic fine sediment loading from peatland drainage. We selected nine streams that were initially impacted by fine sediment accumulation, and were restored 3–7 years (median: 6 years) prior to our sampling. We also sampled two types of control streams: nine near-natural reference and ten impacted streams.

The effects of stream mosses, sand sedimentation and enhanced dispersal on stream communities and ecosystem functions (III) were studied in a mesocosm experiment. We conducted our experiment in the Kainuu Fisheries Research Station of Natural Resources Institute Finland (LUKE) (64.24 °N and 27.31 °E) that houses six 25 x 1.5 m parallel outdoor stream channels designed for experimental research.

The extent of land use, fine sediment and especially nutrient pollution levels in the streams in the Nordic boreal region are overall rather low compared to the situation in, for example, Central Europe (e.g. Hering *et al.,* 2006; Elbrecht *et al.,* 2016). Thus, the field studies reflect the responses stream biota and ecosystem functions to low-to-moderate land use impact scenarios.

3.2 Data

The subprojects of this thesis included a wide variety of data: measurements of physical and chemical habitat characteristics (I, II) samples of leaf-decaying bacteria and fungi (II), diatoms (I), macrophytes (I, II), riparian plants (II), benthic macroinvertebrates (I, II, III) and fish (I). Ecosystem functioning was measured as leaf decomposition (II, III) and periphyton accrual rate (II, III).

3.2.1 Habitat measurements

In paper I, we used water chemistry variables and land use information to quantify the degree of diffuse pollution at each site. For papers I and II, we obtained water chemistry data from a national database (I) (OIVA, http://www.ymparisto.fi/oiva) or collected water samples by using national standards (National Board of Waters 1981) (II). A geographical information system (GIS) was used to delineate catchments, and land use was quantified by Corine Land Cover data (CLC) (I, II). Water pH was measured from water samples (I) or *in situ* with YSI Professional Plus -meter (YSI Inc., Yellowsprings, Ohio, USA) (II).

In paper I, we quantified hydromorphological alteration by conducting River Habitat Survey (RHS; Raven, Holmes, Dawson, & Everard, 1998) and complemented it by an additional evaluation of the degree of channelization for timber transport. Both surveys were conducted at the 500-m standard length for a RHS survey to capture potential modifications of a stream reach. Because RHS does not take into account channelization for timber transport, the degree of channelization was estimated at ten evenly distributed RHS points on a 3-point scale: 0 - no modification, 1 - moderate alteration and 2 - intense alteration. The sum of these values was then used as a channelization score (CS), ranging from 0 to 20. Because all biological sampling focused on riffles, we further calculated a channelization intensity score (CI) by the mean value across those CS estimates that represented riffle habitats (values from 0 to 2). CI thus describes the intensity of morphological alteration at a sampling site and CS in the whole reach.

In paper II, substrate size distribution was estimated in 15 randomly placed 0.25 m^2 quadrates as percentage cover of ten size classes from fine sediments (ø < 0.2 cm) to large boulders (ø > 25 cm) (modified Wentworth scale). Volume of large woody debris (LWD, dm^3 m^{-2}) was quantified by measuring (length x width) all wood particles > 5 cm in diameter within bank full channel width. Hydraulic conditions were measured by adding a tracer injection pulse (NaCl, 10 min pulse)

(Stofleth, Shields, & Fox, 2008) and then applying OTIS-P modelling (Runkel, 1998) to estimate transient storage of a reach. OTIS-P modelling was also used to calculate the hydraulic retention factor (R_h; Morrice, Valett, Dahm, & Campana 1997).

3.2.2 Biological sampling

Diatoms (I) were sampled from five randomly selected stones at each site. The upper surface of stones was washed with water into a jar using a tooth brush, and the dislodged material was preserved in ethanol. From each sample, 400 diatom valves were counted and identified to species level, and the relative abundance of species was used in data analyses.

In paper I, macrophytes (both vascular plants with underwater roots and bryophytes) were surveyed in five 20-m sections at each site. Abundance of vascular plants was estimated as percentage cover of each species at each section; abundance of bryophyte species was estimated as percentage cover in two 1 x 2 m plots per section. Frequency of vascular plants was estimated by dividing the section into 100 equally-sized quadrats and then counting how many of these were occupied by each species. For bryophytes, the frequency was calculated as the number of occurrence in the ten plots per the five 20-m sections. Mean values across sections were then calculated for each site. For data analyses, we combined the estimates of abundance and frequency to a Vegetation Index (VI): $2^{(\text{abundance}+\text{frequency}-1)}$ (Ilmavirta & Toivonen, 1986). To calculate VI, estimates were ranked to seven classes (0%=0, <0.5%=1, 0.5–1%=2, 1–5%=3, 5–25%=4, 25–50%=5, 50–75%=6, 75–100%=7; bryophyte frequency: 0%=0, 10%=1, 20%=2, 30%=3, 40–50%=4, 60–70%=5, 80–90%=6, 100%=7). In paper II, only bryophytes were sampled from 15 randomly placed 0.25 m^2 quadrates across a reach, and species' coverages were recorded at each quadrate.

In papers I and II, benthic macroinvertebrates were sampled by taking four 30-s kick-net samples covering most microhabitats present at a site. This method is known to capture about 75% of taxa present in a given reach, mainly missing species with sporadic occurrence in streams (Mykrä, Ruokonen, Muotka, 2006). In the experimental study (III), macroinvertebrates were sampled by taking four Surber samples (mesh size: 0.5 mm, sampling area: 290 cm^2) by disturbing the bottom sediment with hand for 30 s. Invertebrates were preserved in 70% ethanol in the field, and samples were later sorted in the laboratory. All invertebrates were identified and counted, mainly to species or genus (except dipterans and oligochaetes which were identified at a coarser level).

In paper I, fish were sampled by electric fishing with one to three passes. Fish species and their densities (fish per 100 m^2) were recorded at each site. To maintain comparability between sites, only data from the first pass were used in the data analysis.

3.2.3 Ecosystem functions

In papers II and III, we measured periphyton accrual rate and leaf decomposition. Periphyton accrual rate was measured by incubating five 25 cm^2 ceramic tiles in each reach for 21 days (II) or four tiles for 48 days (III). Chlorophyll a was measured by spectrophotometry in the laboratory. To measure leaf decomposition, (II) we collected alder (*Alnus incana* L.) leaves prior to abscission and air-dried them at +23 °C for three weeks and then incubated 6 g of leaves in the stream in mesh bags for 21 days. The samples were then ashed and converted to ash-free dry mass, and the percentage of leaf mass loss was calculated. In paper III, we fastened 2 g of leaf material with paper clips to create leaf packs. Four leaf packs were placed in each flume on the third week of the experiment (day 22) so that the total incubation period was 27 days.

3.2.4 DNA analyses

In paper II, we extracted bacterial and fungal DNA from the incubated leaf samples. The 16S rDNA region of bacteria was amplified with primers 519F 5′-CAGCMGCCGCGGTAATWC-3′ and 926trP1 5′-CCTCTCTATGGGCAGTCGGTGATCCGT CAATTCCTTTRAGTTT-3. The 18S rDNA region of fungi was amplified with primers ITS1F 5′-CTTGGTCATTTAGAGGAAGTAA-3′ and 58A2R-P15′-CCTCTCTATGGGCAGTCGGTGATCTGCGTTCTTCATCGAT-3′. The amplicons were sequenced using the Ion Torrent™ semiconductor system (Thermo Fisher Scientific Inc., Waltham, USA). Sequences were analyzed using Quantitative Insights Into Microbial Ecology (QIIME) version 1.8.0 (Caporaso *et al.,* 2010). The sequence library was split by samples and quality filtered for each sequence using default settings in QIIME. A total of 1 464 869 and 1 122 516 sequences were retained for bacteria and fungi, respectively. The sequences were clustered as operational taxonomic units (OTUs, 97% similarity) using the Usearch algorithm (Edgar, 2010).

3.3 Study design

In paper I, we explored the independent and interactive effects of hydromorphological channel alteration (mainly channelization for water transport of timber) and diffuse pollution on species assemblages. For this purpose, we grouped our study sites based on their deviation from reference conditions for diffuse pollution and hydromorphological alteration. The sites were classified as unimpacted by diffuse pollution from agriculture if total phosphorus concentration was at the reference, or only slightly elevated, level of that defined for Finnish streams (< 35 μg L^{-1} for streams draining mineral lands, < 40 μg L^{-1} for streams draining peatlands, < 60 μg L^{-1} for streams draining clay catchments, Vuori, Mitikka, Vuoristo, 2009). Sites were classified as impacted by diffuse pollution if nutrient concentrations were clearly elevated (phosphorus values > 60 μg L^{-1}, corresponding to the 'moderate-or-poorer' nutrient status, Vuori *et al.,* 2009). We classified sites as hydromorphologically unaltered if the CI index was ⩽ 0.1, corresponding to < 10% of the section length channelized moderately or < 5% severely. The sites classified as impacted by channelization had CI ⩾ 0.2, corresponding to ⩾ 20% of section length channelized moderately or > 10% severely. This classification scheme resulted in four treatment groups: (i) least impacted sites with both stressors absent (or present at very low levels) (N = 20), (ii) hydromorphologically altered, channelized sites with minor or no diffuse pollution (N = 25), (iii) sites with clear diffuse pollution but with no or only minor hydromorphological alteration (N = 25), and (iv) sites altered by both diffuse pollution and altered hydromorphology (N = 21).

In paper II, we allocated streams to different treatment groups based on restoration methods and forestry (drainage) impact. This resulted in four treatment groups: streams restored mostly with boulders (n=5), streams restored with wood (n=4), near-natural streams (n=9) and forestry impacted streams (n=10). The near-natural references resembled the impacted streams in all other characteristics but the near-absence of drainage activities in their watersheds. The impacted streams were affected by drainage to the same extent as were the restored streams prior to restoration.

In paper III, the experiment ran for 48 days, in August to September 2014. Four 5.8 m long and 20 cm wide rustproof plate subflumes were placed parallel to each other in each of the six channels. Thus, the total number of subflumes was 24. Before the start of the experiment, the bottom of each subflume was covered by a uniform 10-cm layer of gravel which was washed carefully to make sure that the subflumes did not harbor any macroinvertebrates before the experimental treatments were implemented. Water flow into the channels was adjusted such that every channel had similar mean flow velocity (0.25–0.30 m s^{-1}) and mean water depth (10–15 cm). The experimental treatments were (i) addition of habitat architecture (*Fontinalis antipyretica* mosses), (ii) sand (to mimic land-use induced sedimentation) and (iii) addition of benthic invertebrates (to mimic enhanced connectivity/dispersal). Mosses and sand were allocated randomly across the four subflumes in each channel using a fully crossed factorial design. The aided-dispersal treatment was implemented at the whole-channel level, with all subflumes in three randomly selected channels receiving extra loads of invertebrates, while the other set of 3x4 subflumes only received invertebrates from the upstream sections of the experimental arena.

3.4 Statistical methods

In paper I, we used three complementary approaches to assess multiple-stressor impacts on stream communities: (i) taxonomic richness, (ii) community ordinations, and (iii) assessment metrics. We assessed the ecological status of each study site by using Ecological Quality Ratios (EQR, or Observed-to-Expected value [O/E-ratio]) from the national EU Water Framework Directive (WFD) assessment which is based on the reference condition approach. For diatoms, macroinvertebrates and macrophytes, we used the number of expected taxa (O/E-taxa; Moss, Furse, Wright, & Armitage, 1987), or taxonomic completeness, which is widely used as a measure of biological condition in freshwater bioassessment (e.g. Hawkins, 2006). Fish assemblages were assessed using the Fish Index for WFD assessment in Finland (FiFI; Vehanen, Sutela, Korhonen, 2010). The EQRs indicate a range in biological condition from values around 1 (undisturbed reference condition) to 0 (poor status with the largest deviation from reference conditions).

We used Non-metric Multidimensional Scaling (NMS) ordination to visualize the effect of hydromorphological alteration and diffuse pollution (I), restoration (II) and experimental treatments (III) on community composition of different organism groups. Bray-Curtis dissimilarity was used as the distance measure. Two-way factorial permutational multivariate analysis of variance (PERMANOVA) (Anderson, 2001) was used to test the significance of the main effects of and interaction between diffuse pollution and hydromorphological alteration on community structure (I), the effect of stream restoration (II) and the main effects and interactions of mosses, sand sedimentation and enhanced dispersal on macroinvertebrate community composition (III). Homogeneity of multivariate dispersion between treatment combinations was tested prior to PERMANOVA (Anderson, 2001).

We performed two-way ANOVAs separately for each organism group to test whether hydromorphological alteration or diffuse pollution have significant independent and/or interactive effects on taxon richness and ecological status (I). To deal with the potential problems of higher-than-possible additive effects of stressors on response variables, we used the multiplicative risk model (Sih, Englund, & Wooster, 1998), and thus the response variables were $\log_{10}(x+1)$-transformed prior to analysis. The effect of diffuse pollution and hydromorphological alteration on trout density was only visually explored because no trout occurred in any of the sites in two of the stream groups

In paper II, we tested for differences between treatments in the physical stream habitat and microbial responses by using generalized linear models (GLM); for other biological response variables, we used linear mixed-effects models (LMM; function lme in R-package nlme; Pinheiro *et al.,* 2015). In LMM, treatments were fixed effect, and samples nested within streams were treated as random effects. We also included VarIdent function in the model to allow heterogeneity in variance structure among treatments. Proportional response variables were logit transformed prior to analysis (Warton & Hui, 2011). The fit of models was inspected using residual plots and were found to satisfy the assumptions of normality and heterogeneity of residuals for parametric analysis. The results are given as treatment contrasts.

In paper III, we analyzed differences among treatments in algal accrual ($\mu g\ m^{-2}\ d^{-1}$), leaf mass loss (%), organic matter standing stock (g) and macroinvertebrate response variables using linear mixed effects models (LMM; function lme in R-package nlme; Pinheiro & Bates, 2000; Pinheiro *et al.,* 2017), following the top-down strategy recommended by Zuur, Ieno, Walker, Saveliev & Smith (2009). Thus, our initial 'full model' included the main effects of moss, sand and dispersal as fixed factors, and channels and both samples and flumes nested within channels as random variables. We used the comparisons of log-likelihoods of preceding models based on the restricted maximum likelihood estimation. As our initial random effects (channels, subflumes nested within channels, and samples nested within the effects) were all found to be non-significant (i.e. they did not improve the model fit significantly), they were removed from all models (Zuur *et al.,* 2009). Following the same logic, all non-significant three- and two-way interactions were dropped. Thus, our final analysis consisted of generalized least square models (GLS in R-package nlme; Pinheiro & Bates, 2000) with only significant interactions and all main effects included. A variance structure (VarIdent) was included in the models to allow for heterogeneity in variance among moss treatments; species richness and algal accrual rate were $\log_e(x+1)$, and leaf mass loss percentage arcsine-transformed.

In paper III, we used indicator species analysis (IndVal; Dufrêne & Legendre, 1997) in the R package labdsv (Roberts, 2012) to identify potential indicator taxa for each treatment. IndVal analysis determines an indicator value (IV) for a species in each a priori defined site group (in our case, treatment). The indicator value for a taxon varies from 0 to 100, and it attains its maximum value when all individuals of a taxon occur at all sites of a single group. The significance of the indicator value for each taxon was tested by a Monte Carlo randomization test with 1000 permutations. We considered species with IV > 60 (and significant at $\alpha = 0.05$) as strong indicator taxa.

4 Results & Discussion

4.1 Disentangling the effects of diffuse pollution and morphological channel alteration (I)

Diffuse pollution had a negative effect on macroinvertebrate taxonomic richness, but not on richness of diatoms, macrophytes or fish. Taxonomic richness was not affected by hydromorphological alteration in any of the four groups, and neither did hydromorphological alteration and diffuse pollution have any significant interactive effects.

The assemblage structure of each organism group was strongly affected by diffuse pollution, but not by hydromorphological alteration. Trout density was highest at the reference sites with an average of 6.1 individuals 100 m^{-2}. By contrast, sites with only diffuse pollution or both stressors present had no trout. In hydromorphologically altered sites, trout density was on average 4.1 individuals 100 m^{-2}.

Diffuse pollution reduced the EQR of diatoms, macroinvertebrates and fish, but not of macrophytes. Hydromorphological alteration had no effect on the EQRs. There were no significant interactive effects on EQRs.

The low effect of hydromorphological alteration to stream communities is likely related to the nature of the alteration. Channelization for timber transport was typically conducted by removing the largest boulders and bole wood from the channel to facilitate timber floating (Nilsson *et al.,* 2005). This practice causes distinctive changes to reach-scale stream habitat structure (Helfield, Capon, Nilsson, Jansson, & Palm, 2007; Marttila *et al.,* 2016), but the near-bed habitat characteristics often remain largely unmodified (Muotka & Syrjänen, 2007). Thus, the habitat characteristics that change due to the channelization might be irrelevant at the scale of benthic biota (Lepori *et al.,* 2005). Our results do not suggest that hydromorphological conditions are generally unimportant for the stream biota, but that for ecological responses to become detectable, the severity of alteration needs to be more substantial than is typically the case in boreal streams channelized for timber transport. Diffuse pollution had a clear effect on community composition and assessment metrics, suggesting that stream communities adapted to oligotrophic conditions change readily at rather low levels of diffuse pollution. At the studied degradation levels, the combination of these two stressors did not produce a response that would have differed significantly from that expected based on single stressor effects. On a continental-scale comparison (e.g. Hering *et al.,* 2006, Elbrecht *et al.,* 2016), however, both stressors were at low-to-moderate levels in our study sites, thus representing a low-impact scenario for European running waters. Morphological stream restoration is unlikely to be ecologically beneficial if the detrimental effects of diffuse pollution and associated water quality problems cannot be alleviated (Palmer *et al.,* 2010, Sundermann *et al.,* 2011, Stranko *et al.,* 2011). In streams affected by stressors related to agricultural diffuse pollution, stream management should focus on reducing land-use impacts, particularly at the land-water interface between the stream and its riparian forest (Gregory, Swanson, McKee, & Cummins 1991; Lammert & Allan, 1999; Sponseller *et al.,* 2001). Lack of interactions between the stressors suggests that mitigation of these two stressors separately in a multiple-stressor environment should not produce unexpected ecological outcomes, at least not under the degradation gradients encompassed by our study. To conclude, our results emphasize that to cost-efficiently improve ecological condition of boreal streams, reducing diffuse pollution from agriculture should be a priority over local scale restoration of in-stream habitat.

4.2 Restoration of forestry impacted streams (II)

We found that restoration had a significant effect on the physical stream habitat, with contrasting responses between boulder- and wood-restorations. Boulder-restored streams had less fine sediments than did the impacted or wood-restored streams, whereas difference to near-natural streams was negligible, suggesting that boulder restoration was more effective at restoring natural habitat structure.

The volume of large woody debris (LWD) was lower in the impacted and boulder-restored than in near-natural channels, but wood-restored streams had more LWD than the impacted streams. Wood-restoration tended to enhance hydraulic retention, whereas boulder-restoration did not. This result suggests that wood is more effective at restoring hydrological retention and water residence time, thus promoting the tendency of the channel to flood.

Bryophyte cover was higher in near-natural streams than in any other treatment. Bryophytes were also more abundant in the boulder-restored than in the impacted streams, suggesting positive effect of boulder-restoration on bryophytes. Bryophyte richness was similar in the boulder-restored and near-natural streams, whereas wood-restored streams supported less bryophyte species than did either near-natural or boulder-restored streams. The composition of bryophyte assemblages in the impacted and wood-restored streams differed from the near-natural assemblages, but the restored streams did not differ from the impacted streams. Thus, the restoration signal on bryophyte community structure was not very strong, suggesting that bryophyte assemblages were still on a trajectory towards recovery which may take much longer than the 3–7 years post-restoration period of this study (Louhi *et al.,* 2011).

Benthic macroinvertebrates did not show clear signs of recovery. However, EPT richness was lower in the impacted and wood-restored than in near-natural streams but did not differ between boulder-restored and near-natural streams. The composition of benthic macroinvertebrate assemblages in both types of restored streams differed from the near-natural but not from the impacted streams. The low responsiveness of macroinvertebrates may partly reflect the relatively short recovery period of our restored streams. In more strongly modified landscapes, stream macroinvertebrates have been unresponsive to restoration mainly because of dispersal limitation (Tonkin *et al.,* 2014). For example, in lowland streams in Germany, benthic macroinvertebrates did not show any response even 20 years post-restoration (Leps, Sundermann, Tonkin, Lorenz, & Haase, 2016). However, as several headwater reaches in the River Iijoki basin remain in near-pristine condition (Suurkuukka *et al.,* 2014), availability of colonists should not limit post-restoration recolonization in our streams. In fact, one could expect colonization of boulder-restored reaches by mosses to facilitate the establishment of benthic macroinvertebrates, but there seems to be a considerable time lag between the recovery of mosses and macroinvertebrate colonization.

Riparian plant richness did not differ between treatments. Total plant cover was lowest in the wood-restored streams. The cover of ferns was higher in the wood-restored and near-natural streams than in the impacted streams. Graminoids were more abundant in the impacted and boulder-restored than in the reference streams, whereas they did not differ between the wood-restored streams and the near-natural references. Riparian plant assemblages in the wood-restored streams differed from those in the impacted streams, but resembled more the composition in the near-natural streams. The observed responses of riparian plant assemblages to wood restoration suggest that wood addition changes the tendency of the channel to flood and thus causes changes in riparian moisture conditions, resulting in plant assemblages that resemble the near-natural state.

There were no differences in bacterial or fungal OTU richness, evenness or composition between the treatments. Similarly, periphyton accrual rate and leaf decomposition were unaffected by sedimentation and, correspondingly, restoration. The land use impact and restoration did not result in changes in water quality, which could be a major reason for low responsiveness of microbiota and ecosystem functions (Gessner & Chauvet, 2002; Gulis & Suberkropp, 2002; Tolkkinen *et al.,* 2015). On the other hand, the leaf bags and periphyton tiles were not buried by sediments because of the low flow period when the study was conducted (J. Turunen, personal observation), which could also limit responses of these ecosystem functions and microbiota to sedimentation (Danger, Cornut, Elger, & Chauvet, 2012; Mustonen *et al.,* 2016).

The results suggest that restoration success in forestry impacted headwater streams may vary depending on whether boulder additions or wood are used for restoration. Addition of stones has a direct influence on substrate quality, and it is therefore more effective at restoring in-stream biodiversity, whereas addition of large wood alters stream hydrology and may have strong effects on riparian communities. Thus, it is likely that a combination of these methods will yield the best ecological outcome. Our results thus emphasize the need to restore, protect and manage streams and their riparian forests in an integrated effort because any change to one of the two interlinked ecosystems will also affect the other one (Hjälten, Nilsson, Jörgensen, & Bell, 2016).

4.3 Effects of mosses, sedimentation and dispersal (III)

Mosses, sand sedimentation and enhanced dispersal had mainly simple main effects on response variables. Mosses had a negative effect on leaf decomposition, periphyton accrual rate and grazing invertebrates, but a positive effect on organic matter retention and detritus feeders. Mosses reduced macroinvertebrate richness and diversity but increased invertebrate density. Mosses also buffered some of the effects of sand and had a stronger effect in structuring macroinvertebrate communities than did sand sedimentation.

Sand reduced periphyton accrual because of scouring and shading (Mustonen *et al.,* 2016, Louhi *et al.,* 2017) but had no effect on leaf decomposition. Sand reduced invertebrate density but not richness or diversity. However, density of some macroinvertebrate taxa, such as *Leptophlebia* sp., *Heptagenia sulphurea* and Chironomidae, were negatively impacted by sand. Enhanced dispersal decreased periphyton accrual rate and increased decomposition due to increased density of invertebrate consumers. Dispersal increased invertebrate density and richness and thus had strong effect on invertebrate community composition, but mosses and sand retained a distinct imprint on community structure even under intensive dispersal, and the communities were not homogenized, suggesting a strong environmental control over community composition.

Large *Fontinalis* mosses are known to retain effectively organic matter (Muotka & Laasonen, 2002, Koljonen *et al.,* 2012), and they thus increased detrivore abundances, highlighting the indirect importance of mosses in fueling detritus-based food webs in headwater streams. Negative effects of mosses on periphyton accrual were likely related to shading and nutrient competition that resulted in lower periphyton production rate in the presence of mosses. It is also possible that reduction of current velocity by mosses played a role in reducing periphyton accrual rate (Horner & Welch, 1981). Mosses may have reduced decomposition rate because the organic matter retained by mosses provides an additional food resource for shredders and thus reduced shredder aggregation to leaf packs.

These results suggest that moss is an important habitat component structuring boreal streams and also influences their ecosystem functions. Sedimentation clearly had an impact on invertebrate community composition but less so than did mosses. It is likely that a large part of the negative effects of excessive sedimentation is caused by indirect effects of moss eradication due to sediments rather than fine sediments *per se*. Thus, recovery of mosses after sedimentation (or restoration) is of high importance for the full recovery of boreal stream ecosystems. Our results suggest that local-scale factors (sedimentation, moss cover) does have an impact on community composition even under extensive dispersal. Thus, restoration that changes key habitat structures is likely to result in observable biodiversity responses despite of the homogenizing forces of dispersal.

5 Conclusions

Protecting ecosystems and their services is a major challenge for humanity. In streams and rivers, hydropmorphological alteration (e.g. channelization, damming) and land use -induced stressors (e.g. nutrient, sediment, pesticide and metal pollution) rank at the top of the ecosystem changes that threat the biodiversity and functioning of these systems (Malmqvist & Rundle, 2002; Vörösmarty *et al*, 2010). The restoration of ecosystems from an impaired state to the desired "natural" state is the main goal of the majority of restoration projects (Palmer, Hondula, Koch, 2014). Despite restoration ecology as a science has obviously advanced during the past decades, there is still considerable lack of understanding how restoration should be conducted to attain its goals, how ecological communities recover after restoration, and what the trajectory towards the desired ecosystem functions and community assembly is (Palmer, Falk, Zedler, 2006). In the context of stream restoration, most restoration actions are commonly limited to reach scale habitat enhancement, despite the acknowledged limitations of this approach (Palmer *et al.,* 2010, Louhi *et al.,* 2011, Sundermann *et al.,* 2011).

This thesis demonstrates that catchment level land use and the consequent diffuse pollution (nutrients, fine sediments) is a major driver altering boreal stream assemblages, overruling any effects of hydromorphological channel alteration, such as channelization for timber transport. Thus, stream restoration is likely to be more effective if mitigation of catchment level stressors is the priority in restoration programs rather than reach scale habitat modifications.

Excessive sedimentation is a major stressor to boreal headwater streams that results in biodiversity loss, although ecosystem functions do not necessarily change from natural conditions. Once the sources of sediment erosion are controlled, reach scale restoration methods, such as addition of boulders and wood, can improve both stream and riparian biodiversity in sediment-stressed streams. However, the improvement of in-stream habitat and biodiversity are specific to the restoration measures applied. The results suggest that both addition of boulders and wood should be applied for a better restoration outcome, highlighting the importance of managing streams and their riparian zones in an integrated effort, as these ecosystem are highly intertwined by reciprocal energy subsidies (Baxter, Fausch, & Saunders, 2005; Wallace, Eggert, Meyer, & Webster, 2015). Recovery of stream mosses is an important goal in restoration of boreal headwater streams, as they retain organic matter, modify ecosystem functioning and have substantial effects on community composition of stream biota.

Management of streams should be done mainly at the catchment scale with emphasis on mitigation of excessive erosion, loading of fine sediments and nutrients and maintenance of natural hydrology. Conserving and restoring the integrity of riparian forests will provide ecological benefits to streams by protecting streams from solar heating, diffuse pollution, and by supplying streams with woody debris and other organic matter that fuels stream food webs (Gregory *et al.,* 1991; Wallace *et al.,* 1997; Johnson & Almlöf, 2016). The present restoration practices often put large emphasis on restoring salmonid habitats in which they could be successful (Palm, Brännäs, Lepori, Nilsson, & Stridsman 2007; Whiteway *et al.,* 2010; Louhi, Vehanen, Huusko, Mäki-Petäys, & Muotka, 2016). However, stream ecosystems as a whole would likely benefit from more variable reach scale restoration approaches that include, for example, restoration of natural hydrological retentivity, flooding tendency in floodplain areas, debris accumulations and aided re-colonization of key species, such as mosses. The present use of woody debris in restoration programs is often very shy compared to volumes recorded in near-pristine boreal streams (Liljaniemi, Vuori, Ilyashuk, & Luotonen, 2002) and should be increased. However, it is also important to take into account the socio-economical values and needs for streams that can sometimes compromise the application of ecologically optimal restoration programs.

References

Allan, J. D. (2004). Landscapes and riverscapes: the influence of land use on stream ecosystems. *Annual Review of Ecology and Systematics*, *35*(1), 257–284. doi: 10.1146/annurev.ecolsys.35.120202.110122

Anderson, M. J. (2001). A new method for non-parametric multivariate analysis of variance. *Austral Ecology*, *26*(1), 32–46. doi: 10.1111/j.1442-9993.2001.01070.pp.x

Baxter, C. V., Fausch, K. D., & Saunders, W. C. (2005). Tangled webs: reciprocal flows of invertebrate prey link streams and riparian zones. *Freshwater Biology*, *50*(2), 201–220. doi: 10.1111/j.1365-2427.2004.01328.x

Beisel, J.-N., Usseglio-Polatera, P., & Moreteau, J.-C. (2000). The spatial heterogeneity of a river bottom: a key factor determining macroinvertebrate communities. *Hydrobiologia*, *422*(0), 163–171. doi: 10.1023/A:1017094606335

Benton, T. G., Vickery, J. A., & Wilson, J. D. (2003). Farmland biodiversity: is habitat heterogeneity the key? *TRENDS in Ecology and Evolution*, *18*(4), 182–188. doi: 10.1016/S0169-5347(03)00011-9

Bernhardt, E. S., Palmer, M. A., Allan, J. D., Alexander, G., Barnas, K., Brooks, S., … Sudduth, E. (2005). Synthesizing U.S. river restoration efforts. *Science*, *308*(5722), 636–637. doi: 10.1126/science.1109769

Bond, N. R., & Lake, P. S. (2003). Local habitat restoration in streams: Constraints on the effectiveness of restoration for stream biota. *Ecological Management & Restoration*, *4*(3), 193–198. doi: 10.1046/j.1442-8903.2003.00156.x

Brown, B. L. (2003). Spatial heterogeneity reduces temporal variability in stream insect communities. *Ecology Letters*, *6*(4), 316–325. doi: 10.1046/j.1461-0248.2003.00431.x

Brown, B. L., & Swan, M. C. (2010). Dendritic network structure constrains metacommunity properties in riverine ecosystems. *Journal of Animal Ecology*, *79*(3), 571–580. doi: 10.1111/j.1365-2656.2010.01668.x

Brown, B. L., & Swan, M. C. (2017). Metacommunity theory meets restoration: isolation may mediate how ecological communities respond to stream restoration. Ecological Applications, *27*(7), 2209–2219. doi: 10.1002/eap.1602

Buck, O., Niyogi, D. K., & Townsend, C. R. (2004). Scale-dependence of land use effects on water quality of streams in agricultural catchments. *Environmental Pollution*, *130*(2), 287–299. doi: 10.1016/j.envpol.2003.10.018

Butchart, S. H. M., Walpole, M., Collen, B., van Strien, A., Scharlemann, J. P., Almond, R. E., …Watson, R. (2010). Global biodiversity: indicators of recent declines. *Science*, *328*(5982), 1164–1168. doi: 10.1126/science.1187512

Caporaso, J. G., Kuczynski, J., Stombaugh, J., Bittinger, K., Bushman, F. D., Costello, E. K., …Knight, R. (2010). QIIME allows analysis of high-throughput community sequencing data. *Nature Methods*, *7*(5), 335–336. doi: 10.1038/nmeth.f.303

Ceballos, G., Ehrlich, P. R., Barnosky, A. D., García, A., Pringle, R. M., & Palmer, T. M. (2015). Accelerated modern human–induced species losses: entering the sixth mass extinction. *Science Advances*, *1*(5), 1–5. doi: 10.1126/sciadv.1400253

Ceballos, G., Ehrlich, P. R., & Dirzo, R. (2017). Biological annihilation via the ongoing sixth mass extinction signaled by vertebrate population losses and declines. *Proceedings of The National Academy of Sciences*, *114*(30), 6089–6096. doi: 10.1073/pnas.1704949114

Crutzen, P. J., (2002). Geology of mankind. *Nature*, *415*, 23. doi: doi:10.1038/415023a

Danger, M., Cornut, J., Elger, A., & Chauvet, E. (2012). Effects of burial on leaf litter quality, microbial conditioning and palatability to three shredder taxa. *Freshwater Biology*, *57*(5), 1017–1030. 10.1111/j.1365-2427.2012.02762.x

Dearing, J. A., & Jones, R. T. (2003). Coupling temporal and spatial dimensions of global sediment flux through lake and marine sediment records. *Global Planet Change*, *39*(1-2), 147–168. doi: 10.1016/S0921-8181(03)00022-5

Dirzo, R., Young, H. S., Galetti, M., Ceballos, G., Isaac, N. J. B., & Collen, B. (2014). Defaunation in the Anthropocene. *Science*, *345*(6195), 401–406. doi: 10.1126/science.1251817

Dudgeon, D., Arthington, A. H., Gessner, M. O., Kawabata, Z.-I., Knowler. D. J., Lévêque, C., …Sullivan, C. A. (2006). Freshwater biodiversity: importance, threats, status and conservation challenges. *Biological Reviews*, *81*(2), 163–182. doi: 10.1017/S1464793105006950

Dufrêne, M., & Legendre, P. (1997). Species assemblages and indicator species: the need for a flexible asymmetrical approach. *Ecological Monographs*, *67*(3), 345–366. doi: 10.1890/0012-9615(1997)067[0345:SAAIST]2.0.CO;2

Edgar, R. C. (2010). Search and clustering orders of magnitude faster than BLAST. *Bioinformatics*, *26*(19), 2460–2461. doi: 10.1093/bioinformatics/btq461

Ekholm, P., Kallio, K., Salo, S., Pietiläinen, O.-P., Rekolainen, S., Laine, Y., & Joukola, M. (2000). Relationship between catchment characteristics and nutrient concentrations in an agricultural river system. *Water Research*, *34*(15), 3709–3716. doi: 10.1016/S0043-1354(00)00126-3

Elbrecht, V., Beermann, A. J, Goessler, G., Neumann, J., Tollrian, R., Wagner, R., …Leese, F. (2016). Multiple-stressor effects on stream invertebrates: a mesocosm experiment manipulating nutrients, fine sediment and flow velocity. *Freshwater Biology*, *61*(4), 362–375. doi: 10.1111/fwb.12713

Gessner, M. O., & Chauvet, E. (2002). A case for using litter breakdown to assess functional stream integrity. *Ecological Applications*, *12*(2), 498–510. doi: 10.1890/1051-0761(2002)012[0498:ACFULB]2.0.CO;2

Gulis, V., & Suberkropp, K. (2002). Leaf litter decomposition and microbial activity in nutrient-enriched and unaltered reaches of a headwater stream. *Freshwater Biology*, *48*(1), 362–375. doi: 10.1046/j.1365-2427.2003.00985.x

Gregory, S. V., Swanson, F. J., McKee, W. A., & Cummins, K. W. (1991). An ecosystem perspective of riparian zones. *BioScience*, *41*(8), 540–551. doi: 10.2307/1311607

Greenwood, M. J., Harding, J. S., Niyogi, D. K., & McIntosh, A. R. (2012). Improving the effectiveness of riparian management for aquatic invertebrates in a degraded agricultural landscape: stream size and land-use legacies. *Journal of Applied Ecology*, *49*(1), 213–222. doi: 10.1111/j.1365-2664.2011.02092.x

Hassan, M. A., Church, M., Lisle, T. E., Brardinoni, F., Benda, L., & Grant, G. E. (2005). Sediment transport and channel morphology of small, forested streams. *Journal of the American Water Resources Association*, *41*(4), 853–876. doi: 10.1111/j.1752-1688.2005.tb03774.x

Hawkins, C. P. (2006). Quantifying biological integrity by taxonomic completeness: its utility in regional and global assesments. *Ecological Applications*, *16*(4), 1277–1294. doi: 10.1890/1051-0761(2006)016[1277:QBIBTC]2.0.CO;2

Helfield, J. M., Capon, S. J., Nilsson, C., Jansson, R., & Palm, D. (2007). Restoration of rivers used for timber floating: effects on riparian plant diversity. *Ecological Applications*, *17*(3), 840–851. doi: 10.1890/06-0343

Hering, D., Johnson, R. K., Kramm, S., Schmutz, S., Szoszkiewicz, K. & Verdonschot P. F. M. (2006). Assessment of European streams with diatoms, macrophytes, macroinvertebrates and fish: a comparative metric-based analysis of organism response to stress. *Freshwater Biology*, *51*(9), 1757–1785. doi: 10.1111/j.1365-2427.2006.01610.x

Hilderbrand, R. H., Watts, A. C., & Randle. A. M. (2005). The myths of restoration ecology. *Ecology and Society*, *10*(1), 19. doi: 0.5751/ES-01277-100119

Hjälten, J., Nilsson, C., Jörgensen, D., & Bell, D. (2016). Forest–stream links, anthropogenic stressors, and climate change: implications for restoration planning. *Bioscience*, *66*(8), 646–654. doi: 10.1093/biosci/biw072

Horner, R. R., & Welch, E. B. (1981). Stream periphyton development in relation to current velocity and nutrients. *Canadian Journal of Fisheries and Aquatic Sciences*, *38*(4), 449–457. doi: 10.1139/f81-062

Huttunen, K.-L., Mykrä, H., Oksanen, J., Astorga, A., Paavola, R., & Muotka, T. (2017). Habitat connectivity and in-stream vegetation control temporal variability of benthic invertebrate communities. *Scientific Reports*, *7*(1), 1448. doi: 10.1038/s41598-017-00550-9

Ilmavirta, V., & Toivonen, H. (1986). Comparative studies on macrophytes and phytoplankton in ten small brown-water lakes of different trophic status. *Aqua Fennica*, *16*(1), 125–142.

Johnson, R. K., & Almlöf, K. (2016). Adapting boreal streams to climate change: effects of riparian vegetation on water temperature and biological assemblages. *Freshwater Science*, *35*(3), 984–997. doi: 10.1086/687837

Jones, J. I., Duerdoth, C. P., Collins, A. L., Naden, P. S., & Sear, D. A. (2014). Interactions between diatoms and fine sediment. *Hydrological Processes*, *28*(3), 1226–1237. doi: 10.1002/hyp.9671

Jähnig, S. C., Brunzel, S., Gacek, S., Lorenz, A. W., & Hering, D. (2009). Effects of re-braiding measures on hydromorphology, floodplain vegetation, ground beetles and benthic invertebrates in mountain rivers. *Journal of Applied Ecology*, *46*(2), 406–416. doi: 10.1111/j.1365-2664.2009.01611.x

Kemp, P., Sear, D., Collins, A., Naden, P., & Jones, I. (2011). The impacts of fine sediment on riverine fish. *Hydrological Processes*, *25*(11), 1800–1821. doi: 10.1002/hyp.7940

Koljonen, S., Louhi, P., Mäki-Petäys, A., Huusko, A., & Muotka, T. (2012). Quantifying the effects of in-stream habitat structure and discharge on leaf retention: implications for stream restoration. *Freshwater Science*, *31*(4), 1121–1130. doi: 10.1899/11-173.1

Kreutzweiser, D. P., & Capell, S. S. (2001). Fine sediment deposition in stream after selective forest harvesting without riparian buffers. *Canadian Journal of Forest Research*, *31*(12), 2134–2142. doi: 10.1139/x01-155

Kreutzweiser, D. P., Capell, S. S., & Good, K. P. (2005). Effects of fine sediment inputs from a logging road on stream insect communities: a large-scale experimental approach in a Canadian headwater stream. *Aquatic Ecology*, *39*(1), 55–66. doi: 10.1007/s10452-004-5066-y

Lammert, M., & Allan, J. D. (1999). Assessing biotic integrity of streams: effects of scale in measuring the influence of land use/cover and habitat structure on fish and macroinvertebrates. *Environmental Management*, *23*(2), 257-270. doi: 10.1007/s002679900184

Lecerf, A., & Richardson, J. S. (2010). Litter decomposition can detect effects of high and moderate levels of forest disturbance on stream condition. *Forest Ecology and Management*, *259*(12), 2433–2443. doi: 10.1016/j.foreco.2010.03.022

Leibold, M. A., Holyoak, M., Mouquet, N., Amarasekara, P., Chase, J. M., Hoopes, M. F., … Gonzalez, A. (2004). The metacommunity concept: a framework for multi-scale community ecology. *Ecology letters*, *7*(7), 601–613. doi: 10.1111/j.1461-0248.2004.00608.x

Lepori, F., Palm, D., Brännäs, E., & Malmqvist, B. (2005). Does restoration of structural heterogeneity in streams enhance fish and macroinvertebrate diversity? *Ecological Applications*, *15*(6), 2060–2071. doi: 10.1890/04-1372

Leps, M., Sundermann, A., Tonkin, J. D., Lorenz, A. W., & Haase, P. (2016). Time is no healer: increasing restoration age does not lead to improved invertebrate communities in restored river reaches. *Science of the Total Environment*, *557-558*(1), 722–732. doi: 10.1016/j.scitotenv.2016.03.120

Liljaniemi, P., Vuori, K.-M., Ilyashuk, B., & Luotonen, H. (2002). Habitat characteristics and macroinvertebrate assemblages in boreal forest streams: relations to catchment silvicultural activities. *Hydrobiologia*, *474*(1-3), 239–251. doi: 10.1023/A:1016552308537

Lorenz, A. W., Korte, T., Sundermann, A., Januscke, K., & Haase, P. (2012). Macrophytes respond to reach-scale river restorations. *Journal of Applied Ecology*, *49*(1), 202–212. doi: 10.1111/j.1365-2664.2011.02082.x

Louhi, P., Mykrä, H., Paavola, R., Huusko, A., Vehanen, T., Mäki-Petäys, A., & Muotka, T. (2011). Twenty years of stream restoration in Finland: little response by benthic macroinvertebrate communities. *Ecological Applications*, *21*(6), 1950–1961. doi: 10.1890/10-0591.1

Louhi, P., Vehanen, T., Huusko, A., Mäki-Petäys, A., & Muotka, T. (2016). Long-term monitoring reveals the success of salmonid habitat restoration. *Canadian Journal of Fisheries and Aquatic Sciences*, *73*(12), 1733–1741. doi: 10.1139/cjfas-2015-0546

Louhi, P., Richardson, J. S., & Muotka, T. (2017). Sediment addition reduces the importance of predation on ecosystem functions in experimental stream channels. *Canadian Journal of Fisheries and Aquatic Sciences*, *74*(1), 32–40. doi: 10.1139/cjfas-2015-0530

Malmqvist, B. & Rundle, S. (2002). Threats to the running water ecosystems of the world. *Environmental Conservation*, *29*(2), 134–153. doi: 10.1017/S0376892902000097

Marttila, M., Louhi, P., Huusko, A., Mäki-Petäys, A., Yrjänä, T., & Muotka, T. (2016). Long-term performance of in-stream restoration measures in boreal streams. *Ecohydrology*, *9*(2), 280–289. doi: 10.1002/eco.1634

Matthaei, C. D., Piggot, J. J., & Townsend, C. R. (2010). Multiple stressors in agricultural streams: interactions among sediment addition, nutrient enrichment and water abstraction. *Journal of Applied Ecology*, *47*(3), 639–649. doi: 10.1111/j.1365-2664.2010.01809.x

Morrice, J. A., Valett, H. M., Dahm, C. N., & Campana, M. E. (1997). Alluvial characteristics, groundwater-surface exchange and hydrological retention in headwater streams. *Hydrological Processes*, *11*(3), 253–267. doi: 10.1002/(SICI)1099-1085(19970315)11:3<253::AID-HYP439>3.0.CO;2-J

Moss, D., Furse, M. T., Wright, J. F., & Armitage, P. D. (1987). The prediction of the macro-invertebrate fauna of unpolluted running-water sites in Great Britain using environmental data. *Freshwater Biology*, *17*(1), 41–52. doi: 10.1111/j.1365-2427.1987.tb01027.x

Muotka, T., & Laasonen, P. (2002). Ecosystem recovery in restored headwater streams: the role of enhanced leaf retention. *Journal of Applied Ecology*, *39*(1), 145–156. doi: 10.1046/j.1365-2664.2002.00698.x

Muotka, T., & Syrjänen, J. (2007). Changes in habitat structure, benthic invertebrate diversity, trout populations and ecosystem processes in restored forest streams: a boreal perspective. *Freshwater Biology*, *52*(4), 724–737. doi: 10.1111/j.1365-2427.2007.01727.x

Mustonen, K.-R., Mykrä, H., Louhi, P., Markkola, A., Tolkkinen, M., Huusko, A., …Muotka, T. (2016). Sediments and flow have mainly independent effects on multitrophic stream communities and ecosystem functions. *Ecological Applications*, *26*(7), 2116–2129. doi: 10.1890/15-1841.1

Mykrä, H., Ruokonen, T., & Muotka, T. (2006). The effect of sample duration on the efficiency of kick-sampling in two streams with contrasting substratum heterogeneity. *Verhandlungen des Internationalen Verein Limnologie*, *29*(1), 1351–1355. doi: 10.1080/03680770.2005.11902901

National Board of Waters. (1981). *The analytical methods used by National Board of Waters. Report 213*. Helsinki, Finland: National Board of Waters.

Nilsson, C., Lepori, F., Malmqvist, B., Törnlund, E., Hjerdt, N., Helfield, J. M., … Lundqvist, H. (2005). Forecasting environmental responses to restoration of rivers used as log floatways: an interdisciplinary challenge. *Ecosystems*, *8*(7), 779–800. doi: 10.1007/s10021-005-0030-9

Paavilainen, E., & Päivänen, J. (1995). *Peatland forestry: ecology and principles*. Berlin: Springer-Verlag.

Palm, D., Brännäs, E., Lepori, F., Nilsson, K., & Stridsman, S. (2007). The influence of spawning habitat restoration on juvenile brown trout (Salmo trutta) density. *Canadian Journal of Fisheries and Aquatic Sciences*, *64*(3), 509–515. doi: 10.1139/f07-027

Palmer, M. A., Ambrose, R. F., & Poff, N. L. (1997). Ecological theory and community restoration ecology. *Restoration Ecology*, *5*(4), 291–300. doi: 10.1046/j.1526-100X.1997.00543.x

Palmer, M. A., Falk, D. A., & Zedler, J. B. (2006). Ecological theory and restoration ecology. In D. A., Falk, M. A., Palmer, & Zedler, J. B. (ed), *Foundations of Restoration Ecology* (pp. 1-10). Washington D. C.: Island Press

Palmer, M. A., Menninger, H. L., & Bernhardt, E. S. (2010). River restoration, habitat heterogeneity and biodiversity: a failure of theory or practice. *Freshwater Biology*, *55*(s1), 1–18. doi: 10.1111/j.1365-2427.2009.02372.x

Palmer, M. A., Hondula, K. L., & Koch, B. J. (2014). Ecological restoration of streams and rivers: shifting strategies and shifting goals. *Annual Review of Ecology, Evolution, and Systematics*, *45*(1), 247–269. doi: 10.1146/annurev-ecolsys-120213-091935

Paul, M. J., & Meyer, J. L. (2001). Streams in the urban landscape. *Annual Review of Ecology and Systematics*, *32*(1), 333–365. doi: 10.1146/annurev.ecolsys.32.081501.114040

Pedersen, M. L., Kristensen, K. K., & Friberg, N. (2014). Re-Meandering of lowland streams: will disobeying the laws of geomorphology have ecological consequences? *PLoS ONE*, *10*(3), doi: 10.1371/journal.pone.0108558

Pinheiro, J. C., & Bates, D. M. (2000). *Mixed effects models in S and S-Plus*. New York, USA: Springer-Verlag.

Pinheiro, J., Bates, D., DebRoy, S., Sarkar, D., & R Core Team. (2015). nlme: Linear and nonlinear mixed effects models. R package version 3.1–122. http://www.r-project.org/package=nmle

Pinheiro, J., Bates, D., DebRoy, S., Sarkar, D., & the R Development Core Team. (2017). nlme: linear and nonlinear mixed effects models. R package version 3.1–131. http://www.r-project.org/package=nmle

Poff, N. L., Brinson, M. M., & Day, J. W. Jr. (2002). Aquatic ecosystems & global climate change: Potential impacts on inland freshwater and coastal wetland ecosystems in the United States. Prepared for the Pew Center on global climate change, 1–45.

Raven, P. J., Holmes, N. T. H., Dawson, F. H., & Everard, M. (1998). Quality assessment using river habitat survey data. *Aquatic Conservation: Marine and Freshwater Ecosystems*, *8*(4), 477–499. doi: 10.1002/(SICI)1099-0755(199807/08)8:4<477::AID-AQC299>3.0.CO;2-K

Roberts, D. W. (2012). labdsv: ordination and multivariate analysis for ecology. R package version 1.5–0. http://CRAN.R-project.org/package=labdsv

Rosemond, A. D., Benstead, J. P., Bumpers, P. M., Gulis, V., Kominoski, J. S., Manning, D. W. P., …Wallace, B. J. (2015). Experimental nutrient additions accelerate terrestrial carbon loss from stream ecosystems. *Science*, *347*(6226), 1142–1145. doi: 10.1126/science.aaa1958

Runkel, R. L. (1998). One-Dimensional Transport with Inflow and Storage (OTIS): A Solute Transport Model for Streams and Rivers. U.S. Geological Survey Water-Resources Investigations Report.

Sala, O. E., Chapin, F. S., Armesto, J. J., Berlow, E., Bloomfield, J., Dirzo, R., …Wall, D. H. (2000). Global Biodiversity Scenarios for the Year 2100. *Science*, *287*(5459), 1770–1774. doi: 10.1126/science.287.5459.1770

Sih, A., Englund, G., & Wooster, D. (1998). Emergent impacts of multiple predators on prey. *TRENDS in Ecology and Evolution*, *13*(9), 350–355. doi: 10.1016/S0169-5347(98)01437-2

Sponseller, R. A., Benfield, E. F., & Valett, H. M. (2001). Relationships between land use, spatial scale and stream macroinvertebrate communities. *Freshwater Biology*, *46*(10), 1409–1424. doi: 10.1046/j.1365-2427.2001.00758.x

Stoddard, J. L., Larsen, D. P., Hawkins, C. P., Johnson, R. K., & Norris, R. H. (2006). Setting expectations for the ecological condition of streams: the concept of reference condition. *Ecological Applications*, *16*(4), 1267–1276. doi: 10.1890/1051-0761(2006)016[1267:SEFTEC]2.0.CO;2

Stofleth, J. M., Shields, F. D., & Fox, G. A. (2008). Hyporheic and total transient storage in small, sand-bed streams. *Hydrological Processes*, *22*(12), 1885–1894. doi: 10.1002/hyp.6773

Stranko, S. A., Hilderbrand, R. H., & Palmer, M. A. (2011). Comparing the fish and benthic macroinvertebrate diversity of restored urban streams to reference streams. *Restoration Ecology*, *20*(6), 747–755. doi: 10.1111/j.1526-100X.2011.00824.x

Sundermann, A., Antons, C., Cron, N., Lorenz, A. W., Hering, D., & Haase, P. (2011). Hydromorphological restoration of running waters: effects on benthic invertebrate assemblages. *Freshwater Biology*, *56*(8), 1689–1702. doi: 10.1111/j.1365-2427.2011.02599.x

Sutherland, A. B., Meyer, J. L., & Gardiner, E. P. (2002). Effects of land cover on sediment regime and fish assemblage structure in four southern Appalachian streams. *Freshwater Biology*, *47*(9), 1791–1805. doi: 10.1046/j.1365-2427.2002.00927.x

Suurkuukka, H., Virtanen, R., Soursa, V., Soininen, J., Paasivirta, L., & Muotka, T. (2014). Woodland key habitats and stream biodiversity: does small scale terrestrial conservation enhance the protection of stream biota? *Biological Conservation*, *170*(1), 10–19. doi: 10.1016/j.biocon.2013.10.009

Tews, J., Brose, U., Grimm, V., Tielbörger, K., Wichmann, M. C., Schwager, M., & Jeltsch, F. (2004). Animal species diversity driven by habitat heterogeneity/diversity: the importance of keystone structures. *Journal of Biogeography*, *31*(1), 79–92. doi: 10.1046/j.0305-0270.2003.00994.x

Tolkkinen, M., Mykrä, H., Markkola, A.-M., Aisala, H., Vuori, K.-M., Lumme, J., …Muotka, T. (2013). Decomposer communities in human impacted streams: species dominance rather than richness affects leaf decomposition. *Journal of Applied Ecology*, *50*(5), 1142–1151. doi: 10.1111/1365-2664.12138

Tolkkinen, M., Mykrä, H., Annala, M., Markkola, A. M., Vuori, K.-M., & Muotka, T. (2015). Multi-stressor impacts on fungal diversity and ecosystem functions in streams: natural vs. anthropogenic stress. *Ecology*, *96*(3), 672–683. doi: 10.1890/14-0743.1

Tonkin, J. D., Stoll, S., Sundermann, A. & Haase, P. (2014). Dispersal distance and the pool of taxa, but not barriers, determine the colonization of restored river reaches by benthic invertebrates. *Freshwater Biology*, *59*(9), 1843–1855. doi: 10.1111/fwb.12387

Tornwall, B. M., Swan, C. M., & Brown, B. L. (2017). Manipulation of local environment produces different diversity outcomes depending on location within a river network. *Oecologia*, *184*(3), 663–674. doi:10.1007/s00442-017-3891-7

Turunen, J. (2008). Development of Finnish peatland area and carbon storage 1950–2000. *Boreal Environment Research*, *13*(4), 319–334.

Vehanen, T., Sutela, T., & Korhonen, H. (2010). Environmental assessment of boreal rivers using fish data — a contribution to the Water Framework Directive. *Fisheries Management and Ecology*, *17*(2), 165–175. doi: 10.1111/j.1365-2400.2009.00716.x

Venail, P. A., MacLean, R. C., Bouvier, T., Brockhurst, M. A., Hochberg M. E., & Mouquet, N. (2008). Diversity and productivity peak at intermediate dispersal rate in evolving metacommunities. *Nature*, *452*, 210–214. doi: 10.1038/nature06554

Vuori, K.-M., & Joensuu, I. (1996). Impact of forest drainage on the macroinvertebrates of small boreal headwater stream: Do buffer zones protect lotic biodiversity? *Biological Conservation*, *77*(1), 87–95. doi: 10.1016/0006-3207(95)00123-9

Vuori, K.-M., Joensuu, I., Latvala, J., Jutila, E., & Ahvonen, A. (1998). Forest drainage: a threat to benthic biodiversity of boreal headwater streams? *Aquatic Conservation: Marine and Freshwater Ecosystems*, *8*(6), 745–759. doi: 10.1002/(SICI)1099-0755(1998110)8:6<745::AID-AQC310>3.0.CO;2-X

Vuori, K.-M., Mitikka, S., & Vuoristo, H. (2009). Pintavesien ekologisen tilan luokittelu. Osa I: Vertailuolot ja luokan määrittäminen, Osa II: Ihmistoiminnan ympäristövaikutusten arviointi. Retrieved from https://helda.helsinki.fi/handle/10138/41785

Vörösmarty, C. J., McIntyre, P. B., Gessner, M. O., Dudgeon, D., Prusevich, A., Green, P., …Davies, P. M. (2010). Global threats to human water security and river biodiversity. *Nature*, *467*, 555–561. doi:10.1038/nature09440

Wagenhoff, A., Townsend, C. R., & Matthaei, C. D. (2012). Macroinvertebrate responses along broad stressor gradients of deposited fine sediment and dissolved nutrients: a stream mesocosm experiment. *Journal of Applied Ecology*, *49*(4), 892–902. doi: 10.1111/j.1365-2664.2012.02162.x

Wallace, J. B., Eggert, S. L., Meyer, J. L., & Webster, J. R. (1997). Multiple trophic levels of a forest stream linked to terrestrial litter inputs. *Science*, *277*(5322), 102–104. doi: 10.1126/science.277.5322.102

Wallace, J. B., Eggert, S. L., Meyer, J. L., & Webster, J. R. (2015). Stream invertebrate productivity linked to forest subsidies: 37 stream-years of reference and experimental data. *Ecology*, *96*(5), 1213–1228. doi: 10.1890/14-1589.1

Warton, D. I., & Hui, F. K. C. (2011). The arcsine is asinine: the analysis of proportions in ecology. *Ecology*, *92*(1), 3–10. doi: 10.1890/10-0340.1

Waters, T. F. (1995). *Sediment in streams: Sources, biological effects and control*. Bethesda, Maryland: American Fisheries Society.

Whiteway, S. L., Biron, P. M., Zimmermann, A., Venter, O., & Grant, J. W. A. (2010). Do in-stream restoration structures enhance salmonid abundance? A meta-analysis. *Cananadian Journal of Fisheries and Aquatic Sciences*, *67*(5), 831–841. doi: 10.1139/F10-021

Winking, C., Lorenz, A. W., Sures, B. & Hering, D. (2014). Recolonisation patterns of benthic invertebrates: a field investigation of restored former sewage channels. *Freshwater Biology*, *59*(9), 1932–1944. doi: 10.1111/fwb.12397

WWF, (2016). *Living planet report 2016. Risk and resilience in a new era*. Gland, Swizerland: WWF International.

Zuur, A. F., Ieno, E. N., Walker, N. J., Saveliev, A. A, & Smith, G. M. (2009). *Mixed effects models and extensions in ecology with R. Statistics for biology and health.* New York, USA: Springer-Verlag.

Original articles

I Turunen J, Muotka T, Vuori K-M, Karjalainen SM, Rääpysjärvi J, Sutela T & Aroviita J (2016). Disentangling the responses of boreal stream assemblages to low stressor levels of diffuse pollution and altered channel morphology. Science of the Total Environment 544: 954–962.

II Turunen J, Aroviita J, Marttila H, Louhi P, Laamanen T, Tolkkinen M, Luhta P-L, Kløve B & Muotka T (2017). Differential responses by stream and riparian biodiversity to restoration of forestry-impacted streams. Journal of Applied Ecology 54: 1505–1514.

III Turunen J, Louhi P, Mykrä H, Aroviita J, Putkonen E, Huusko A & Muotka T (2017). Habitat structure controls community assembly and stream ecosystem functioning under extensive dispersal and anthropogenic disturbance. Manuscript.

Original publications are not included in the electronic version of the dissertation.

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UNIVERSITY of OULU
OULUN YLIOPISTO

ISBN 978-952-62-1781-9 (Paperback)
ISBN 978-952-62-1782-6 (PDF)
ISSN 0355-3191 (Print)
ISSN 1796-220X (Online)