2	Does the buffer width matter: testing the effectiveness of forest certificates in the
3	protection of headwater stream ecosystems
4	Jussi Jyväsjärvi <sup>1</sup> , Iina Koivunen <sup>1</sup> and Timo Muotka <sup>1,2</sup>
5	
6	<sup>1</sup> University of Oulu, Ecology and Genetics Research Unit, P.O. Box 3000, FI-90014, Oulu, Finland
7	<sup>2</sup> Finnish Environment Institute, Freshwater Centre, P.O. Box 413, FI-90014, Oulu, Finland
8	
9	
10	Corresponding author: Jussi Jyväsjärvi
11	email: jussi.jyvasjarvi@oulu.fi
12	Running title: Effectiveness of stream buffers
13	
14	Keywords: forestry, buffer management, decomposition, ecosystem processes, benthic invertebrates
15	
16	
17	
18	
19	
20	

2.1	Abstract
Z I	- ADSITACI

Forest harvest has multiple impacts on adjoining freshwater ecosystems, particularly headwater streams which typically receive minimal protection against forestry. However, evidence on the effectiveness of differently sized riparian buffers remains limited. Using data from two discrete regions of Finland, we assessed the effectiveness of riparian buffers in providing protection for the riparian and stream environment, benthic invertebrate diversity and species composition, and ecosystem functioning of boreal headwater streams. Our study included streams with both wide (> 15 m) and narrow (< 15 m) riparian buffers, enabling comparison of the two dominant forest certificates (FSC and PEFC). Compared to unharvested reference streams, nutrient concentrations as well as stream and riparian light intensity and temperature were higher at forestry-impacted sites. The amount of woody debris, cover of aquatic mosses and particulate organic matter standing stock were strongly reduced in streams draining harvested forests, especially in narrowly buffered streams. Changes in light and nutrient conditions induced a transition towards more autotrophic conditions. Organic matter decomposition rates were elevated in forestry-impacted sites only in the southern region. Forest harvest decreased macroinvertebrate diversity and evenness, and altered community composition in the northern region, but much weaker changes were observed in the southern region. Our findings support the retention of riparian buffers, but also confirm that their effectiveness depends on the environmental context and thus remains poorly predictable. Our results also suggest that the widely applied PEFC certification does not provide sufficient protection for stream ecosystems and more stringent protocols are needed to ensure ecological sustainability of forestry.

42

41

43

### 1. Introduction

45

Global efforts to reduce the consumption of non-renewable energy have provoked a worldwide surge 47 of bioeconomy (EC, 2018). This is placing increasing pressure on the exploitation of natural resources, and in forest-rich countries a prominent environmental impact of this development is the loss and modification of forests. Intensified forestry not only degrades forest ecosystems but also imposes a substantial threat to adjacent freshwater ecosystems (Laudon et al., 2011; Jonsson et al., 51 2017). The uppermost parts of fluvial watercourses (hereafter, headwater streams) represent up to 80% of the total stream network length (Bishop et al., 2008) and are key habitats for biological diversity (Finn et al., 2011). Headwater ecosystems also regulate the availability of resources to downstream habitats 55 (Alexander et al., 2007). Given their small size and close intertwining with the surrounding forests, headwaters are often considered the most vulnerable part of riverine networks (Wallace and Eggert, 2015), yet recent studies imply that they are largely neglected during forestry planning and management (Richardson et al., 2012; Kuglerová et al., in review). Various protective measures have been taken to mitigate the effects of forestry on adjacent stream ecosystems. The most conventional method is to leave an unmanaged strip of vegetation (henceforth, 60 riparian buffer) between the stream and the harvest (Richardson et al., 2012). Retention of riparian buffers reduces nutrient and sediment transport from land, maintains natural in-stream thermal and light regimes and provides terrestrial resource subsidies to stream food webs (Kreutzweiser et al., 2009; Richardson and Sato, 2015). In most jurisdictions the retention of buffer strips is voluntary (Ring et al., 2017). For example, the Finnish Forest Act requires protection of riparian forests, but does not provide any specifications for the width, type or quality of the riparian buffers. In production forests, similar statutory protection

are ecologically, economically and socially sustainably used, forest owners are required to obtain a certificate for the wood they produce. Globally, there are two major forest certification systems: Program for the Endorsement of Forest 72 Certification (PEFC) and the Forest Stewardship Council (FSC). Both require some level of protective buffer between the harvested forest and the adjoining freshwater ecosystem. According to the Finnish FSC, the protective riparian buffer must comprise at least 15 meters of intact forest 74 (Finnish FSC Association, 2010). The principles of PEFC are less stringent and only require that the 76 riparian buffer should be at least 5 meters wide, and careful thinning can be allowed (PEFC Finland, 2014). While both certificates are currently available the PEFC certification is much more widely applied in Finland (95 % of certified forests; see Lopatin et al., 2016). 79 The riparian buffer retention measures of either certificate are, however, poorly supported by 80 scientific evidence. Several lines of evidence suggest that the protection of environmental conditions, key ecosystem processes and stream biodiversity requires 30-m wide riparian buffers (Sweeney and Newbold, 2014) and safeguarding the riparian plant and wildlife biodiversity may necessitate even more extensive (> 40 m) buffers (Marczak et al., 2010; Selonen and Kotiaho, 2013). A recent 84 comparison of contemporary riparian buffer practices among major forestry countries (Canada, Sweden and Finland) revealed that the average width of the riparian buffer around small forest 86 streams was far less than recommended by scientific consensus (Kuglerová et al, in review). These results also indicated considerable inconsistencies in riparian retention practices within each of the three countries, reflecting the lack of clear guidelines for buffer retention protocols. The discrepancies in riparian buffer management stem from region-specific differences but also indicate the shortage of systematic research regarding the effectiveness of riparian buffers on adjoining freshwater 91 ecosystems. Given the noticeable contribution of Nordic countries, particularly Sweden and Finland, to global forestry and forest economy (FAO, 2019), scientific evidence on the importance of riparian

does not exist; instead, their conservation is based on forest certificates. To verify that their forests

buffers and concrete guidelines for ecologically justified buffer widths is imperative for steering sustainable use of forests in northern Europe.

Here, we evaluated the importance of riparian buffer width to the protection of headwater stream ecosystems, particularly macroinvertebrate diversity and species composition, as well as key ecosystem functions. We focused on small streams draining recent clear-cut areas. Previous research has demonstrated that forestry impacts on adjoining streams are often complex and dependent on the environmental context (see Richardson and Béraud, 2014). To examine whether and how the responses differ within a single jurisdiction, we repeated our monitoring scheme in two regions differing in geographical location, climate, forest management practices and land use. In both regions, riparian buffer widths varied between 0-35+m, thus demonstrating the adaptation of buffer retention principles of either the PEFC or FSC certificate.

We hypothesise that, regardless of the region, streams receiving minimal protection (buffer < 15 m) deviate from the unharvested reference streams in terms of macroinvertebrate assemblages and ecosystems functioning while streams with wider riparian buffers (> 15 m) remain largely unaffected by forest harvest, resembling the reference streams. We anticipate that the environmental conditions inherent to near-pristine headwater streams and their riparian forests (e.g. high shade, low temperature, low nutrient levels) are compromised in poorly buffered streams. We anticipate that a narrow buffer decreases the quantity of particulate organic matter of terrestrial origin and intensifies light availability and primary production, resulting in transition towards autotrophy. Finally, the two study regions are expected to differ in their responses to nearby forestry; while the abiotic responses (light, temperature, organic matter standing stocks) are expected to be coherent across the regions, we expect that more pervasive land use in the southern region results in lower-quality reference sites. This is expected to obscure the signal of any individual land use type and therefore results in less pronounced biological differences between the reference and forestry-impacted streams.

## 2. Material and methods

We selected 23 small streams (orders 1 – 2) for the study, twelve in northern-central Finland (hereafter "northern" region) and 11 in south-western Finland ("southern" region; Fig. 1). The two regions differ in terms of climate, topography and intensity of land use (Table 1). The northern region constitutes headwaters of River Iijoki basin. The area represents a transitional zone between middle boreal and northern boreal ecoregions and is characterised by mires and mixed forests (Table 1). The southern region combines headwater tributaries of Rivers Karvianjoki, Isojoki and Kyröjoki. It is characterized by a flat coastal landscape dominated by a mixture of peatlands, forests and arable land (Table 1).

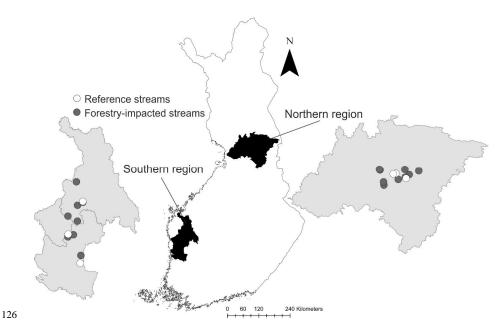


Fig. 1. Geographical locations of the study regions and of reference and forestry-impacted streams within each region.

	Northern region	Southern region
Latitude (°N) <sup>1</sup>	65°34' N	62°12' N
Longitude (°E) <sup>1</sup>	27°51' E	22°16' E
Altitude (m, a.s.l.) <sup>1</sup>	117	275
Annual mean air temperature (°C)	0	4.1
Annual mean precipitation (mm)	567	681
Built areas (%) <sup>2</sup>	1.0	3.3
Open mires (%) <sup>2</sup>	11.4	4.1
Coniferous forests (%) <sup>2</sup>	57.4	49.4
Deciduous forests (%) <sup>2</sup>	0.4	1.3
Mixed forests (%) <sup>2</sup>	8.6	11.5
Arable land (%) <sup>2</sup>	0.9	15.5

<sup>&</sup>lt;sup>1</sup> Central position of the study sites

Three of the study sites in each region did not have any recent (< 50 - 60 y) forestry actions nearby (> 300 m from the stream or at least 1.5 km upstream of a study site) and were used as reference streams. The remaining streams drained recent (3 - 6 y old) clear-cuts and sampling sites were located at the downstream end of a clear-cut. The streams were selected from a larger number of candidate sites (see Kuglerová et al., in review) so that the width of the forested riparian buffer between the stream and the clear-cut ranged from 0 to > 35 m. This range is well representative of Finnish riparian buffer practices (Kuglerová et al., in review). Typical of Finnish forestry, a great majority of our study streams (> 90 %) had clear-cuts and riparian buffers on one side of the stream while the other side

remained intact. Buffer width was calculated from three measurements taken within a 50-m study section. For the one-sided buffers, only the forestry-impacted side was considered and for the few two-sided buffers, the buffer width was measured on both sides and average of these measurements was used in the analyses. The following additional criteria were used for site selection: i) each site should contain a 50-m long continuous riffle section, ii) reference and forestry-impacted sites were spatially interspersed (Fig. 1), and iii) none of the sites were in the vicinity of an open mire, lake or spring outlet.

#### 2.2 Environmental measurements

Substratum structure was determined in 15 randomly distributed 0.25 m<sup>2</sup> plots using a modified Wentworth scale (see Mykrä et al., 2008). Water samples were collected once (August) and they were analysed for electrical conductivity, total phosphorus (TP), phosphate (PO<sub>4</sub>), total nitrogen (TN), nitrate-N (NO<sub>3</sub>), dissolved organic carbon (DOC) and pH following national standards. Catchment characteristics were determined using ArcMap Desktop 10.5 and CORINE 2018 land use data. Amount of large woody debris (LWD) was measured by summing the volume of wood particles (Ø > 5 cm) within the bankfull channel for each 50 m study section. We recorded temperature (°C) and light intensity (lux) in the stream channel and in the riparian forest (1 m from the stream, 1 m above the ground) in 1-h intervals with waterproof loggers (HOBO Pendant, Onset, Massachusetts) from late June to early October.

## 9 2.3 Sampling of benthic invertebrates and organic matter standing stock

Benthic macroinvertebrates and fine and coarse organic matter (FPOM and CPOM) were sampled by eight Surber samples ( $0.1~\text{m}^2$ ,  $500~\mu\text{m}$  mesh size) distributed randomly along the 50~m study reach. Each sample was preserved in 70% ethanol and invertebrates were later sorted from the other material and identified in the laboratory, mostly to species or genus level. Six of the eight samples were randomly selected for macroinvertebrate identification. The remaining material in each Surber sample

<sup>&</sup>lt;sup>2</sup> Mean across the river basin(s)

was fractionated into FPOM and CPOM using 0.2 mm and 1 mm sieves, respectively, and the sieved 165 material was dried for 48 h at 60 °C and weighed. The samples were combusted then for 4 h at 550 °C and reweighed to obtain ash-free dry mass (AFDM, g m<sup>-2</sup>). 167 2.4 Algal biomass accrual and organic matter decomposition Stream biofilm was sampled twice (July and August) in 2018 by incubating 10 cm × 10 cm 169 unglazed ceramic tiles (n = 10 per site) in the stream for 4 - 5 weeks. After incubation, biofilm was 170 scraped off into 100 ml distilled water and the suspension was filtered to 0.45 um filter papers (Whatman GF/F, Kent, UK). Chlorophyll a concentration (n = 5) was determined according to 173 Huttunen et al. (2012). Another five samples were dried at 60 °C for 24 h, weighed, combusted for 4 h at 550 °C and reweighed to convert dry mass to AFDM. Autotrophic index (AI) was calculated 174 as the ratio of biofilm AFDM and chlorophyll a. Mean values of the two samplings were used in 175 statistical analyses. 176 Total decomposition rate (including both macroinvertebrates and microbes) was measured using coarse mesh (8 mm) leaf bags which allowed leaf-shredding invertebrates to enter. Four grams of 178 179 dried birch (Betula pendula) leaves were enclosed in 15 × 15 cm nylon bags. Five bags were placed 180 onto the stream bed in early September and were removed after 5 – 6 weeks. In the laboratory, 181 litter bags were gently cleaned under tap water to remove any accumulated sediments. The 182 remaining leaf material was dried 48 h at 60 °C and ashed (4 h at 550 °C).

To measure microbial-mediated organic matter (cellulose) decomposition we used standardized cotton-strip assays (Tiegs et al., 2013). The cotton strips were prepared using unprimed 12–oz. cotton fabric, following Tiegs et al. (2013). One pre-weighed strip was inserted into each leaf bag.

After incubation the strips were gently cleaned, and decomposition was terminated by submerging the strips into 96% ethanol for 60 sec. The strips were dried for 48 h in 50 °C and weighed. Tensile strength loss (a surrogate for microbial decomposition rate) was measured by placing a 1-cm-long

portion of a cotton strip in the grips of a tensiometer (Zwick/Roell Z010, Germany) mounted on a
motorized test stand; the strip was then pulled at a fixed rate (2 cm min<sup>-1</sup>) until the strip tore. The
initial tensile strength (N) was determined as an average of 10 control strips processed identically
to the treatment strips. Tensile-strength loss was expressed as percent of the initial tensile-strength
lost per incubation period. No temperature correction was done for the decomposition data as the
potential within- and among-group differences in stream water temperature were considered
inherent to our study design.

## 2.5 Data analyses

198

199

203

204

205

206

209

210

211

The forestry-impacted sites were classified into two groups based on their average buffer width measured at three locations within the 50 m study reach. The sites with less than 15 m buffers (hereafter "Narrow") represent the typical buffer width of the PEFC certified forests whereas the sites with wider buffers (> 15 m; "Wide") follow the guidelines of the FSC certificate. Principal component analysis (PCA) was used to characterize environmental variation among the site groups (Reference, Wide and Narrow). For individual variables, the differences between the reference (baseline) and the two forestry-impacted site groups were determined with Generalized Linear Models (GLMs) with a gaussian link function. If test assumptions were not satisfied, log<sub>10</sub>transformation was applied to response variable. For each benthic macroinvertebrate sample, we calculated total density (individuals m<sup>-2</sup>), total species richness, number of EPT taxa (Ephemeroptera, Plecoptera, Trichoptera) and Pielou's evenness. Linear mixed effects-models (LMM) were applied to macroinvertebrate metrics and other biotic response variables with multiple measurements per stream (chlorophyll a, Autotrophic index, CPOM, FPOM and decomposition rates). LMM models were constructed using lme4 and lmerTest packages in R (R Core Team, 2019) and included buffer treatment as fixed effect and individual samples nested within stream as random effects. For count data (species and EPT number), we used generalized linear mixed models (GLMMs) with poisson error distribution with a log link function.

214 Patterns in macroinvertebrate species composition were visualized with non-metric multidimensional scaling (NMDS) using metaMDS function of vegan package (Oksanen et al., 2019) of the R. 215 Differences in species composition among stream groups were tested using nonparametric 216 permutational multivariate analysis of variance (PERMANOVA) with adonis function in vegan. 217 PERMANOVAs were run using the Bray-Curtis similarity coefficient on log<sub>10</sub>-transformed 218 abundance data, and statistical significance was estimated based on 9999 permutations. All six Surber 219 220 samples per site were used in PERMANOVA and the argument strata in the adonis2 function was used to circumvent spatial autocorrelation among replicates within each stream. A significant global test was ensued by pairwise PERMANOVAs. The among-group differences in environmental conditions were also tested with PERMANOVA, based on a Euclidean distance matrix. 223

### 3. Results

224

236

237

## 3.1 Environmental conditions

The median width of narrow riparian buffers was 6.75 m for the northern region (n = 4) and 7.0 m 227 for the southern region (n = 5), whereas the medians for wide buffers were 24.5 m (n = 5) and 23 m (n = 3) for the northern and southern region, respectively. For the northern region, the first two PCs 228 explained 58.6% of the variance of environmental data. The stream groups were well separated along 229 the first PC, which correlated positively with light availability and water and air temperature (Fig. 2a; Table 2), thus representing a buffer width gradient. The second PC represented a water chemistry 232 gradient with TP, NO<sub>3</sub> and DOC concentrations correlating positively with PC2 (Fig. 2a; Table 2). Environmental conditions differed among the stream groups (PERMANOVA;  $F_{2.9} = 2.75$ , P = 0.016), 233 with the narrowly-buffered sites differing from the reference (P = 0.05) based on, for example, lower 234 moss cover and a less large woody debris (Fig. 2a, Table 2). 235

11

Table 2 Mean values of the measured environmental variables for the three stream groups (reference, wide buffer [> 15 m] and narrow buffer [< 15 m]) in each study region.

	Northern region			Southern region			
	Reference	Wide	Narrow	Reference	Wide	Narrow	
Catchment area (km²)	2.7	4.9	2.9	10.3	8.9	9.3	
Open mires (%)	5.2	5.0	0.0	8.6	6.3	3.3	
Coniferous forests (%)	57.9	55.9	33.1	75.9	66.2	68.9	
Mixed forests (%)	26.3	4.0	28.8	2.4	0.0	3.9	
Arable land (%)	0.0	0.0	0.0	2.2	3.4	0.9	
pH	7.0	6.8	7.1	6.9	7.1	6.8	
Electrical conductivity (mS m <sup>-1</sup> )	2.4	2.0	2.8	3.4	4.9	3.5	
$TP (\mu g L^{-1})$	11.5	13.6	12.0	24.9	50.8	71.5	
$PO_4 (\mu g L^{-1})$	6.2	5.2	3.6	12.5	15.7	19.3	
$NO_3$ (µg L <sup>-1</sup> )	14.4	28.6	26.2	88.2	158.7	205.1	
DOC (mg L <sup>-1</sup> )	5.8	11.1	10.9	4.9	5.3	14.2	
Channel width (cm)	227	152	112	248	265	212	
Channel depth (cm)	17.3	18.3	15.7	19.7	21.3	12.4	
Substrate size (Wenthworth scale)	4.7	5.1	5.1	4.8	4.9	4.8	
Large woody debris (m <sup>3</sup> a <sup>-1</sup> )	0.032	0.011	0.006	0.459	0.010	0.011	
Current velocity (m s <sup>-1</sup> )	19.2	24.5	16.3	31.5	16.6	18.0	
Moss cover (%)	49.6	31.4	14.8	14.0	8.0	8.8	

240241

242

243

244

PCA for the southern region followed largely the same pattern. The first two PCs explained 53.7% of the variance and the stream groups were separated only along PC1, which represented clear-cut impact and water quality gradients (Fig. 2b; Table 2). The among-group difference bordered on significance ( $F_{2,9} = 1.77$ , P = 0.052) and only the pairwise comparison between the reference and narrowly buffered streams approached significance (P = 0.076).

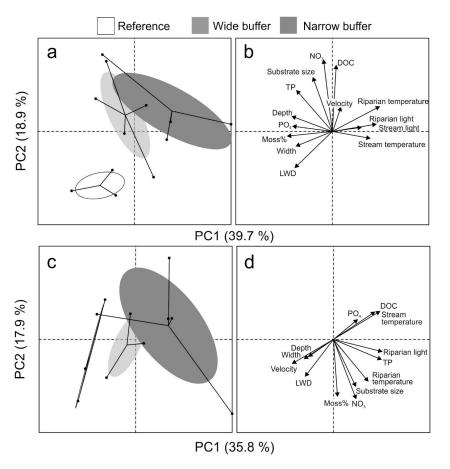


Fig. 2. PCA ordinations of the environmental characteristics of the northern (upper panel) and southern (lower panel) streams, showing (a and c) separation of the three stream groups in the ordination space and (b and d) correlations (i.e., arrow lengths) between the principal components and environmental variables. Ellipses depict ±95% CI around group centroids.

Narrowing of the riparian buffer altered the light and thermal regimes of the stream-riparian ecotone.

Riparian light intensity was higher in narrowly buffered sites compared to reference sites in both

regions (GLM; t = 2.33, P = 0.048 for northern; t = 2.78, P = 0.022 for southern sites; Fig. 3a). Riparian air temperature differed between the reference and narrow-buffered streams only in the northern region (t = 4.57, P = 0.001; Fig. 3b). Stream light intensity did not differ among the stream groups (Fig. 3c), whereas water temperature tended to increase in forestry-impacted streams, albeit significantly so only in the northern widely buffered streams (Fig. 3d).

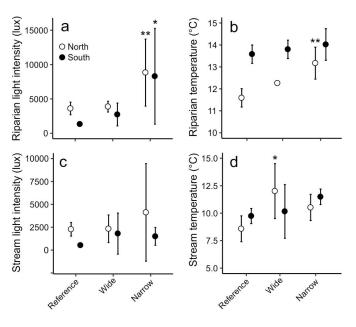


Fig. 3. Mean ( $\pm 95\%$  CI) a) riparian light intensity, b) riparian air temperature, c) stream light intensity and d) stream water temperature in late June to early October in the three buffer width categories in each study region. All comparisons are made against the reference (GLM); significant differences are denoted by asterisks (\* P < 0.05; \*\* P < 0.01).

- 3.2 Primary productivity, organic matter standing stock and decomposition processes
- 270 Chlorophyll a accrual rates were generally higher in forestry-impacted than in reference streams (Fig.
- 271 4a). The autotrophic index showed an opposite pattern, with lower values than reference for both
- buffer types in the southern streams (LMM: t = -2.88, P = 0.02 for wide buffers; t = -3.10, P = 0.015
- for narrow buffers) and for wide buffers in the northern region (t = -1.96, P = 0.01) (Fig. 4b).
- 274 In both study regions, CPOM standing stock showed a weak (P = 0.09 0.17) decreasing trend
- towards the wide- and narrow-buffered streams (Fig. 4c). The amount of FPOM showed a similar
- 276 negative trend, but significantly so for the northern streams (Fig. 4d). Unexpectedly, both CPOM and
- 277 FPOM were nearly equal in widely- and narrowly buffered streams (Fig. 4c and 4d).
- 278 Leaf decomposition rate was enhanced towards narrowly buffered streams in the southern region (t =
- 2.34, P = 0.047 for wide buffers; t = 2.47, P = 0.038 for narrow buffers), but not in the northern region
- 280 (t = 0.90, P = 0.39 for wide buffers; t = -0.29, P = 0.77 for narrow buffers) (Fig. 4e). Likewise,
- 281 microbial-mediated decomposition (loss of cotton strip tensile strength) was enhanced in the southern
- region's forest-impacted streams, but significantly so only for narrow buffers (t = 2.38, P = 0.044; t = 0.044; t
- 283 = 1.75, P = 0.11 for wide buffers), whereas no differences were observed in the northern region (t = 1.75, P = 0.11)
- 284 -1.81, P = 0.10 for wide buffers; t = -0.25, P = 0.80 for narrow buffers) (Fig. 4f).

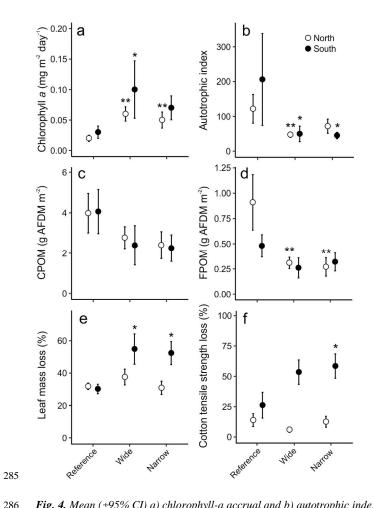


Fig. 4. Mean ( $\pm 95\%$  CI) a) chlorophyll-a accrual and b) autotrophic index (AFDM:Chl a), ash-free dry mass of c) coarse (CPOM; > 1 mm) and d) fine (FPOM; 0.2 – 1 mm) particulate organic matter and e) leaf mass loss and f) cotton strip tensile strength loss during the decomposition assay in the three stream groups in each region. All comparisons are made against the reference (LMM); significant differences are denoted by asterisks (\* P < 0.05; \*\* P < 0.01).

291

287

## 3.3 Benthic macroinvertebrate density, diversity and community composition

Benthic macroinvertebrate data of the northern region comprised 60 taxa, whereas the southern region's data contained 49 taxa. Total macroinvertebrate densities ranged between 617 - 6599 and 872 - 3401 individuals per m<sup>2</sup> for the northern and southern regions, respectively. Total densities did not differ between the reference and forestry-impacted streams in either region (all P > 0.05). For the northern region, total number of taxa was marginally lower in the narrowly buffered sites compared to reference (t = -1.77, P = 0.07; Fig. 5a), while no such pattern was observed in the southern region (Fig. 5a). In the northern region, the narrowly buffered stream lacked a notable proportion of EPT taxa (t = -2.61, P = 0.009; Fig. 5b). Macroinvertebrate evenness was likewise significantly lower in the narrowly buffered streams in the northern region (t = -3.51, t = 0.007; Fig. 5c), but not in the southern region (t = -0.74, t = 0.47; Fig. 5c). All community metrics were lower in the southern reference sites than in the northern ones (see Fig. 5), indicating lower reference-site quality in the southern region.

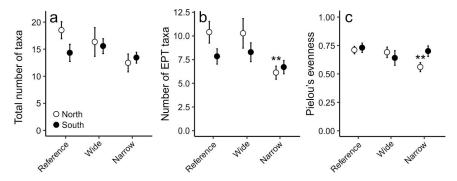


Fig. 5. Mean ( $\pm 95\%$  CI) a) number of macroinvertebrate taxa, b) number of ephemeropteran, trichopteran and plecopteran (EPT) taxa and c) Pielou's evenness index in the three buffer width categories in each region. All comparisons are made against the reference; significant differences are denoted by asterisks (\*\* P < 0.01).

Macroinvertebrate species composition differed among the stream groups in the northern region (PERMANOVA;  $F_{2.69} = 9.27$ , P = 0.029), but not in the southern region ( $F_{2.69} = 3.26$ , P = 0.84). Pairwise PERMANOVAs for the northern streams indicated that the species composition of the narrowly buffered streams differed marginally from the reference assemblages ( $F_{2.69} = 11.75$ , P = 0.08), whereas wide buffer assemblages did not ( $F_{2.69} = 8.26$ , P = 0.12). NMDS ordinations indicated for both study regions that the streams with very narrow ( $\leq 10$  m) riparian buffers deviated most from the reference assemblages (Fig. 6a and b).

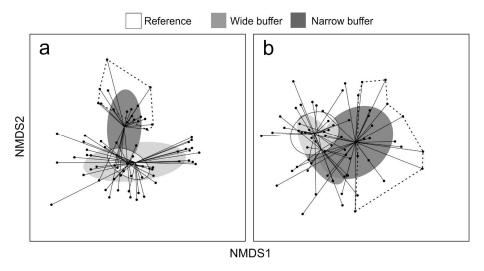


Fig. 6. Nonmetric multidimensional scaling (NMDS) ordinations of macroinvertebrate assemblages in the a) northern and b) southern streams. Solid lines connect each sample to the corresponding group centroid and ellipses depict  $\pm 95\%$  CI around the centroids. Dashed polygons delineate samples taken from streams with  $\leq 10$  m riparian buffers.

#### 4. Discussion

327

## 4.1 Environmental conditions

329	Our findings highlight that narrow ( $<$ 15 m) riparian buffers are insufficient in mitigating the forestry-
330	induced alteration of headwater streams and their riparian forests. It should be noted that we used
331	space-for-time (SFT) substitution design in our study. SFT assumes that drivers of ecological change
332	through time are the same as those that drive changes in space. We acknowledge that this design has
333	inherent weaknesses as it may confound temporal and spatial effects (Damgaard, 2019) but it was
334	unfeasible to conduct a well replicated before-after-control-impact (BACI; Underwood, 1994) design
335	within the limited project period. The amount of large woody debris (LWD) was reduced in forestry-
336	impacted streams, especially those with the narrowest buffers. LWD affects the movement and
337	storage of organic material, nutrients and streambed sediments and maintains the diversity of meso-
338	scale habitats. As a result of clear-cuts, the amount of wood in the stream channel typically decreases
339	(Wallace et al., 2001).
340	Moss cover was lower in forestry-impacted streams. Aquatic mosses influence stream processes and
341	biodiversity mainly by providing sheltered microhabitats and fine detritus for benthic animals
342	(Turunen et al., 2020). Bryophytes typically thrive in headwater streams where canopy shading limits
343	algal growth (Stream Bryophyte Group, 1999). Clear-cutting of riparian forests increases the amount
344	of light and thus, algal and vascular plant productivity (Kiffney et al., 2003), potentially outcompeting
345	bryophytes (González-Mancebo et al., 2004). In our data, light intensities in the stream channel and
346	the riparian forest increased, especially at narrowly buffered sites (see also Kiffney at al., 2003).
347	The pattern of increased light intensity was less pronounced in the stream channel. This is due most
348	likely to increased DOC content in the narrowly buffered sites. Terrestrially derived DOC typically
349	makes water brown-colored, thus enhancing light attenuation (Karlsson et al., 2009). Forest clear-

cutting and subsequent site preparations have been observed to increase DOC input into adjacent streams (Piirainen et al., 2007; Laudon et al., 2009), which was also suggested by our results.

Water temperature in the stream channel was higher in the narrowly buffered than in the reference sites. This is in accordance with Kiffney et al. (2003), who reported an increase of insolation, thermal radiation and stream water temperature in recently harvested and buffered (10 m) streams compared to unharvested streams. On the other hand, Gomi et al. (2006) showed that in some cases even a 10 m buffer can mitigate the logging-induced increase of water temperature, but the efficiency of the buffer was related to north-south orientation of the stream, and thus differences in exposure to insolation. The retention of riparian buffers is not critical only for protecting streams from local forestry-induced impacts but also for adapting fluvial ecosystems to climate change (Thomas et al., 2016). By providing shade, thermal refugia and detrital input, wide and longitudinally continuous riparian buffers may contribute importantly to climate change adaptation of riverine networks through suppressing the warming of the riparian soil and stream water and maintaining energy flow (Palmer et al., 2009).

# 4.2 Organic matter decomposition

361

365

366

367

We observed strongly divergent patterns in both microbial and invertebrate-mediated organic matter decomposition rates between the study regions. While in the southern region decomposition rates were accelerated towards the narrowly buffered streams, data from the northern region did not suggest any differences between the reference and forestry-impacted streams. This observation underlines the context-specificity of responses to forestry. For example, Kreutzweiser et al. (2008) and Lecerf and Richardson (2010) noted that forest harvest resulted in lowered decomposition rates compared to reference streams, whereas Kreutzweiser et al. (2010) did not observe any effect of forestry on decomposition, and McKie and Malmqvist (2009) documented an accelerated rate of both microbial and detritivore-mediated decomposition in streams draining recent (3 – 5 y old) clear-cuts. Our southern streams exhibited considerable variation in NO<sub>3</sub> and PO<sub>4</sub> concentrations among differently

buffered streams (see Table 2) and, given the well-known role of nutrients in regulating particularly microbial decomposition rates (Ferreira et al., 2015; Gulis and Suberkropp, 2003), the increased nutrient runoff is the most likely explanation for the stronger response of decomposition rates to forest harvest in the southern region. Also increased stream temperatures in the forestry-impacted streams may have contributed to enhanced decomposition processes as organic matter decomposition tends to be higher in warmer conditions (Martínez et al., 2014). In our decomposition analyses, we did not correct decomposition rates for the temperature as we expected forestry actions to influence stream temperatures, thereby rendering within- and among-group differences in temperature inherent to our study design. However, we tested also the temperature-corrected data and the results remained the same. This implies that thermal conditions played a minor role in regulating decomposition rates and verifies that the decomposition patterns were primarily driven by the differences in nutrient levels.

# 4.3 Benthic organic matter standing stocks

Our observation of reduced biomass of FPOM and CPOM in forestry-impacted streams is in line with some earlier evidence (Kiffney and Richardson, 2010). However, responses of CPOM and FPOM to forest harvest have been highly variable (Göthe et al., 2009; Richardson and Béraud, 2014). The reasons for this inconsistency may be related to site-specific differences in logging practices, soil preparation and processing of harvest residues that can greatly modify the amount, quality and fate of organic material delivered to the stream (Jackson et al., 2007). In our forestry-impacted streams, the quantities of CPOM and FPOM virtually equaled, regardless of the buffer width. One potential explanation for the reduced organic matter standing stock in both forestry-impacted stream groups could be the intensified discharge dynamics due to nearby forestry actions. Finnish forest harvests are often accompanied by intensive peatland drainage (Nieminen et al., 2017), resulting in more frequent and extreme spates during high rainfalls, which is a key determinant of CPOM/FPOM export in headwater streams (Cuffney and Wallace, 1989). The observed reduction of organic matter

standing stock potentially alters the physical structure of the stream ecosystem (Eggert et al., 2012) and is likely to further intensify the reliance of stream biota on autochthonous production (see below).

## 4.4 Algal productivity and level of autotrophy

As expected, increased insolation stimulated algal productivity in forestry-impacted streams. Along with the concurrent reduction in CPOM/FPOM, this induced a transition towards autotrophy (see also Wootton, 2012; Kaylor and Warren, 2017). A classic paradigm in stream ecology dictates that forested headwater streams are heterotrophic and predominantly fueled by allochthonous material from the riparian forest (e.g. Tank et al., 2010). However, recent evidence challenges this paradigm, suggesting that autochthonous production is of disproportionate importance to stream biota, even when in low levels in apparently donor-controlled ecosystems (e.g. Brett et al., 2017).

## 4.5 Benthic invertebrates

Forest harvest in the vicinity of a stream typically reduces benthic diversity, causes uneven abundance distributions and alters community composition (e.g. Zhang et al., 2009). While all these community-level responses were detected in our northern streams, the responses were much weaker in the southern region. This result underlines the fact that the impacts of human disturbance, including those related to forestry, are highly context specific. The lack of congruence in macroinvertebrate responses may be linked to region-specific differences in historical and contemporary land use, which has a strong influence on the quality of the regional reference condition. In our northern regions, forestry is the dominant land use and our reference streams mainly drain relatively mature forests. In contrast, land use in the southern region is a mixture of more intense land use types (see Table 1), which has likely resulted in compromised stream biodiversity even in regional reference conditions (see Harding et al., 1998), thereby obscuring the detection of local forestry impacts

# 4.6 Towards a better optimization of riparian buffers

422 Buffer width requirements must be economically practicable as exceedingly wide buffers would impose economic costs on forest owners. However, defining an 'ecologically optimal riparian buffer' is challenging because of i) inconsistent scientific evidence, ii) focus on a single or a limited set of 425 indicators, and iii) the traditional separation of terrestrial and freshwater realms in ecological research and ecosystem management. Future research should evaluate the optimization of riparian buffers in 426 427 a more holistic way, by integrating biodiversity values and ecosystem processes of both the stream 428 and the riparian forest to measure and protect cross-ecosystem multidiversity (Allan et al., 2014) and multifunctionality (Hector and Bagchi, 2007) across a gradient of riparian buffers of varying widths. 430 Recent scientific literature has offered novel solutions to riparian buffer management to more meaningfully compromise between economic profit and ecological change. Rather than the conventional 'one size fits all' -type fixed-width buffers, flexible buffers would enable allocation of 432 conservation efforts to locations of particularly high biodiversity or otherwise of special ecological, 433 hydrological or biogeochemical importance (Richardson et al., 2012; Kuglerová et al., 2014). Oldén 434 et al. (2019) showed that careful thinning (30%) within 30-m wide riparian buffers can be allowed 436 for without threatening the diversity of riparian plant communities. Similarly, Kreutzweiser et al. (2010) concluded that partial harvesting of > 30 m wide riparian buffers does not pose any major 437 risks to stream biodiversity and ecosystem functioning. Partial harvesting of riparian buffers also 438 439 decreases the predominance of coniferous trees, diversifying the allochthonous base of stream food 440 webs and thus potentially enhancing stream biodiversity (Jonsson et al., 2017). Intentional smallscale harvesting of riparian forest may be advisable as it emulates the patchy disturbance typical of 441 natural forest succession (Sibley et al., 2012); however, from the perspective of stream biodiversity, 442 it is unlikely to be useful, or even acceptable, unless the riparian buffer is at least 15 m, and preferably 443 25 - 30 m wide. 444

4.7 Comparison of the forest certificates

Our results suggest that PEFC -compliant buffer retention measures will not support stream ecosystem processes and biodiversity at a level comparable to reference conditions. Albeit some deviation from reference conditions was observed also in the streams complying with the FSC 448 449 certificate, we can safely conclude that while the FSC certificate performs reasonably well in 450 providing protection for stream biodiversity and ecosystem functioning, PEFC does not. Dias et al. 451 (2015) reached a similar conclusion for Mediterranean stream corridors and Kuuluvainen et al. (2019) 452 for boreal forests, but neither of these directly tested for the biological effectiveness of the certificates. The responses of stream ecosystems to forestry impacts are context-dependent and vary across 454 biological groups (see Richardson and Béraud, 2014; Lunn et al., 2017), presenting a major challenge 455 to forest management at the stream-forest interface. In our streams, diversity responses to the apparent but complex environmental alterations caused by adjacent forest harvest varied between regions, 456 457 implying that biological consequences of forest harvest remain to some extent unpredictable and therefore forests adjoining headwater streams should be managed with extreme caution.

#### 459 Author contributions

JJ and TM conceived the idea and designed the study. JJ, IK and TM collected the data. IK
identified macroinvertebrates and was responsible for most of the laboratory work. JJ analyzed the
data. JJ led the writing of the manuscript and all authors contributed to drafts and edited the paper
and gave final approval for publication.

64 Declaration of competing interest

The authors declare no conflicts of interest

# 6 Acknowledgements

We thank the members of our field and lab crew: Sanna Räisänen, Venla Virtanen, Sanni Litjo,
Eveliina Lampinen, Carmen Bartrina Galan and Joel Nyberg. Our study was funded by the Academy
of Finland in the SOurce STream PROtection (SOSTPRO) project organized through the ERA-NET

- 470 co-funded call JPI Water Works 2016. We thank John S. Richardson, Lenka Kuglerová, Claire
- 471 Ruffing, Darshanaa Chellaiah and Angie Nicolas for collaboration and support during the project.
- 472 We also appreciate the insightful comments of the two anonymous reviewers on a previous draft of
- 473 our article.
- 474 References
- 475 Alexander, R.B., Boyer, E.W., Smith, R.A., Schwarz, G.E., Moore, R.B., 2007. The role of
- headwater streams in downstream water quality. J. Am. Water Resour. Assoc. 43, 41–59.
- 477 Allan, E., Bossdorf, O., Dormann, C.F., Prati, D., Gossner, M.M., Tscharntke, T., ... Böhm, S.,
- 478 2014. Interannual variation in land-use intensity enhances grassland multidiversity. Proc. Natl.
- 479 Acad. Sci. 111, 308–313.
- 480 Bishop, K., Buffam, I., Erlandsson, M., Fölster, J., Laudon, H., Seibert, J., Temnerud, J., 2008.
- Agua Incognita: the unknown headwaters. Hydrol. Process. 22, 1239–1242.
- 482 Brett, M.T., Bunn, S.E., Chandra, S., Galloway, A.W., Guo, F., Kainz, M.J., ... Rasmussen, J.B.,
- 483 2017. How important are terrestrial organic carbon inputs for secondary production in
- freshwater ecosystems?. Freshw. Biol. 62, 833–853.
- 485 Cuffney, T.F., Wallace, J.B., 1989. Discharge-export relationships in headwater streams: the
- 486 influence of invertebrate manipulations and drought, J. North Am. Benthol. Soc. 8, 331–341.
- 487 Damgaard, C., 2019. A critique of the space-for-time substitution practice in community ecology.
- 488 Trends Ecol. Evol. 34, 416–421.
- 489 Dias, F.S., Bugalho, M.N., Rodríguez-González, P.M., Albuquerque, A., Cerdeira, J.O., 2015.
- 490 Effects of forest certification on the ecological condition of Mediterranean streams. J. Appl.
- 491 Ecol. 52, 190–198.
- 492 EC, 2018. A sustainable Bioeconomy for Europe: strengthening the connection between economy,

- society and the environment. https://ec.europa.eu/research/bioeconomy/. Accessed May 2020.
- Eggert, S.L., Wallace, J.B., Meyer, J.L., Webster, J.R., 2012. Storage and export of organic matter
- in a headwater stream: responses to long-term detrital manipulations. Ecosphere 3, 1–25.
- 96 Ferreira, V., Castagneyrol, B., Koricheva, J., Gulis, V., Chauvet, E., Graça, M.A., 2015. A meta-
- analysis of the effects of nutrient enrichment on litter decomposition in streams. Biol. Rev. 90,
- 498 669–688.
- 499 Finn, D.S., Bonada, N., Múrria, C., Hughes, J.M., 2011. Small but mighty: headwaters are vital to
- stream network biodiversity at two levels of organization. J. North Am. Benthol. Soc. 30, 963–
- 501 980.
- 502 Food and Agriculture Organization of the United Nations (FAO), 2019. FAOSTAT, Forestry
- production and Trade, http://www.fao.org/faostat/en/#data/FO. Accessed May 2020.
- 504 Forest Stewardship Council, 2010. Finnish FSC-standard. https://fi.fsc.org/preview.suomen-fsc-
- 505 standardi.a-142.pdf. Accessed May 2020.
- 506 Gomi, T., Moore, R.D., Dhakal, A.S., 2006. Headwater stream temperature response to clear-cut
- 507 harvesting with different riparian treatments, coastal British Columbia, Canada. Water Resour.
- 508 Res., 42, W08437.
- 509 González-Mancebo, J.M., Losada-Lima, A., Patinő J., 2004. Forest floor bryophytes of laurel forest
- 510 in Gomera (Canary Islands): life strategies and influence of the tree species. Lindbergia 29, 5–
- 511 16.
- 512 Göthe, E., Lepori, F., Malmqvist, B., 2009. Forestry affects food webs in northern Swedish coastal
- 513 streams. Fundam. Appl. Limnol. 175, 281–294.
- 514 Gulis, V., Suberkropp, K., 2003. Leaf litter decomposition and microbial activity in nutrient-
- enriched and unaltered reaches of a headwater stream. Freshw. Biol. 48, 123–134.

- 516 Harding, J.S., Benfield, E.F., Bolstad, P.V., Helfman, G.S., Jones, E.B.D., 1998. Stream
- biodiversity: the ghost of land use past. Proc. Natl. Acad. Sci. 95, 14843–14847.
- 518 Hector, A., Bagchi, R., 2007. Biodiversity and ecosystem multifunctionality. Nature 448, 188.
- 519 Huttunen, K.L., Mykrä, H., Muotka, T., 2012. Temporal variability in taxonomic completeness of
- 520 stream macroinvertebrate assemblages. Freshw. Sci., 31, 423-441.
- 521 Jackson, R.C., Batzer, D.P., Cross, S.S., Haggerty, S.M., Sturm, C.A., 2007. Headwater streams and
- 522 timber harvest: channel, macroinvertebrate, and amphibian response and recovery. For. Sci.
- 523 53, 356–370.
- 524 Jonsson, M., Burrows, R.M., Lidman, J., Fältström, E., Laudon, H., Sponseller, R.A., 2017. Land
- use influences macroinvertebrate community composition in boreal headwaters through altered
- stream conditions. Ambio 46, 311–323.
- 527 Karlsson, J., Byström, P., Ask, J., Ask, P., Persson, L., Jansson, M., 2009. Light limitation of
- nutrient-poor lake ecosystems. Nature 460, 506–509.
- 529 Kaylor, M.J., Warren, D.R., 2017. Linking riparian shade and the legacies of forest management to
- fish and vertebrate biomass in forested streams. Ecosphere, 8, e01845.
- 531 Kiffney, P.M., Richardson, J.S., 2010. Organic matter inputs into headwater streams of
- southwestern British Columbia as a function of riparian reserves and time since harvesting.
- 533 Forest Ecol. Manag. 260, 1931–1942.
- 534 Kiffney, P.M., Richardson, J.S., Bull, J.P., 2003. Responses of periphyton and insects to
- experimental manipulation of riparian buffer width along forest streams, J. Appl. Ecol. 40,
- 536 1060–1076.
- Kreutzweiser, D.P., Capell, S.S., Holmes, S.B., 2009. Stream temperature responses to partial-
- 538 harvest logging in riparian buffers of boreal mixedwood forest watersheds. Can. J. For. Res.

- 539 39, 497–506.
- 540 Kreutzweiser, D.P., Good, K.P., Capell, S.S., Holmes, S.B., 2008. Leaf-litter decomposition and
- 541 macroinvertebrate communities in boreal forest streams linked to upland logging disturbance.
- 542 J. North Am. Benthol. Soc. 27, 1–15.
- 543 Kreutzweiser, D., Muto, E., Holmes, S., Gunn, J., 2010. Effects of upland clearcutting and riparian
- partial harvesting on leaf pack breakdown and aquatic invertebrates in boreal forest streams.
- 545 Freshw. Biol. 55, 2238–2252.
- 546 Kuglerová, L., Ågren, A., Jansson, R., Laudon, H., 2014. Towards optimizing riparian buffer zones:
- 547 Ecological and biogeochemical implications for forest management. Forest Ecol. Manag. 334,
- 548 74–84.
- 549 Kuglerová, L., Jyväsjärvi, J., Ruffing, C., Muotka, T., Jonsson, A., Andersson, E., Richardson, J.S,
- 550 2020. Cutting edge: A comparison of contemporary practices of riparian buffer retention
- around headwaters in Canada, Finland and Sweden. Water Resour. Res., in review.
- 552 Kuuluvainen, T., Lindberg, H., Vanha-Majamaa, I., Keto-Tokoi, P., Punttila, P., 2019. Low-level
- retention forestry, certification, and biodiversity: case Finland. Ecol. Proc. 8, 47.
- Laudon, H., Hedtjärn, J., Schelker, J., Bishop, K., Sørensen, R., Ågren, A., 2009. Response of
- dissolved organic carbon following forest harvesting in a boreal forest. AMBIO 38, 381-386.
- Laudon, H., Sponseller, R., Lucas, R., Futter, M., Egnell, G., Bishop, K., Ågren, A., Ring, E.,
- 557 Högberg, P., 2011. Consequences of more intensive forestry for the sustainable management of
- forest soils and waters. Forests 2, 243–260.
- 559 Lecerf, A., Richardson, J.S., 2010. Litter decomposition can detect effects of high and moderate
- levels of forest disturbance on stream condition. Forest Ecol. Manag. 259, 2433–2443.
- Lopatin, E., Trishkin, M., Gavrilova, O., 2016. Assessment of compliance with PEFC forest

- certification indicators with remote sensing. Forests 7, 85.
- 563 Lunn, T., Munks, S., Carver, S., 2017. The impacts of timber harvesting on stream biota An
- expanding field of heterogeneity. Biol. Cons. 213, 154–166.
- 565 Marczak, L.B., Sakamaki, T., Turvey, S.L., Deguise, I., Sylvia, L., Wood, R.,..., 2010. Are forested
- buffers an effective conservation strategy for riparian fauna? An assessment using meta-
- 567 analysis. Ecol. App. 20, 126–134.
- Martínez, A., Larrañaga, A., Pérez, J., Descals, E., Pozo, J., 2014. Temperature affects leaf litter
- decomposition in low-order forest streams: field and microcosm approaches. FEMS Microbiol.
- 570 Ecol. 87, 257–267.
- 571 McKie, B.G., Malmqvist, B., 2009. Assessing ecosystem functioning in streams affected by forest
- 572 management: increased leaf decomposition occurs without changes to the composition of
- 573 benthic assemblages. Freshw. Biol. 54, 2086–2100.
- 574 Mykrä, H., Aroviita, J., Kotanen, J., Hämäläinen, H., Muotka, T., 2008. Predicting the stream
- 575 macroinvertebrate fauna across regional scales: influence of geographical extent on model
- 576 performance. J. North Am. Benthol. Soc. 27, 705–716.
- 577 Nieminen, M., Sallantaus, T., Ukonmaanaho, L., Nieminen, T. M., Sarkkola, S., 2017. Nitrogen and
- 578 phosphorus concentrations in discharge from drained peatland forests are increasing. Sci. Total
- 579 Environ. 609, 974–981.
- 580 Oksanen, J., Blanchet, F.G., Friendly, M., Kindt, R., Legendre, P., McGlinn, D., Minchin, P.R.,
- 581 O'Hara, R.B., Simpson, G.L., Solymos, P., Stevens, M.H.H., Szoecs, E., Wagner, H., 2019.
- vegan: Community Ecology Package. R package version 2.5.4.
- 583 Oldén, A., Selonen, V.A.O., Lehkonen, E., Kotiaho, J.S., 2019. The effect of buffer strip width and
- selective logging on streamside plant communities. BMC Ecology, 1–9.

- Palmer, M.A., Lettenmaier, D.P., Poff, N.L., Postel, S.L., Richter, B., Warner, R., 2009. Climate
- 586 change and river ecosystems: protection and adaptation options. Environ. Manage. 44, 1053–
- 587 1068.
- 88 PEFC Finland, 2014. PEFC Finland Standard. Criteria for PEFC Forest Certification. PEFC FI
- 589 1002:2014.
- 90 Piirainen, S., Finér, L., Mannerkoski, H., Starr, M., 2007. Carbon, nitrogen and phosphorus
- 591 leaching after site preparation at a boreal forest clear-cut area. Forest Ecol. Manag. 243, 10–18.
- 592 R Core Team, 2019. R: a language and environment to statistical computing. R Foundation for
- 593 Statistical Computing, Vienna, Austria.
- 594 Richardson, J.S., Béraud, S., 2014. Effects of riparian forest harvest on streams: A meta-analysis. J.
- 595 Appl. Ecol. 51, 1712–1721.
- 596 Richardson, J.S., Danehy, R.J., 2007. A synthesis of the ecology of headwater streams and their
- riparian zones in temperate forests. For. Sci. 53, 131–147.
- 598 Richardson, J.S., Naiman, R.J., Bisson, P.A., 2012. How did fixed-width buffers become standard
- 599 practice for protecting freshwaters and their riparian areas from forest harvest practices?
- 600 Freshw. Sci. 31, 232–238.
- 601 Richardson, J.S., Sato, T., 2015. Resource subsidy flows across freshwater-terrestrial boundaries
- and influence on processes linking adjacent ecosystems. Ecohydrology 415, 406–415.
- Ring, E., Johansson, J., Sandström, C., Bjarnadóttir, B., Finér, L., Lībiete, Z....., 2017. Mapping
- 604 policies for surface water protection zones on forest land in the Nordic–Baltic region: Large
- differences in prescriptiveness and zone width. Ambio 46, 878–893.
- Selonen, V.A.O., Kotiaho, J.S., 2013. Buffer strips can pre-empt extinction debt in boreal
- streamside habitats. BMC Ecology 13, 24.

- 608 Sibley, P.K., Kreutzweiser, D.P., Naylor, B.J., Richardson, J.S., Gordon, A.M., 2012. Emulation of
- 609 natural disturbance (END) for riparian forest management: synthesis and recommendations.
- 610 Freshw. Sci. 31, 258–264.
- 611 Stream Bryophyte Group, 1999. Roles of bryophytes in stream ecosystems. J. N. Am. Benthol. Soc.
- 612 18, 151–184.
- 613 Sweeney, B.W., Newbold, J.D., 2014. Streamside forest buffer width needed to protect stream
- water quality, habitat, and organisms: A literature review. J. Am. Water Resour. Assoc. 50,
- 615 560–584.
- 616 Tank, J.L., Rosi-Marshall, E.J., Griffiths, N.A., Entrekin, S.A., Stephen, M.L., 2010. A review of
- allochthonous organic matter dynamics and metabolism in streams. J. North Am. Benthol. Soc.
- 618 29, 118–146.
- 619 Thomas, S.M., Griffiths, S.E, Ormerod, S.J., 2016. Beyond cool: adapting upland streams for
- 620 climate change using riparian woodlands. Glob. Chang. Biol. 22, 310–324.
- 621 Tiegs, S.D., Clapcott, J.E., Griffiths, N.A., Boulton, A.J., 2013. A standardized cotton-strip assay
- for measuring organic-matter decomposition in streams. Ecol. Indic. 32, 131–139.
- 623 Turunen, J., Muotka, T., Aroviita, J., 2020. Aquatic bryophytes play a key role in sediment-stressed
- boreal headwater streams. Hydrobiologia 847, 605–615.
- 625 Underwood, A.J., 1994. On beyond BACI: sampling designs that might reliably detect
- environmental disturbances. Ecol. Appl. 4, 3–15.
- Wallace, J.B., Webster, J.R., Eggert, S.L., Meyer, J.L., Siler, E.R., 2001. Large woody debris in a
- headwater stream: long-term legacies of forest disturbance. Int. Rev. Hydrobiol. 86, 501–513.
- 629 Wallace, J.B., Eggert, S.L., 2015. Terrestrial and longitudinal linkages of headwater streams.
- 630 Southeast. Nat. 14, 65–86.

- Wootton, J.T., 2012. River food web response to large-scale riparian zone manipulations. PLoS One
- 632 7, 12.
- Zhang, Y., Richardson, J.S., Pinto, X., 2009. Catchment-scale effects of forestry practices on
- benthic invertebrate communities in Pacific coastal streams. J. Appl. Ecol. 46, 1292–1303.