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Research article

Riparian buffers mitigate downstream effects of clear-cutting on instream metabolic rates

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ABSTRACT

Clear-cutting of forests with little or no regard for riparian buffers alters the local abiotic habitat of streams within and downstream of clear-cuts by increasing temperature, incident light, suspended sediments and resource inputs such as carbon and inorganic nutrients. It is also well documented that streams with narrow or non-existent riparian buffers affect local stream ecosystem processes. Here, we ask whether ecosystem processes can also be affected downstream of clear-cuts. We tested this in nine headwater streams that run through recently harvested clear-cuts (1–6 years ago) with varying buffer widths (<10 and ≥ 15 m) in northern Sweden. We compared biofilm (periphytic algal and bacterial mats) and whole stream metabolic rates in stream reaches situated upstream of the clear-cuts, in the clear-cuts and downstream of the clear-cuts. We found that biofilm gross primary productivity (GPP) in streams with thin buffers (<10 m) increased, on average, by 54 % downstream of clear-cuts in July, but that the net effect on the whole ecosystem was still a decrease in ecosystem productivity due to high respiration rates. In September, the situation was different as there was a 50 % decrease in biofilm GPP downstream of clear-cuts, and the net effect was again a decrease in ecosystem productivity. Wide buffer zones (>15 m) could mitigate these longitudinal changes for both biofilm and whole stream metabolism, except in one stream that was dominated by fine sediments. Importantly, the magnitude of downstream propagation in biofilm GPP was related to the magnitude of responses in the clear-cut, which in turn was driven by nutrient concentrations. To upscale the potential magnitude of clear-cutting in Sweden, we estimated that nearly 6 % (or 57,400 km) of the total forested stream length is situated within and 100 m downstream of clear-cuts that were harvested 1–6 years ago. Based on this study, we conclude that clear-cut effects on stream ecosystem processes are not only local, but can also be propagated to downstream recipient waters if riparian buffer width in the clear-cut is less than 15 m.

1. Introduction

Clear-cut forestry is still the dominant management strategy in boreal regions (Högberg et al., 2021). The most common tool for reducing the impacts of clear-cutting on surface waters is the retention of riparian buffers, which are uncut strips of forest along streams, rivers and lakes (Richardson et al., 2012). However, this practice is often not well regulated and thus riparian buffers rarely exceed 15 m in width in the boreal zone (Kuglerová et al., 2020), and 10 m in Sweden (Ring et al., 2023). When large areas are harvested and riparian forests are removed or compromised, stream channels are exposed to increased incident light, temperatures, and loads of sediment, dissolved carbon and nutrients (Broadmeadow and Nisbet, 2004). Along with these changes follow ecological effects to the streams, which include local alterations to ecosystem metabolic rates, primary producer biomass (Bechtold et al., 2017; Myrstener et al., 2023) and species composition (Göthe et al., 2009; Ring et al., 2023). Ultimately, the abiotic changes such as warming of water as well as alterations of the basal levels of the food web can be critical for fish populations, such as brown trout and Arctic char, two ecologically and socioeconomically important species in the boreal zone (Albertson et al., 2018). Eventually, water in the stream flows past the clear-cut area and enters a forested area again, and although the direct external stressors from the clear-cut are absent (e.g. light intensity), the water might still bear legacy of the clear-cut, with

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elevated temperatures, turbidity and concentrations of dissolved nutrients and carbon when compared to areas upstream of the clear-cut (Hassan et al., 2005; Kreutzweiser et al., 2008; MacDonald and Coe, 2007). Indeed, temperature increases can be sustained for hundreds of meters downstream of extensive riparian thinning (Arismendi and Groom, 2019; Roon et al., 2021), and intense forestry has been shown to have landscape scale effects on stream dissolved organic carbon (DOC) concentrations (Oni et al., 2015). These findings raise questions about the magnitude and extent of the downstream propagation of biological effects from clear-cutting (Feijó-Lima et al., 2018), and whether contemporary mitigation practices (riparian buffers) are effective.

While studies on local effects of clear-cutting have been conducted for decades (e.g., Burrows et al., 2021; Göthe et al., 2009; Jyväsjärvi et al., 2020, Kiffney et al., 2003), only a handful of studies have focused on the downstream transmission of ecological processes in relation to upstream forestry disturbance. For example, metabolic rates have been studied downstream of wastewater effluents (Bernhardt et al., 2018; Ledford and Toran, 2020) and large wildfires (Nichols et al., 2024). Nevertheless, the far more widespread effects of forestry have not been explored in this context. This is potentially explained by the inherent complexity of studying longitudinal changes in running waters, where streams naturally change downstream as the channels increase in size, as described by the River Continuum Concept (Vannote et al., 1980). Furthermore, it is difficult to isolate stream segments when evaluating aquatic ecosystem functions (Demars et al., 2015), which is necessary for comparing reaches upstream and downstream of a disturbed reach (clear-cuts in this case). This can be overcome by analyzing biofilm metabolism, as biofilms (periphytic algal and bacterial mats) account for a large part of the metabolism in headwater streams (Battin et al., 2016). Lastly, longitudinal studies of streams in managed forests are complicated by the mosaic of different stands (species, age, size and historical management, Warren et al., 2016), which limits the possibility of an ideal controlled study. For example, Erdozain et al. (2022) compared streams in an intensely managed forest with adjacent forested control streams and found lower autochthony of collector-feeder invertebrate taxa downstream of intensely managed forests. Their streams, however, not only differed in management intensity, but also had large differences in deciduous cover, complicating the interpretations of their results. Ultimately, we believe difficulties associated with, for example, appropriate controls have led to a paucity of ecological studies of forestry-induced downstream propagation effects. Yet, to understand the effectiveness of contemporary mitigation practices that are supposed to protect surface waters in production forests, we need to know how ecological impairments might propagate downstream. This is especially important in countries like Sweden, where riparian buffers that are supposed to reduce impacts are voluntary and based on non-binding guidelines, resulting in poorly designed buffers (Kuglerová et al., 2024). Empirical evidence that monitors the outcomes of mitigation measures locally and on a catchment scale is needed to advance best management practices.

The magnitude of downstream propagation of ecological effects associated with forestry is likely coupled to the intensity and extent of forestry operations (Erdozain et al., 2021) and to the biotic and abiotic changes within the clear-cut (Roon et al., 2021). Careful consideration of buffer strips can mitigate habitat effects within clear-cuts (Kiffney et al., 2003), and these considerations are particularly important when the catchment (or stream) size is small relative to the size of the clear-cut (Coats and Jackson, 2020; Swartz et al., 2020). Additionally, local differences in soil properties (e.g. occurrence of fine sediments Rosenfeld et al., 2011) and high hydrological connectivity can increase the downstream propagation of sediments and nutrients (Kreutzweiser et al., 2008). Moreover, downstream effects on stream function could have biological causes e.g. changes in grazing pressure or changes to the biofilm community. Although this was never explicitly tested, Erdozain et al. (2021) indicated there were downstream changes in invertebrate diversity and richness due to forestry in two catchments in southeastern Canada, which in turn could affect primary producers and metabolic rates. Finally, changes to biofilm communities are to be expected after large habitat alterations (Neif et al., 2017), and this could potentially affect both downstream rates and seasonality of productivity patterns (Guasch and Sabater, 1995; Hoellein et al., 2010).

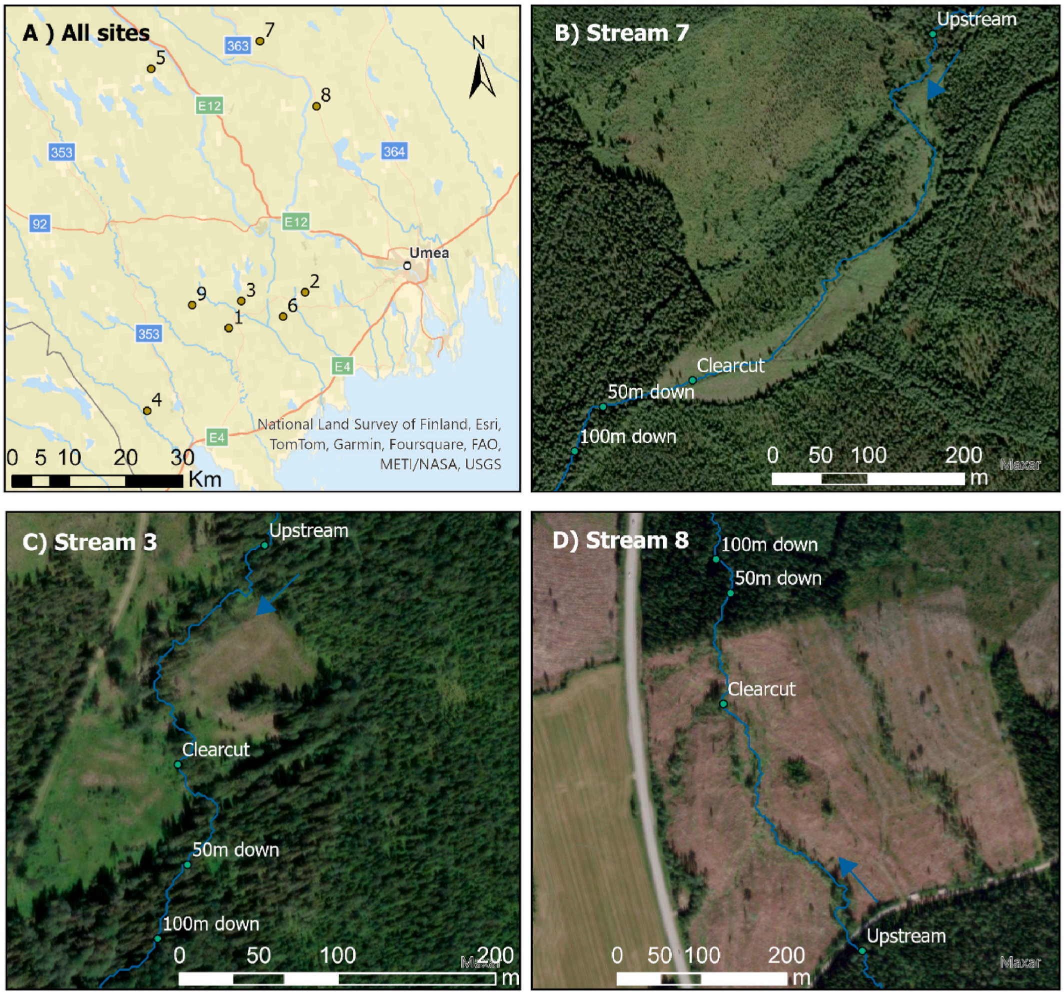
In this study, we ask whether clear-cutting affects the metabolic rates of downstream forested stream reaches, and whether the use of riparian buffers within the clear-cut can mitigate this propagation effect. We tested this by surveying nine streams, which run through recent clear-cuts (harvested between 1 and 6 years ago) with different riparian buffer widths (<10 and $\geq$ 15 m). We estimated biofilm and whole stream metabolic rates in reaches situated upstream of the clear-cut, within the clear-cut and downstream of the clear-cut, and used the upstream reach as a reference, or background condition, to which we compare the downstream metabolic rates. We hypothesized that downstream gross primary production (GPP) and ecosystem respiration (ER) would be higher than in upstream reaches due to increased availability of nutrients, organic matter and higher temperatures, but that this effect is lower in streams with wider buffer zones in the clear-cut. To put our results in a broader spatial context, i.e. to explain what proportion of forested streams in Sweden might be subject to clear-cut effects, we quantified the total length of forest streams in Sweden that are situated within or 100m downstream of a recent clear-cut (harvested 1–6 years ago).

2. Methods

2.1. Study sites

We conducted this study in summer and autumn 2021 in nine streams located in the county of Västerbotten, all within 1 h driving distance from Umeå, northern Sweden (Fig. 1A). Each stream was divided into four reaches (“locations” hereafter): (1) upstream of the clear-cut, (2) within the clear-cut, (3) 50 m downstream and (4) 100 m downstream of the clear-cut (Fig. 1B–D), with the reaches upstream and downstream of the clear-cuts being forested. Downstream length was counted as the length along the course of the stream. Measurements of stream chemistry, biofilms and metabolism were all conducted within these same locations. This design enabled us to analyze direct effects of the clear-cut on downstream locations, rather than using a different control stream with ultimately different habitat settings (Arismendi and Groom, 2019). Upstream and downstream locations were situated in mature production forest stands (for at least 150 m of the stream length) while the clear-cut location was situated at the downstream end of the clearcut (Fig. 1B–D). We did attempt to identify suitable control streams, i.e., with forested stream reaches of at least 500 m without clear-cuts, wetlands, lakes or other significant change in the surrounding forest (e.g., thinned stand), but we were not successful due to the heterogeneous forest landscape and intense forestry in the region.

For the region encompassing the nine streams, the mean annual temperature is ~0–1 °C and approximately 50 % of the annual precipitation falls as snow. At all sites, the vegetation is typical of the Fennoscandian boreal forest, with an overstory dominated by Norway spruce (*Picea abies*) and Scots pine (*Pinus sylvestris*), and the understory vegetation consisting mainly of bryophytes and *Vaccinium* spp. All streams are first and second order (discharge <50 L s^{-1}), situated in catchments with forestry as the main land-use, and run through areas that were clear-cut between 2014 and 2020 (Table 1). The site selection was non-random. First, we analyzed open-access GIS data on clear-cuts (harvested in 2014–2020) intersected by streams within the desired region to find streams that had similar land-use, i.e. production forest (>10 m in average height) with no recent forest operation (thinning and/or clear-cutting) for the upstream and downstream stream reaches (at least 150 m of the stream length). This initial condition was fulfilled in only 25 potential sites because this landscape is dense with mires, lakes, agricultural fields and intensively managed stands (and clear-cuts).



National Land Survey of Finland, Esri, TomTom, Garmin, Foursquare, FAO, METI/NASA, USGS

Fig. 1. A) Location of all studied streams in northern Sweden, and three examples of studied stream with B) no riparian buffer, C) wide (>15 m) riparian buffer and D) thin (<10 m) riparian buffer. Aerial photos of the three types of streams (B–D), stream numbers 3, 7 and 8 (Table 1), show the reaches studied for estimating whole stream metabolic rates. Blue lines represent streams, blue arrows represent flow direction and green dots represent sampling points for oxygen loggers (hereafter “locations”).

Table 1
Stream locations and characteristics. Thin buffer widths are <10 m with multiple gaps and wide buffers are ≥15 m wide.

Stream	Age of clear-cut	Coordinates (WGS84)	Stream length on clear-cut (m)	Buffer width (m ±SD)	Buffer category
1	2015	63.7525, 19.6034	169	9 ± 7	Thin
2	2019	63.8001, 19.8843	116	7 ± 4	Thin
3	2017	63.794, 19.6549	178	18 ± 10	Wide
4	2016	63.6310, 19.2921	141	6 ± 5	Thin
5	2014	64.1696, 19.3890	81	7 ± 8	Thin
6	2017	63.764, 19.7996	212	15 ± 7	Wide
7	2018	64.201, 19.7909	517	3 ± 3	Thin
8	2020	64.092, 19.976	430	8 ± 8	Thin
9	2017	63.7933, 19.478	161	16 ± 7	Wide

After excluding streams that were not accessible (gates blocking the roads) or too recently ditched, the final selection of nine streams was based on achieving a variety of buffer widths in two categories: <10 and ≥ 15 m, measured from aerial photographs in ArcGIS Pro (Esri, 2023) at 10 stratified transects. The final selection, while fulfilling our criteria, nevertheless showed variation in the forest age surrounding the streams in the upstream and downstream locations (ranged from 30 to 80 years), the size of the clear-cut (the length of the stream within the clear-cut, Table 1) and substrate conditions (ranging from stream bottoms dominated by fine-grained particles to streams with no sand at all).

2.2. Physico-chemical parameters

We recorded incident light in lux and water temperature in ^{o}C every hour using Hobo pendant loggers (Onset Computer Corporation, Borne, U.S.A.) deployed at four locations in each stream, together with the tiles (see next section on Biofilm metabolism). The locations were 20–40 m upstream of the clear-cut, at the end of the clear-cut, 50 m downstream and 100 m downstream of the clear-cut (Fig. 1). Lux was converted to photosynthetically active radiation (PAR) using a conversion factor of 0.0185 (Thimijan and Heins, 1983). The lux loggers were tested against each other under 25 °C and they ranged 24.7–25.1 °C. We sampled water four different times at each of the four locations in each stream (9 streams, 36 locations) to measure concentrations of nitrate (NO_3^-), ammonium (NH_4^+), total phosphorus (TP) and DOC. Dissolved inorganic nitrogen (DIN) represents the sum of NO_3^- and NH_4^+. Water was filtered (0.45 μm) on site and kept refrigerated at 4 °C (DOC) or frozen at −20 °C (DIN, TP) before colorimetric analysis of NO3-N (ISO 13395:1996; Method G-384-08 Rev. 2), NH4-N (ISO 11732:2005; Method G-171-96 Rev. 12), and TP (ISO 6878:2004; Method G-297-03 Rev. 1) with a QuAAtro39 (Seal Analytical).

2.3. *Biofilm metabolism*

Local biofilm metabolism was estimated using ceramic tiles (4.8 × 2.3 cm) for GPP and wood tiles (made of birch veneers, 5 × 2 cm) for community respiration (CR). Two different tiles, ceramic and wood, were used because autotrophs (periphytic algae) often dominate inorganic surfaces (tiles), while heterotrophic organisms (bacteria and fungi) favor organic substrates (Myrstener et al., 2018). At each stream location (upstream, within clear-cut, 50 m and 100 m downstream), four ceramic and four wood tiles were deployed for 21 days, once in July and once in August. After retrieval, tiles were stored at 4 °C and incubated in the lab within 24 h of collection for estimates of GPP and CR. Incubations were conducted by adding one tile each to a 50 mL tube and filling them with oxygen saturated stream water. The water used in the incubation was collected from the same locations as the tiles with no modifications other than bubbling with air to saturation. Dissolved oxygen saturation (YSI ProDO, USA) was measured pre- and post-incubation and the instrument was calibrated each morning before the experiment started. Ceramic tiles were incubated for 3 h in light chambers at 12 °C for estimation of autotrophic oxygen production, and both ceramic and wood tiles were incubated for 3h in dark chambers (12 °C) for estimation of total oxygen consumption. We chose 12 °C for all incubations as a way of standardizing conditions between streams and because this was the average temperature of all streams during the study. We also chose the same temperature for all streams so that the GPP and CR represent the biomass growth over the whole deployment, rather than being influenced by the differences in temperature during the incubations. An additional three blanks (stream water only), treated the same way as the tiles, were used to correct for any water column changes in dissolved oxygen. Metabolic rates were calculated as the difference in dissolved oxygen between start and finish of incubations, correcting for any dissolved oxygen change in the blanks, and presented as per surface area (g O_2 cm^{-2} hr^{-1}). GPP was calculated for ceramic tiles as the mass of oxygen produced during light incubation plus oxygen consumed during dark incubation. We calculated CR as the mass of oxygen consumed during dark incubation of wood tiles.

2.4. *Whole stream metabolism*

Whole stream metabolism was modelled for the upstream, clear-cut and 100 m downstream locations in three of the streams (streams 3, 7 and 8) during ca 90 days from mid-July to early October. We chose those streams to represent both wide and narrow buffers (Fig. 1B–D and Table 1). We also chose streams that lacked substantial inputs of water from ditches or ground water ~200 m upstream of the logger sites because this disrupts the oxygen signal. At each stream, we recorded dissolved oxygen at 10-min intervals using miniDOT loggers (Precision Measurement Engineering Inc., USA). Oxygen loggers were calibrated before and after deployment using 100 % oxygen saturation and 0–5 % oxygen saturation. There was no notable drift during deployment. Metabolism was estimated at these locations using the single-station diel oxygen method where GPP and ecosystem respiration (ER) were estimated using Bayesian inverse modelling (Hall and Hotchkiss, 2017). We used our time series data for dissolved oxygen, dissolved oxygen saturation (DOsat), water temperature, light (from lux loggers), together with a modelled gas exchange rate coefficient (K) and stream depth (z). The main equation for GPP and ER was:

$$\Delta \text{dissolved oxygen} / \Delta t = (\text{GPP} - \text{ER})/z + K(\text{DOsat} - \text{dissolved oxygen})$$

where the change in oxygen over time (O_2 m^{-3}) equals all oxygen produced by photosynthesis (GPP, g O_2 m^{-2} d^{-1}) minus all oxygen consumed by respiration of both autotrophs and heterotrophs (ER, g O_2 m^{-2} d^{-1}), and the rate of gas exchange between the water and air (K, d^{-1}). We modelled three parameters (GPP, ER and K) but with daily priors (the starting point from which the model predicts a parameter) for Ks based on nighttime regression analysis and discharge-K relationships (following Rocher-Ros et al., 2020). Finally, we filtered data for erroneous model days by using the mean average error between the observed and the modelled DO concentrations. All days with a mean average error larger than 0.25 were removed. All remaining days were visually inspected to further exclude erroneous model estimates as the model can be poor, even if the model has a small error, if GPP is very low. Following these guidelines, we removed 25 % of analyzed days across all streams. We are aware that the footprint of the downstream oxygen loggers might incorporate signals from the water of upstream locations. These are, however, headwater streams with multiple waterfalls per reach that completely mix (and thereby oxygenate) the water, causing short oxygen turnover lengths. Still, we tested for correlations in metabolic rates between loggers and this was highest for ER in stream 8 ($r^2 = 0.37$). With that, we are certain that our estimates of whole stream GPP and ER to a large degree represent metabolic rates, which are produced in the represented location (i.e. good separation between upstream, clear-cut and downstream locations). There may have been a modest downstream transport of oxygen in stream 8, the stream with the highest correlation between ER in the clear-cut and downstream site, but this effect is not expected to be large enough to affect the direction of change between logger locations. ER in this location was also highly autocorrelated ($r^2 = 0.5$, $p < 0.01$), as daily values of ER depended on the previous day's ER, for at least three days (lag3). This indicates low daily variability in ER, and therefore we would expect some correlation between locations even without any overlap in logger footprint.

2.5. *Data analyses*

We evaluated the change in biofilm metabolic rates (GPP and CR) in clear-cut, 50 m and 100 m downstream locations compared to their upstream location. This was done using t-tests to determine if the change in GPP was different from 0. We used R for all statistical analyses (Version 4.1.2; R Core Team, 2021).

We evaluated the drivers of downstream changes in biofilm GPP and CR per season using partial least square regressions (PLSR) with the R package "pls" and leave-one-out cross-validation (Mevik and Wehrens, 2023). We used the change in GPP and CR in the 100 m downstream locations compared to their upstream location as the response variable. We separated data for July (summer) and September (autumn). PLSR identifies the relationship between predictor (X) and response variables (Y) through a linear, multivariate model and produces latent variables that maximize the explained variability in Y and reduces the original multidimensionality (similar to a principal component analysis). We opted for PLSR due to the high number of predictor variables compared to the low number of observations (Carrascal et al., 2009). The predictor variables were: average light (PAR), TP, DIN, average temperature, DOC as well as the absolute change in upstream-downstream locations for those above mentioned parameters. Finally, we included GPP of the clear-cut as a predictor variable. The most important predictor variables were identified based on variables important in projection (VIP scores) above 1.0.

Differences in weekly whole stream metabolic rates between locations and season were evaluated using a mixed effect model (lme4 package, Bates and Maechler, 2009) with location (upstream, clear-cut and 100 m downstream) and season (summer and autumn) as fixed factors and week as a random factor. We grouped July and August as summer and September and October as autumn. We used weekly averages of the daily metabolism estimates to minimize effects of autocorrelation. Pairwise comparisons were made using function emmeans with the Tukey HSD method (package emmeans, Lenth, 2023).

2.6. Mapping clear-cut stream length

We quantified the proportion of the total forested stream length in Sweden that is situated within a clear-cut harvested between 2014 and 2020 and 100 m downstream from those clear-cuts. This was done to put the “100 m” reach length into a larger perspective within Sweden. Stream networks were extracted from a hydrologically corrected digital elevation model with 1 m resolution using the deterministic 8 (D) flow routing algorithm (O’Callaghan and Mark, 1984) with a 6 ha stream initiation threshold (Paul et al., 2023). The digital elevation model was corrected by carving a channel of known streams and road culverts across roads (Lidberg et al., 2017). Ditch channels detected by the algorithm described by Lidberg et al. (2023) were also burned into the digital elevation model to ensure correct flow routing in flat and drained landscapes. Finally, a complete breaching algorithm was used to resolve remaining depressions in the digital elevation model (Lindsay, 2016). To get the total forested stream length of Sweden we used a modified version of the original 6 ha stream network, where we only included the length of stream segments that were on forest land.

The modelled stream network was intersected with clear-cuts, where date of clear-cutting is based on a change analysis from satellite imagery (map from Swedish forest agency). A total of 332,260 clear-cuts with a total area of 11,340 km^2 were harvested between 2014 and 2020. We only included streams that intersected the clear-cuts for at least 50 m. The selected stream segments were then used as seed points to trace downstream flow paths along the D8 flow direction grid. Finally, we used these seeded streams to calculate the length of streams within 100 m downstream of the clear-cuts.

3. Results

3.1. Physical and chemical properties of the streams

Temperature in the studied streams ranged from 6.8 to 15.4 °C, with a mean of 12.7 °C in July and 8.2 °C in September (Table S1). There were only minor longitudinal differences in the temperature among the upstream and downstream locations, where, for example in July, the upstream locations averaged 12.4 °C while downstream locations averaged 12.7 °C. In stream 7, however, the downstream location was 2 °C warmer than the upstream location (Fig. 2). The majority of forested locations (both upstream and downstream of clear-cuts) were dark, with an average light (PAR) over the full season of 14.7 μmol m^{-2} s^{-1} (13.2 μmol m^{-2} s^{-1} in upstream vs 22.9 in downstream locations), which contrasts with the clear-cut locations, which averaged 70.4 μmol m^{-2}

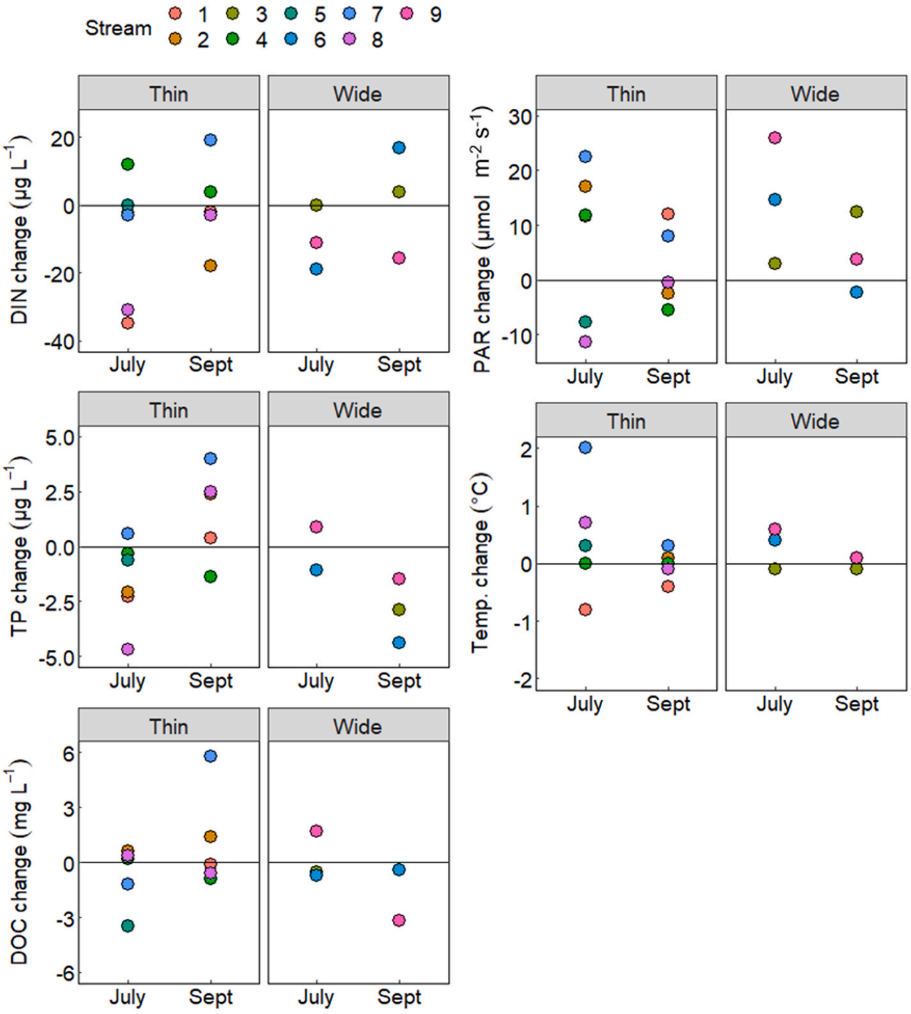


Fig. 2. Change in physico-chemical variables, comparing each 100m downstream location to its upstream locations. A positive value indicates higher values in the downstream location than in the upstream location. Each point represents the average value of two sampling occasions.

s^{-1}. There was no difference in benthic light (PAR) between thin and wide buffer clear-cut locations (51 vs 52 μmol m^{-2} s^{-1}). There was large variation in DOC among streams (9.5–36.3 mg L^{-1}), but not between seasons or among locations within a stream. DIN varied among streams from 21 to 141 μg L^{-1} and TP from 8 to 25 μg L^{-1}. There was a general trend of dilution and thus slightly lower DIN and TP concentrations in downstream locations as compared to upstream ones (Fig. 2), although stream 7 had higher DIN and TP concentrations in the downstream locations. Stream 8 had the highest concentrations of nutrients on a few occasions, likely due to fertilization in an agricultural field further up in the stream network. The levels of DIN and TP increased equally in both upstream and downstream and were <30 μg N L^{-1} and <15 μg P L^{-1} before and after fertilization (Table S1).

3.2. Biofilm metabolism (GPP and CR)

GPP of biofilms as estimated from incubations of ceramic tiles averaged 1.1 μg O_2 cm^{-2} hr^{-1} (range 0.01–3.23) across all sites and sampling dates (Fig. 3A). In July, the average GPP was 1.6 μg O_2 cm^{-2} hr^{-1} in thin buffer streams and 1.0 μg O_2 cm^{-2} hr^{-1} in wide buffer streams. In thin buffer streams in July, GPP was 0.52 μg O_2 cm^{-2} hr^{-1}, or 55 %, higher in the 100 m downstream locations than in the upstream sites ($t = 3.4$, $df = 5$, $P = 0.02$). In wide buffer streams, there was no longitudinal change in GPP. The most important factor driving downstream increases in GPP in thin buffer streams was the magnitude of GPP in the clear-cut (VIP 1.4, loading 0.5), i.e. streams with high GPP in the clear-cut also had high upstream-downstream increases in GPP. Streams with high average DOC and TP also had large downstream increases in GPP (VIP 1.1 and 1.3, loading 0.3 and 0.6), whereas temperature and light were not important variables in the PLS. The two components (clear-cut GPP and stream chemistry) together explained 90 % of the variance in the downstream change in GPP in the PLS model. The most important variables related to high GPP in the clear-cut were DIN (VIP 1.4, loading 0.7) and TP (VIP 1.4, loading 0.8). We also included the relationships between longitudinal changes in physico-chemical variables (upstream-downstream changes) with the downstream changes in GPP in a PLS, and the only important variable (VIP>1) was a negative effect of TP, where a larger longitudinal increase in TP was related to decreases in GPP.

In September, the average GPP was 0.6 μg O_2 cm^{-2} hr^{-1} in thin buffer streams and 0.9 μg O_2 cm^{-2} hr^{-1} in wide buffer streams. In thin buffer streams in September, we found that GPP was on average 50 % lower (decreased with 0.49 μg O_2 cm^{-2} hr^{-1}) 100 m downstream compared to the upstream location ($t = -2.47$, $df = 5$, $P = 0.056$). The clear-cut sites were not significantly different from upstream sites in September, yet there was generally a large drop in productivity as compared to July. PLS analysis on thin buffer sites in September revealed that high light sites had the largest downstream decrease in GPP (VIP 1.6 and loading −0.5). GPP in the wide buffers did not have significant longitudinal patterns. The 50 m downstream locations showed the same pattern as the 100 m downstream locations for both GPP and ER but we did not perform statistics on these locations.

Community respiration (CR) of biofilms, estimated from incubations of birch wood veneers, were of similar rates as GPP and averaged 0.9 μg O_2 cm^{-2} hr^{-1} (range 0.07–3.01) over all streams and sampling periods. Rates of CR had no longitudinal or seasonal pattern, with differences

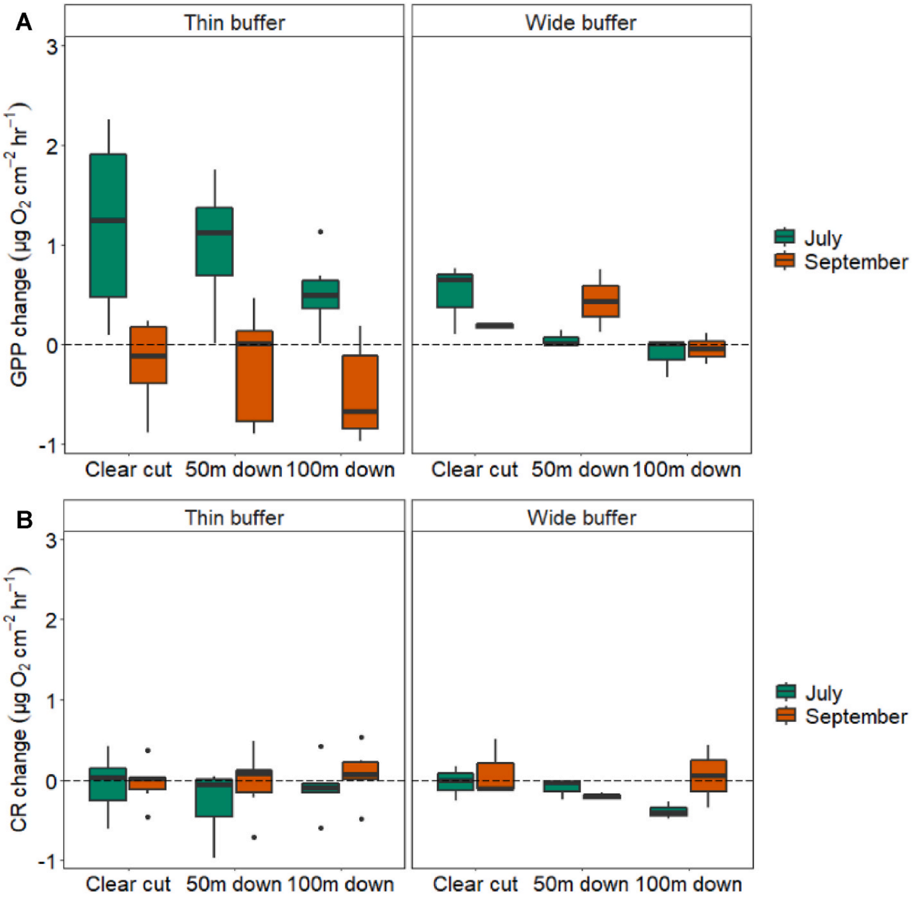


Fig. 3. Change in biofilm GPP (A, μg O_2 cm^{-2} hr^{-1}) and CR (B, μg O_2 cm^{-2} hr^{-1}) in clear-cut, 50 m and 100 m downstream sites compared to each stream's upstream location. A positive value indicates higher gross primary production (GPP) or community respiration (CR) as compared to upstream. The box shows the interquartile range with the median indicated by the black line, the error bars are the maximum (3rd quartile + 1.5*inner quartile range) and minimum (1st quartile – 1.5*inner quartile range) values and outliers outside of the minimum and maximum are indicated by black dots.

between the upstream sites and the other three sites in a stream near zero (Fig. 3B).

3.3. Whole stream GPP and ER

Whole stream GPP and ER estimated from high frequency oxygen data spanning July to October revealed strongly heterotrophic ecosystems where ER was on average an order of magnitude higher than GPP (Fig. 4A–C), with an average net ecosystem productivity of −4.6 g O_2 m^{-2} d^{-1}. Streams 7 and 8 showed a similar pattern, where GPP was sevenfold greater in the clear-cut than in the upstream location, while ER was three times greater in the same streams for the same comparison, which together resulted in a decrease in net ecosystem productivity. This pattern was propagated 100 m downstream for stream 8 (GPP: $t = 5.4$, $df = 33$, $p < 0.01$, ER: $t = 6.2$, $df = 33$, $p < 0.01$). In stream 7, increases in ER rates were propagated downstream ($t = 5.1$, $df = 26$, $p < 0.01$), while GPP levels at 100 m downstream did not differ from levels upstream of the clear-cut ($t = 0.3$, $df = 19$, $p = 0.9$). Stream 3, which was dominated by sandy substrates in the clear-cut and a wide buffer, behaved differently and displayed a sharp decrease in metabolic rates (70 % decrease) in the clear-cut compared to the upstream site, and the low values of GPP and ER were sustained 100 m downstream of the clear-cut (GPP: $t = 4.3$, $df = 20$, $p < 0.01$, ER: $t = 10.9$, $df = 18$, $p < 0.01$). Overall, the effect of season (summer vs autumn) was small compared to the effect of location (upstream vs downstream, Fig. S1).

3.4. Mapping clear-cut stream length

The total length of the modelled forested stream network in Sweden was 1,008,800 km, and the total length of all stream segments within clear-cuts (harvested between 2014 and 2020) was 24,300 km. The total stream length 100 m downstream of clear-cuts was 33,100 km. This means that 2.5 % of the total stream length was found within clear-cuts harvested 1–6 years ago, and 3.3 % of the total stream length was within 100 m downstream of those clear-cuts. In total, 5.8 % of the stream length is thus affected by recent clear-cuts (harvested 1–6 years ago).

4. Discussion

The longitudinal connectivity of flowing waters, where downstream sites are affected by upstream stressors becomes particularly important to consider in the context of forest clear-cutting (Erdozain et al., 2021). In Sweden, 1.1 % of the production forest is clear-cut each year, which creates a mosaic of stands where one fifth of stands are 0–21 years of age and therefore have very little canopy (Nilsson et al., 2023). Superimposed on this mosaic forest landscape are numerous small headwater streams, many of which receive minimal or even no protection in the form of riparian buffers (Kuglerová et al., 2020; Ring et al., 2023). In fact, riparian buffers along headwaters in Sweden rarely exceed 10 m and the thin buffers (<10 m) used in our study represent the current norm of 5–7m wide buffers on average (Ring et al., 2023). Previous studies have shown that abiotic factors such as temperature and DOC can be propagated downstream from clear-cuts (Oni et al., 2015; Roon et al., 2021), but our estimates of metabolic rates are the first to show that ecological functions are also affected downstream of clear-cuts. We found effects on the magnitude of metabolic rates, on the balance between production and consumption and on the seasonality of productivity patterns. Compared to upstream sites, which were represented by

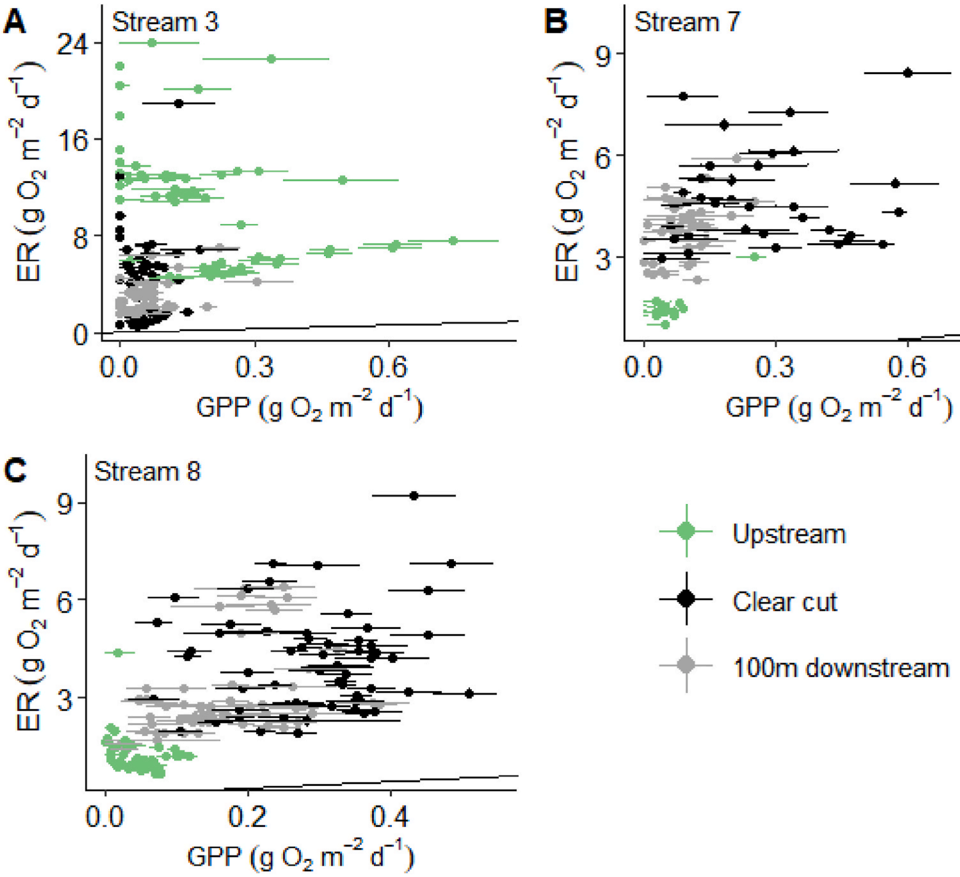


Fig. 4. Whole stream gross primary production (GPP, g O_2 m^{-2} d^{-1}) and ecosystem respiration (ER, g O_2 m^{-2} d^{-1}) at three locations in each of three studied streams, based on one station metabolism. Green color marks the upstream, control location. Each point represents the daily average GPP and ER with error bars that represent uncertainty of parameter estimation reported as 95 % credible intervals (error bars for ER are hardly visible due to the difference in axes). Data incorporate estimates from mid-July to early October. The black line represents a 1:1 relationship so points above the line mean ER was higher than GPP.

even-aged, second-growth stands, downstream locations of clear-cuts with thin buffers had higher overall net ecosystem productivity, higher GPP in July and lower GPP in September. Wide riparian buffers (≥15 m) reduced impacts on biofilm metabolic rates both within and downstream of clear-cuts, and this effect is consistent with findings for abiotic parameters (Roon et al., 2021; Sweeney and Newbold, 2014). The importance of wide buffers is further supported by a Finnish study, which showed that 15 m buffers protected aquatic organisms better than 10 m ones (Jyväsjärvi et al., 2020), although 15 m wide buffers are still not enough to protect the entire stream-riparian ecosystem in most situations (Oldén et al., 2019b, Broadmeadow and Nisbet, 2004). Considering that metabolic rates rarely recovered within 100 m downstream, and clear-cuts effects likely persist longer than 6 years post-harvest, the scope of environmental impact is likely underestimated by our study. In addition, we expect interactive effects to occur when a stream runs through multiple clear-cuts and/or agricultural fields within short distances (Townsend et al., 2008), and this needs to be taken into account when best-management-practices for mitigating forestry impacts are formed.

We suggest that the downstream propagation of biofilm metabolism was potentially caused by a shift in species composition towards high light adapted biofilms. This notion is supported by a study in the same area, where exposing outdoor flumes to minimal shading caused large shifts in algal biofilm composition towards a dominance of filamentous species (Myrstener et al., 2023). With the data set used here, we cannot disentangle what was the direct cause of the downstream propagation of metabolic rates but what we did find was that downstream changes in local biofilm GPP were coupled to high summer GPP within the clear-cut. We further show that this was promoted in streams with higher nutrient concentrations, which is to be expected as these waters are often nutrient-limited (Burrows et al., 2021). The direct effect of inorganic nutrient enrichment from clear-cuts is likely short-term (Löfgren et al., 2009), but effects of increased autotrophic organic matter and organic nutrients can be sustained as long as there is high productivity within the clear-cut due to increased light. Even though a couple of streams showed signs of nutrient enrichment in downstream sites, this was not the main cause for the downstream propagation of metabolic rates. Furthermore, differences in light and temperature were small and not driving downstream propagation patterns, but that is not to say the effect of light was not important. The increase in metabolic rates in the clear-cuts and the probable shift in species dominance was enabled by large increases in light.

The potential shift in species composition could also have caused the disruption of biofilm GPP in September in the thin buffers. Fast growing algae, developed in high light environments, likely have poor adaptation to the dramatic shift towards cool, dark and hydrologically flashy conditions, which prevail in September (Myrstener et al., 2023; Neif et al., 2017). In this study, we did not identify the species on the biofilms and thus cannot confirm or reject this hypothesis. Another possible explanation is an increase in grazers in clear-cut and downstream locations during late August and early September, promoted by the high biofilm biomass during summer (Göthe et al., 2009; Jonsson et al., 2017). However, bottom-up processes likely dominate for these low-productive, boreal waters (Burrows et al., 2021; Jonsson et al., 2017), and overall macroinvertebrate abundance and richness tends to be low (Göthe et al., 2013; Jonsson et al., 2017). Finally, downstream decreases in autumnal GPP could be an effect of longitudinal differences in stream size and increased water velocity. The water level increased drastically by the end of the September deployment, which theoretically could have caused the downstream decrease in GPP. However, this negative effect was lacking in the wide buffers, which makes this hypothesis less likely. The connection between high clear-cut GPP and high downstream propagation remains to be further studied, but we propose that large changes in biofilm composition was one part of the explanation for altered downstream metabolism and changes to the seasonal productivity patterns.

Primary production is low in small streams in second-growth, even-aged northern Scandinavian forests. Headwater streams are generally dark, nutrient poor and acidic, and whole stream GPP was below 1g O_2 m^{-2} d^{-1} in all upstream locations, in line with the few estimates that exist for the same area (Lupon et al., 2020). Low primary productivity is coupled to low food quality for consumers (Guo et al., 2016) and degradation of stream functions, such as nutrient (Skovsholt et al., 2020) and carbon dioxide uptake (Rocher-Ros et al., 2020). The decrease in biofilm GPP in downstream sites as compared to the stream locations upstream of clear-cuts in September is therefore undesirable and calls for increased protection of the ecological functions of our headwaters through the use of sufficient riparian buffer management. From our study, buffers of at least 15 m width should be applied to small streams because they mitigated the metabolic changes better than narrow buffers, and have been shown by others to protect biodiversity (Jyväsjärvi et al., 2020), provide sufficient amount of large wood (Kuglerová et al., 2023) and decrease sediment transport (Hasselquist et al., 2024). For other targets, including temperature control and protection of animal communities on land and in water, 30m or even wider buffers have been shown to be necessary (Sweeney and Newbold, 2014, Broadmeadow and Nisbet, 2004).

The combined use of locally estimated biofilm metabolic rates and whole stream metabolism helps in addressing the question of overlap in oxygen footprint from the open water oxygen method used. The open water method enables detection of change in GPP and ER, while it cannot fully explain lack of change. As we managed to observe large changes (both increases and decreases) in GPP and ER, and these largely correspond to changes in local biofilm metabolic rates, we are comfortable with the conclusions made based on the one station method. Furthermore, these small headwaters all have multiple points of complete mixing, so that oxygen turnover lengths are short (also verified by little overlap between loggers). Unfortunately, with the two-station method, you can never accomplish the spatial or temporal resolution that we accomplished in this study. Low GPP systems are also very sensitive to small changes in hydrological inputs and outputs in a mass balance approach, making the method even more sensitive in dark, boreal waters. The use of oxygen loggers to monitor stream health is increasing and new methods of simplifying the analyses of stream oxygen data are currently being developed, e.g. daily fluctuations and/or frequency distributions of oxygen saturation that are distinct for certain types of land-use (dos Reis Oliveira et al., 2019) can be used to detect relative change. Regardless of the specific method, we encourage the use of oxygen signals together with biofilm estimates to monitor downstream changes in stream health connected to land-use changes of all types, including effects of climate change (Gómez-Gener et al., 2020).

While we report negative effects of clear-cutting on local and downstream ecological patterns, our study raises the question of how far and how long after clear-cutting the downstream propagation of ecological effects persists. To highlight the spatial importance of our study, we estimated the total forested stream length and proportion of streams in Sweden that are situated within or 100 m downstream of a recent clear-cut (harvested 1–6 years ago). We found that, at any given time, up to 3.3 % of all forested streams in Sweden are situated downstream of recent upstream clear-cuts (harvested 1–6 years ago), and another 2.5 % is situated within those same clear-cuts, totaling 57,400 km of streams. This is due to the fact that about 1 % of the production forest is being clear-cut each year. Contemporary monitoring programs are not sufficient to identify potential water quality degradation from clear-cutting because small, forested streams are not systematically monitored; they are hardly even mapped (Bishop et al., 2008; Fovet et al., 2021). Most of the monitoring programs have been developed to evaluate ecological status in large streams and rivers (>10 km^2 catchment area), not situated in forests (Biggs et al., 2017). Yet, here we show that clear-cutting has the potential to affect a distance long enough to have ecologically relevant effects on a catchment scale. In our study, we present changes in metabolic rates, but it is highly likely that other ecological processes and organisms are also affected (Albertson et al., 2018; Roon et al., 2021). These effects should be monitored and mitigation measures must be improved. From our results, buffers of at least 15 m width (on each side of the stream) can mitigate some of the worst impacts. Anything narrower than 15 m is at risk of failing the protective functions that buffers are supposed to provide (Jyväsjärvi et al., 2020; Kuglerová et al., 2023; Oldén et al., 2019a).

CRediT authorship contribution statement

Maria Myrstener: Writing – review & editing, Writing – original draft, Visualization, Validation, Methodology, Investigation, Formal analysis, Data curation, Conceptualization. **Larry A. Greenberg:** Writing – review & editing, Supervision, Conceptualization. **William Lidberg:** Writing – review & editing, Methodology, Formal analysis, Data curation, Conceptualization. **Lenka Kuglerová:** Writing – review & editing, Writing – original draft, Resources, Project administration, Funding acquisition, Conceptualization.

Declaration of competing interest

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

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Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.jenvman.2025.124740.

Data availability

Data are accessible through the Swedish National Data Service: https://doi.org/10.5878/4g5y-nd76.

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