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Riparian forests can mitigate warming and ecological degradation of agricultural headwater streams

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Abstract

1. Riparian forests are commonly advocated as a key management option to mitigate the effects of agriculture on headwater stream biodiversity and ecosystem functions. However, the benefits of riparian forests might be reduced by uninterrupted catchment-scale pollution.
2. We studied the effects of riparian land use on multiple ecological endpoints in headwater streams in an agricultural landscape. We studied stream habitat characteristics, water temperature and algal accrual, and macrophyte, benthic macroinvertebrate and fish communities in 11 paired forested and open agricultural headwater stream reaches that differed in their extent of riparian forest cover but had similar water quality.
3. Hydromorphological habitat quality was higher in forested reaches than in open reaches. Riparian forest had a strong effect on the summer water temperature regime, with maximum and mean water temperatures and temperature variation in forested reaches substantially lower than in open reaches.
4. Macrophyte communities differed between forested and open reaches. The mean abundance of bryophytes was higher in forested reaches but the difference to open reaches was only marginally significant, whereas graminoids were significantly more abundant in open reaches. Within-stream dissimilarity of benthic macroinvertebrate community structure was significantly related to the difference in riparian land use between reach pairs. The relative DNA sequence abundance of pollution-sensitive Ephemeroptera, Plecoptera, and Trichoptera species tended to be higher in forested reaches than in open reaches. Finally, fish densities were not significantly different between forested and open reaches, although densities were higher in forested reaches.
5. This unequivocal evidence for the ecological benefits of forested riparian reaches in agricultural headwater streams suggests that riparian forest can partly mitigate the adverse impacts of agricultural diffuse pollution on biota. The strong effect of forests on stream water temperature suggest that riparian forest could also mitigate harmful effects on headwater stream biodiversity and ecosystem functions of the predicted more frequent high summer temperatures.

KEYWORDS

Biodiversity, diffuse pollution, DNA metabarcoding, land use, water temperature

1 | INTRODUCTION

Despite their small size, headwater streams account for a large portion of the total basin area and the biodiversity of river ecosystems (Bishop et al., 2008; Finn et al., 2011). Small catchment sizes and isolation within river networks cause spatial and temporal stochasticity of environmental conditions and species dispersal. This results in larger between-stream variation and higher species turnover than in higher order channels (Brown & Swan, 2010; Sarremejane et al., 2017). Moreover, many headwater streams are heavily influenced by groundwater discharge (Jyväsjärvi et al., 2015; Turunen et al., 2020; Winter, 2007) and could thus provide thermal refugia for cold stenothermic species during heat waves, highlighting their key importance for the biodiversity of the entire catchment.

However, the very same reasons that make headwater stream habitats and their biota unique in the riverine landscape, leave them particularly vulnerable to anthropogenic disturbance. Land use, such as agriculture, can result in nutrient and pesticide pollution, acidification, excessive sedimentation, and changes of thermal conditions (Allan, 2004; Buck et al., 2004; Sponseller et al., 2001), which—exacerbated by the small water volume of headwater streams—quickly exceed species' tolerance levels.

In headwater streams, agricultural land use not only adversely affects water quality and benthic habitat conditions, it also causes the loss of natural riparian vegetation, which has profound consequences for the stream's ecology (Burrel et al., 2014; Hawkins et al., 1983; Hladyz et al., 2011). Headwater streams and their riparian forests are deeply connected (e.g. Nakano et al., 1999; Turunen et al., 2017). Riparian forests stabilise stream banks and have the ability to reduce nutrient run off, thereby mitigating erosion and eutrophication (Feld et al., 2018). Leaf litter and terrestrial insects fuel the heterotrophic food webs (Perkins et al., 2018; Wallace et al., 1997). Shading and inputs of woody debris affects stream metabolism, nutrient cycling, and water temperature (Johnson & Almlöf, 2016; Warren et al., 2016). Shade and reduced wind speeds in forested riparian zones also create cooler and more humid microclimates with fitness consequences for riparian biota and adult aquatic insects (Carlson et al., 2016; Collier & Smith, 2000; Remsburg et al., 2008). Reciprocally, hatching aquatic insects are a crucial energy subsidy for riparian ecosystems and flooding represents a key disturbance that provides nutrients and increases soil moisture in riparian zones (Baxter et al., 2005; Hjältén et al., 2016).

The influence of reach scale riparian forests on stream water temperature, benthic habitat conditions, water quality, and ecological status in extensively altered catchments has been frequently studied, but results have been highly variable. Some studies report stronger influence of catchment scale land use (Death & Collier, 2010; Harding et al., 2006; Roth et al., 1996; Wahl et al., 2013), while others suggest that reach scale land use and integrity of local riparian forests is a more influential factor (Jones et al., 1999; Lammert & Allan, 1999; Storey & Cowley, 1997). There are at least two factors that may govern the strength of effects that riparian forests have on streams. First, it is likely that under intensive catchment land use and high water pollution, reach scale variation in riparian forest cover will have limited influence on the ecological conditions of a stream because its ecosystem is degraded by intense pollution (Osborne & Kovacic, 1993; Walsh et al., 2007; Feld et al., 2018). However, in slightly to moderately polluted streams, local riparian forests could improve reach scale ecological conditions. Turunen et al. (2019) found that in moderately polluted mid-order streams, occurrence of riparian forests improved the ecological status of macrophytes and increased the abundance of leaf shredding invertebrates despite having no effect on water chemistry, temperature, or benthic habitat conditions. Second, according to predictions of the river continuum concept (Vannote et al., 1980), influence of riparian forests on stream ecosystems should be higher for headwater streams, suggesting that in agricultural headwater streams, the positive effects of riparian forests on stream habitat and ecological status should be stronger than for mid-order channels.

In this study, we explored the effect of reach scale riparian forest cover on stream water temperature, habitat characteristics, periphyton accrual, as well as macrophyte, macroinvertebrate and fish community structure in 11 agricultural headwater streams. We compared forested and open reaches within and across streams. We specifically asked if riparian forest has any influence on species composition and algal accrual irrespective of diffuse pollution, or if diffuse pollution negates potential positive effects of riparian forests. Due to shading effects of the forests, we expected mean and maximum water temperatures and water temperature variation to be lower in forested reaches and that the presence of riparian forest leads to a decrease of algal accrual. Moreover, due to differences in their affinity to light, macrophyte communities were expected to be dominated by graminoids in open reaches, whereas bryophytes were expected to be more abundant in forested reaches. Forests reduce water temperature, improve stream and riparian habitat quality, and provide input of leaf detritus, all of which are expected to have positive effects on the abundance of leaf-shredding invertebrates (especially on stonefly shredders due to their preference for forested riparian habitats) as well as Ephemeroptera, Plecoptera, and Trichoptera (EPT) species. Similarly, we expected higher fish density in forested reaches as a consequence of improved stream habitat quality, terrestrial inputs of prey items and reduced water temperatures.

2 | METHODS

Our study area is located in lowland (<200 m above sea level) catchments of western Finland (63.2–64.8°N, 23.8–25.5°E; Figure 1). Streams in the area are typically slightly acidic and coloured due to dissolved organic carbon and suspended solids. Catchment forests typically consist of half coniferous and half mixed boreal forests that are mostly managed. A substantial proportion of catchment areas is used for agriculture (Table 1). The main anthropogenic impact on these streams comes from diffuse agricultural pollution, channelisation, and conversion of riparian areas to pasture and fields. The agriculture in the area is mostly crop (oat, barley) and animal feed production (*Phleum pratense*, *Festuca pratensis*, *Lolium perenne*, *Dactylis glomerata*).

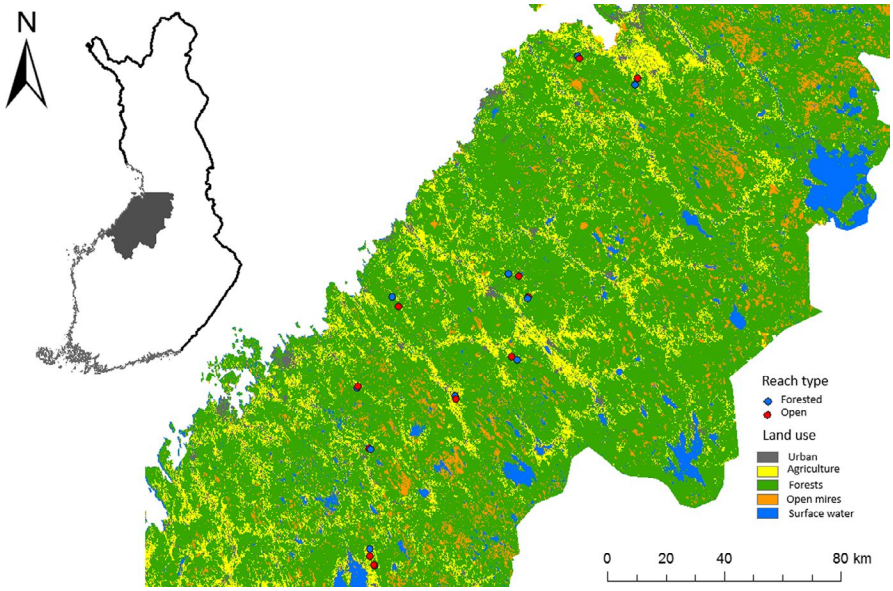

FIGURE 1 A map showing the study area, dominant land uses, and spatial arrangement of the study sites in Finland [Colour figure can be viewed at wileyonlinelibrary.com]

We selected 11 small (mean catchment area 38 km^2) first-order streams that were distinctly impacted by diffuse agricultural pollution (Table 1). These are small perennial low gradient streams that drain former seabed areas with flat terrain. Due to their catchment characteristics, the composition of biological communities in those streams is somewhat atypical in comparison with classic steep gradient headwater streams (sensu Vannote et al., 1980). We used aerial images and conducted field visits to select two 40-mreaches for each stream, one having an extensive cover of riparian forest (hereafter referred to as forested reach) and one having an altered riparian vegetation with reduced forest cover, with shrubs, few trees, and fields (hereafter referred to as open reach). Each reach contained some distinct riffle areas and pool habitat. We aimed to select reaches that would only differ by the integrity of their riparian forest within each stream and were located close to each other (mean distance 1.9 km) to ensure similar diffuse loading and water quality conditions (Table 1). In five of the 11 streams, open reaches were upstream of the forested reaches and in six cases downstream to avoid systematic effects related to relative positions of the reach pairs. The extent of field cover around open reaches was similar to the extent of forests in forested reaches.

2.1 | Water chemistry and physical habitat

Field surveys and sampling were conducted between July and September 2018. We measured several water quality variables for each stream at both open and forested reaches to verify that the level of diffuse pollution was similar between sites (Table 1). The chemical water quality parameters were measured in the laboratory using national standards (https://www.finas.fi/Documents/T003_M38_2018.pdf). Water pH and electrical conductivity were measured in situ using a YSI-professional-plus meter (YSI Inc.).

Water temperature was recorded at an hourly interval using loggers (iButton; Thermochron, Maxim Integrated) from mid-July to the end of August, which typically represents the warmest period of the year in Finland. Loggers were fixed to the river bed at 10–30 cm depth within 0.5 m from the stream margin using iron bars.

Water depth, bank-full channel width, and current velocity were measured at three points in three transects placed evenly along the sampling reach and mean values were calculated for each reach. Substratum size distribution was estimated for 12 randomly placed 0.25-m^2 squares as percentage cover of 10 size classes ranging from fine sediments (ø < 0.2 cm) to large boulders (ø > 25 cm; modified Wentworth scale, see Turunen et al., 2019). The amount of large woody debris (LWD) was quantified by measuring the length and average diameter of all wood pieces with >5 cm diameter from the 40-m reach. The canopy cover of riparian trees was estimated at 10 transects (five transects on each side of the channel). For each transect, we visually estimated the percentage cover of canopy vegetation through a 15 cm diameter cylindrical tube at three points: at the centre of the channel, the stream margin and within the riparian zone 5 m from the margin. Mean cover was calculated for the whole reach.

Hydromorphological conditions were evaluated at eight spots along the 40-m reach (every 5 m). We used the metrics for channelisation and hydromorphological degradation to score habitat conditions as many moderately channelised streams in the area have retained sufficient hydromorphological variability to support near-natural species composition (Turunen et al., 2016). Channelisation was estimated as removal of boulders and degree of straightening and ditching of the channel form (scale 0–2, 0 representing unaltered state and 2 severely channelised). For the hydromorphological degradation score (scale 0–2, 0 representing good status and 2 low status), we evaluated width, depth, flow, and substratum variability. Mean scores across each reach were calculated for both variables.

We used the ArcMap™ (ESRI) GIS software to calculate the percentage of agricultural land in stream catchments by using Corine

TABLE 1 The mean values and range of the key environmental variables. LWD, large woody debris; CV, coefficient of variation

Variable	Forested reaches	Open reaches
Catchment agricultural land use (%)	10 (2–31)	11 (3–28)
Riparian forest cover (100 m) (%)	78 (41–100)	24 (4–82)
Canopy cover (%)	53 (35–64)	19 (0–49)
Bryophyte cover (%)	13 (0–42)	5 (0–15)
Fine sediment cover (%)	19 (0–59)	39 (2–100)
Substrate size	5.6 (2.7–7.3)	3.6 (0.3–6.9)
Volume of LWD (dm^3/m^2)	1.6 (0–8.6)	0.1 (0–0.5)
Channelisation score (0–2)	1.5 (0.8–2)	1.9 (1.5–2)
Hydromorphological degradation score (0–2)	0.8 (0–1.8)	1.4 (0.6–2)
Current velocity (m/s)	0.1 (0.02–0.2)	0.1 (0.04–0.2)
Depth (cm)	12 (8–19)	9 (5–15)
Width (cm)	360 (210–550)	280 (180–460)
Electrical conductivity (uS/cm)	94 (43–202)	81 (40–162)
pH	6.5 (5.3–7.2)	6.6 (5.7–7.3)
Al (μg/L)	360 (150–830)	440 (200–1000)
Fe (μg/L)	7,500 (4800–12,000)	8,000 (3,800–11,000)
S (μg/L)	2,800 (580–7,500)	2,800 (910–7,100)
Suspended solids (mg/L)	14 (4–26)	17.9 (5–46)
Turbidity (FNU)	19.4 (6.1–43)	21.4 (5.1–38)
Total *N* (μg/L)	503 (280–870)	510 (270–720)
NH_4 (μg/L)	37 (5–190)	38 (3–210)
NO_2/NO_3 (μg/L)	290 (82–960)	280 (42–1000)
Total P (μg/L)	153 (73–300)	167 (67–390)
PO_4 (μg/L)	98 (29–190)	100 (26–260)
Mean water temperature (°C)	17.0 (16.2–18.4)	17.7 (16.3–18.7)
Minimum water temperature (°C)	9.2 (8.4–10)	8.6 (6.1–9.6)
Maximum water temperature (°C)	20.9 (19.2–23.2)	23.5 (21.9–25.6)
Temperature variation (CV)	0.19 (0.18–0.22)	0.21 (0.19–0.23)

Land cover 2012 data. In addition, we calculated the riparian forest cover within stream catchments with 100 m long and 25 m wide riparian buffers upstream of the sampling site.

2.2 | Biological sampling

We measured algal accrual at each reach by placing eight unglazed clay tiles in riffle habitat for eight weeks (from mid-July to early September). After incubation in the streams we measured the amount of algae on the tiles using a BenthoTorch™ fluorometer that estimates algal abundance on surfaces in situ (Harris & Graham, 2015). The area measured by the fluorometer was 1 cm^2 for each tile.

Macrophytes were surveyed for the 40-m reaches. We defined macrophytes as any vascular plant or bryophyte growing in the stream channel or directly at the water-land interface. Each reach was visually divided into 100 squares and the frequency of occurrence for each species was estimated by counting the squares of species occurrence (Rääpysjärvi et al., 2016). Species abundance was estimated as average cover per square in which a species occurred. For a summary data analysis, we multiplied abundance estimates with frequency estimates of macrophyte species. Bryophytes were sampled in 12 randomly placed 0.25-m^2 squares across each reach and both species identity and percentage coverage were recorded for each square to calculate mean cover.

For benthic macroinvertebrates, we took four 30-s kick-net samples covering most microhabitats present at a reach. This method is known to capture about 75% of taxa present in a given reach, mainly missing species with sporadic occurrence (Mykrä et al., 2006). Invertebrate sampling was conducted in early September. Samples were preserved in 96% ethanol in the field and the ethanol was replaced within 24 hr to assure a final 96% concentration (Stein et al., 2013). Samples were kept cool (8°C). All individuals were sorted in the laboratory and again preserved in 96% ethanol. Specimens were kept cool (8°C) for subsequent species identification by molecular analyses (see below).

Fish were sampled in mid-July from the riffle habitat of each reach using backpack electrofishing equipment (Hans Grassl, IG200-2). The reaches were fished once, all fish caught recorded (identified to species and their total length measured) to calculate total fish density for each reach.

2.3 | Macroinvertebrate identification

We used the DNA metabarcoding to identify macroinvertebrate species and quantify their relative abundance following workflow described by Elbrecht and Steinke (2019). To detect potential cross-contamination, eight negative controls and one empty well were incorporated in extraction, subsequent polymerase chain reactions (PCRs), and sequencing. Samples of different studies were included for library assembly and high throughput sequencing (Malaise trap samples, spider gut content, and lake grab samples, see Table S1 for a plate map).

Samples were dried over night at 40°C in single-use 20-ml homogenisation chambers. We used the IKA ULTRA-TURRAX Tube Drive Control System (IKA, Staufen im Breisgau, Germany) at 45 ***g*** for 30 min with 10 steel beads (diameter, 5 mm) added to tubes to grind bulk macroinvertebrate samples to a fine powder. Approximately 15 mg of tissue powder from each respective sample was used for DNA extraction with the DNeasy 96 Blood & Tissue Kit (Qiagen). To prevent cross-contamination between samples, tissue was digested

according to manufacturer recommendations in individual 1.5-ml reaction tubes at 56°C for 3 hr, and then transferred into the spin column plate.

For DNA metabarcoding, we utilised a two-step fusion primer strategy (Elbrecht & Steinke, 2019). During the first PCR step a 421-bp fragment of the cytochrome c oxidase subunit I gene was amplified using the BF2 + BR2 primer pair (Elbrecht & Leese, 2017). We used the Qiagen Multiplex PCR Plus Kit (Qiagen, Hilden, Germany) with 0.5 µl DNA (concentration not quantified), 0.2 µM for each primer, 2× Multiplex PCR Master Mix and ddH_2O for a total reaction volume of 25 µl. Polymerase chain reactions were run on an Eppendorf Mastercycler Pro Thermo Cycler with the following program: 95°C for 5 min; 25 cycles of 95°C for 30 s, 50°C for 30 s, and 72°C for 50 s; and final extension at 72°C for 5 min. Amplification success was evaluated on a 1% agarose gels. For the second PCR step, 1 µl PCR product from the first PCR was used as template, and each sample tagged with a unique fusion primer combination (see Table S1 for tagging combinations, Elbrecht & Steinke, 2019). The PCR setup was identical to the previous PCR, but the cycle number was reduced to 20 cycles, the PCR volume increased to 35 µl and the extension time in each cycle was increased to 2 min. Amplification success was again checked with a 1% agarose gel. Products from the second PCR step were cleaned up and normalised using SequalPrep Normalisation Plates (Thermo Fisher Scientific; Harris et al., 2010) following manufacturer protocols. Normalisation success was checked on a 1% agarose gel. Ten µl of each normalised sample were pooled, and the resulting library cleaned up using left-sided size selection with 0.76× SPRIselect (Beckman Coulter), to remove primer dimers from the negative controls. Sequencing was carried out by the Genomics Facility at the University of Guelph using a 600 cycle Illumina MiSeq Reagent Kit v3 and 5% PhiX spike in. Both indexing read steps were skipped, as we used inline tags. The read length of read one was increased to 316 bp, while keeping read 2 at 300 bp.

Raw sequencing data were quality checked using FastQC v0.11.8 and then processed using the R-based JAMP v0.59 pipeline (https://github.com/VascoElbrecht/JAMP) which mostly relies on Usearch v11.0.667 (Edgar, 2010). The data processing commands are available as supporting information (Supporting information, Script S1). Reads were demultiplexed based on fusion primer in-line tagging (Elbrecht & Steinke, 2019) and paired end merged using Usearch, while allowing mismatches of up to 25%. To orient all sequences in forward direction, samples were converted to reverse complement where needed. Primers were trimmed from both ends with Cutadapt v1.18 using default settings, and reads for which no primer could be detected on either side were discarded. Only reads between 411 and 431 bp were retained for further analysis. To discard reads with poor read quality, expected error filtering was applied (Edgar & Flyvbjerg, 2015), using a max expected error of 1. Sequences of all samples were subsequently pooled, dereplicated (minuniquesize = 2), and clustered into molecular operational taxonomic units (OTUs), using cluster_otus with a 97% identity threshold (Edgar, 2013) (includes chimera removal). Individual reads (including singletons) were mapped against the OTU list using usearch global with a minimum match of 97%. OTUs with less than a minimum of 0.01% read abundance for both replicates of one sample, were removed and reads again mapped against the OTU subset. The highest read count in the negative controls for each individual OTU was multiplied by two and subtracted from all other samples, to account for low level tag switching and cross-contamination. OTU taxonomy was assigned using the BOLD reference database (Ratnasingham & Hebert, 2007).

2.4 | Statistical analyses

We calculated standardised effect sizes (Cohen's *d*) (Cohen, 1988) to quantify and compare the responses of univariate variables (water temperature measures, hydromorphological degradation, volume of LWD, algal accrual rate, bryophyte cover, graminoid abundance, macroinvertebrate and EPT richness, EPT and shredder sequence abundance, fish density) to the presence of riparian forest.

To test for differences between forested and open reaches in the univariate response variables, we used linear mixed-effects models (LMM; function lme in R-package nlme; Pinheiro et al., 2017). In LMM, reach type (forested vs. open) was defined as fixed factor and stream identity was treated as random effect. We also included the VarIdent function in the model to allow for heterogeneity in variance structure among treatments. The fit of models was inspected using residual plots and were found to satisfy the assumptions of normality and heterogeneity of residuals for parametric analysis.

To study whether community compositions in forested reaches differed from open reaches we used non-parametric multidimensional scaling (NMDS). First, we visualised the community structure in NMDS ordination space and subsequently ran a permutational multivariate analysis of variance (PERMANOVA; Anderson, 2001) to explore whether observed differences have statistical significance. The permutations were constrained within streams (*strata* option in *adonis* function) to account for the nested design of the study. We ran NMDS ordination for all biological endpoints, except for fish due to a low number of species and limited density, restricting the use of NMDS. NMDS plots were calculated with Bray–Curtis dissimilarities using the function *metaMDS* in the vegan package (Oksanen et al., 2018, version 2.5–2). Environmental variables were fitted using the function *envfit*. Both macrophyte community data (frequency × abundance) and macroinvertebrate sequence abundance were $\log_{10}(x + 1)$ -transformed prior to analysis. In addition, we explored whether within-stream community dissimilarity of macrophytes and macroinvertebrates between forested and open reaches was related to difference in riparian forest cover (measured as Euclidean distance of canopy and riparian forest cover difference).

We further used the indicator species analysis (IndVal; Dufrêne & Legendre, 1997) in the R package labdsv (Roberts, 2012) to identify potential indicator taxa for the reach types. IndVal analysis yields an indicator value (IV) for a species for each a priori defined site group. The IV for a taxon varies from 0 to 100, and attains its

maximum value when all individuals of a taxon occur at all sites of a group. Significance of the indicator value for each taxon was tested through a Monte Carlo randomisation test with 1,000 permutations. We considered species with an IV > 50 (and significant at $\alpha = 0.05$) as strong indicators. All analyses were performed using R software (version 3.6.2; R Core Team, 2019).

3 | RESULTS

The mean riparian forest cover was 78% and the canopy cover 53% in forested reaches, whereas open reaches had coverages of 24% and 19%, respectively (Table 1). Water chemistry was very similar among reaches and thus the difference in local land use did not have an effect on the level of diffuse agricultural pollution between the reaches (Table 1).

The hydromorphological degradation score was lower for forested reaches compared to open reaches ($d = -1.4$; LMM: $t = -3.5$, $p < 0.001$; Figure 2, Table 2) indicating better instream habitat conditions. Forested reaches also exhibited larger volumes of LWD but the difference to open reaches only bordered significance ($d = 0.8$; LMM: $t = 2.0$, $p = 0.078$).

Mean ($d = -0.9$; LMM: $t = -3.8$, $p = 0.003$) and maximum ($d = -2.1$; LMM: $t = -5.9$, $p < 0.001$) water temperatures and their coefficient of variation ($d = -1.3$; LMM: $t = -4.0$, $p = 0.003$) were significantly lower in forested compared to open reaches (Table 2, Figure 2, Figure S1). Algal accrual was not significantly different between reach types ($d = -0.4$; LMM: $t = 1.0$, $p = 0.333$; Table 2, Figure 2).

The PERMANOVA indicated that macrophyte community composition was distinctly different between the forested and open reaches ($F_{1,20} = 3.4$, $p < 0.001$; Figure 3a). Community change correlated with canopy cover, riparian forest cover and hydromorphological degradation score along the NMDS axis 1 and current velocity, pH, and various trace elements (Ba, Ca, K) along the NMDS axis 2 (Figure 3b). The within-stream community dissimilarity of macrophytes was not significantly related to differences in riparian land use between reach types (Figure 4a). Indicator value analysis identified *Viola palustris* as a significant indicator for forested reaches and *Sparganium emersum*, *Carex acuta*, *Calamagrostis purpurea*, *Poa nemoralis*, and *Juncus filiformis* as indicators for open reaches (Table 3). Bryophytes were more abundant in forested reaches but the difference from open reaches was not significant ($d = 0.8$; LMM: $t = 2.2$, $p = 0.050$; Table 2, Figure 2), whereas graminoids dominated the open reaches ($d = -1.3$; LMM: $t = -3.1$, $p = 0.010$; Table 2, Figure 2).

DNA extractions of three macroinvertebrate samples did show low quantity and highly fragmented DNA as well as comparatively weak bands in the PCR. These samples only recovered a few species with low read abundance and were considered failed samples, probably due to DNA degradation. Therefore, the samples were excluded from statistical analysis of the DNA metabarcoding data. All other samples did show good DNA quality and metabarcoding results with an average of 287k ($SD = 44$k) paired end reads per sample.

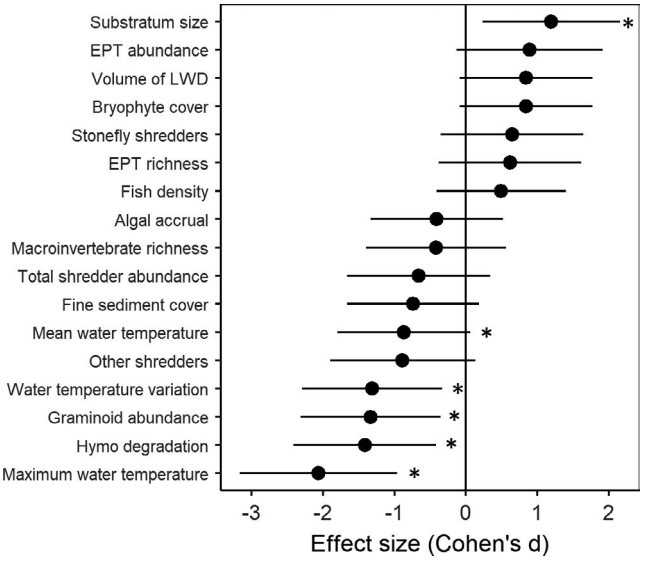

FIGURE 2 Standardized mean effect sizes (Cohen's *d*) and their 95% confidence intervals for different response variables. The effect size describes the influence of riparian forest relative to open reaches so that negative values indicate smaller variable values in forested reaches than in open reaches, and positive values indicate larger variable values in forested reaches than in open reaches. The variable Other shredders (%) consists of macroinvertebrate crustacean, dipteran, and trichopteran shredders. *Significant effect ($p < 0.05$) of the reach type according to linear mixed effect models. EPT, Ephemeroptera, Plecoptera, and Trichoptera; LWD, large woody debris

The PERMANOVA indicated that macroinvertebrate communities were not significantly different between forested and open reaches ($F_{1,17} = 0.96$, $p = 0.177$; Figure 3c). Community change correlated with fine sediment cover, minimum water temperature and catchment area along NMDS axis 1 and with turbidity, current velocity, aluminium and manganese concentration along NMDS axis 2 (Figure 3d). Within-stream community dissimilarity was significantly related to differences in riparian land use between reach types (i.e. the more different the riparian forest cover between the reaches of a stream the more different were the communities; Figure 4b).

The stoneflies *Diura bicaudata* and *Diura nanseni* were determined as indicators for forested reaches (Table 4). The coleopteran *Platambus maculatus* and chironomids *Orthocladius dentifer* and *Psectrocladius octomaculatus* were identified as indicator species for open reaches (Table 4). Neither total macroinvertebrate ($d = -0.4$; LMM: $t = -0.9$, $p = 0.380$) nor EPT richness ($d = 0.6$; LMM: $t = 1.3$, $p = 0.230$) differed between reach types (Figure 2) but relative DNA abundance of EPT species was marginally higher for forested reaches than open reaches ($d = 0.9$; LMM: $t = 2.2$, $p = 0.059$; Figure 2, Table 2). The relative abundance of shredders was not significantly different between the reach types ($d = -0.7$; LMM: $t = -1.5$, $p = 0.181$). When analysing shredders in two groups, stonefly and other shredders, the relative abundance of other shredders (isopod *Asellus aquaticus* and the crane flies *Tipula couckei* and *Tipula pierrei* as well as trichopterans) was marginally higher in open compared to forested reaches ($d = -0.9$; LMM: $t = -2.1$, $p = 0.068$; Figure 2, Table 2), whereas the

TABLE 2 The linear mixed-effects models for different response variables. The estimate for the reach type is the effect of riparian forest relative to open reaches and the intercept denotes the mean of the response variable in open reaches. EPT, Ephemeroptera, Plecoptera, and Trichoptera; LWD, large woody debris; CV, coefficient of variation

Response variable	Fixed effects	Estimate	SE	*df*	*t*	*p*
Mean substratum size (Wentworth)	Intercept	3.6	0.5	10	6.6	<0.001
	Reach type	2.0	0.7	10	2.8	**0.019**
Fine sediments (%)	Intercept	38.7	9.8	10	4	0.003
	Reach type	−20.0	11.5	10	−1.7	0.111
HyMo degradation (0–2)	Intercept	1.4	0.1	10	10.8	<0.001
	Reach type	−0.6	0.2	10	3.5	**<0.001**
Volume of LWD (dm^3/m^2)	Intercept	0.1	0.05	10	2.1	0.058
	Reach type	1.5	0.8	10	2	0.078
Mean water temperature (°C)	Intercept	17.7	0.2	10	71.9	<0.001
	Reach type	−0.7	0.2	10	−3.8	**0.003**
Maximum water temperature (°C)	Intercept	23.5	0.4	10	61.6	<0.001
	Reach type	−2.6	0.4	10	−5.9	**<0.001**
Water temperature variation (CV)	Intercept	0.2	0.003	10	63.7	<0.001
	Reach type	−0.010	0.004	10	−4.0	**0.003**
Algal accrual rate ($\mu g/cm^2$)	Intercept	4.3	1.1	10	4.0	0.003
	Reach type	−1.2	1.1	9	−1.0	0.333
Fish density $\log_{10}$ (ind. 100 m^{-2})	Intercept	0.3	0.1	10	2.1	0.063
	Reach type	0.3	0.2	10	1.9	0.091
Bryophyte abundance (%)	Intercept	5.2	1.6	10	3.3	0.009
	Reach type	8.1	3.6	10	2.2	**0.050**
Graminoid abundance (f*a) [a]	Intercept	560.3	169.3	10	3.3	0.008
	Reach type	−531.2	169.0	10	−3.1	**0.011**
Macroinvertebrate richness	Intercept	67.1	3.9	9	17.2	<0.001
	Reach type	−4.9	5.3	8	−0.9	0.380
EPT richness	Intercept	13.8	1.5	9	9.5	<0.001
	Reach type	2.0	1.6	8	1.3	0.233
EPT abundance (%)	Intercept	42.7	7.0	9	6.1	<0.001
	Reach type	16.0	7.3	8	2.2	0.059
Total shredder abundance (%)	Intercept	23.3	5.1	9	3.8	0.004
	Reach type	−9.8	6.7	8	1.5	0.181
Stonefly shredder abundance (%)	Intercept	3.8	0.9	9	4.2	0.002
	Reach type	3.2	2.2	8	1.5	0.181
Other shredder abundance (%) [b]	Intercept	19.7	6.6	9	3.0	0.015
	Reach type	−13.2	6.2	8	−2.1	0.068

Statistically significant differences are bolded.

[a]Graminoid abundance is a product from frequency and abundance (f*a) estimates.

[b]Other shredders include isopod, dipteran and trichopteran shredder taxa.

mean of relative sequence abundance of stonefly shredders was higher in forested reaches, but the difference to open reaches was not significant ($d = 0.7$; LMM: $t = 1.5$, $p = 0.181$; Figure 2, Table 2).

The fish assemblages consisted of stone loach (*Barbatula barbatula*), European bullhead (*Cottus gobio*), pike (*Esox lucius*), burbot (*Lota lota*), and perch (*Perca fluviatilis*). In addition, brook lamprey (*Lampetra planeri*) larvae were caught in two streams. Total fish density was higher in forested reaches than in open reaches although the difference was not significant ($d = 0.5$; LMM: $t = -1.9$, $p = 0.091$; Figure 2, Table 2).

4 | DISCUSSION

Riparian forests strongly influence local water temperatures, light conditions and input of allochtonous nutrients and detritus and thereby shape community structure in streams (Jones et al., 1999; Sponseller et al., 2001; Turunen et al., 2019). However, local forest patches in extensively altered catchments do not necessarily improve water quality but provide other benefits that can improve the ecological conditions in streams (Harding et al., 2006; Storey & Cowley, 1997; Turunen et al., 2019). For freshwater and biodiversity managers, it is important

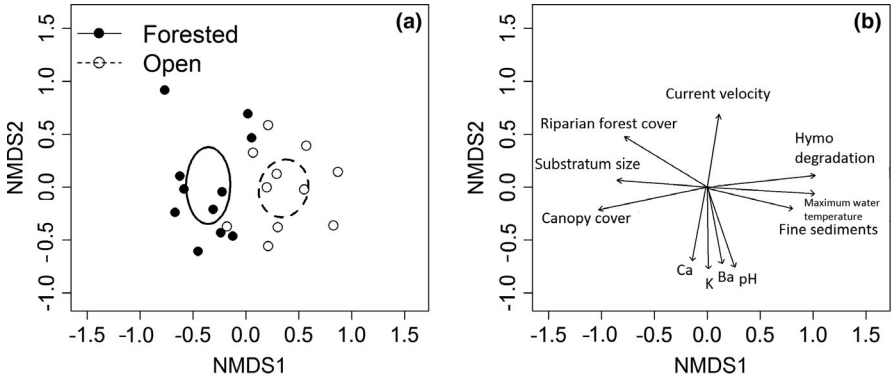

FIGURE 3 Non-parametric multidimensional scaling (NMDS) ordinations of macrophyte (a, b) and macroinvertebrate (c, d) communities of the study sites with 95% confidence ellipses around the group centroid. Vectors indicate the direction and strength of correlation of environmental variables that were significantly ($p < 0.05$) related to community structure

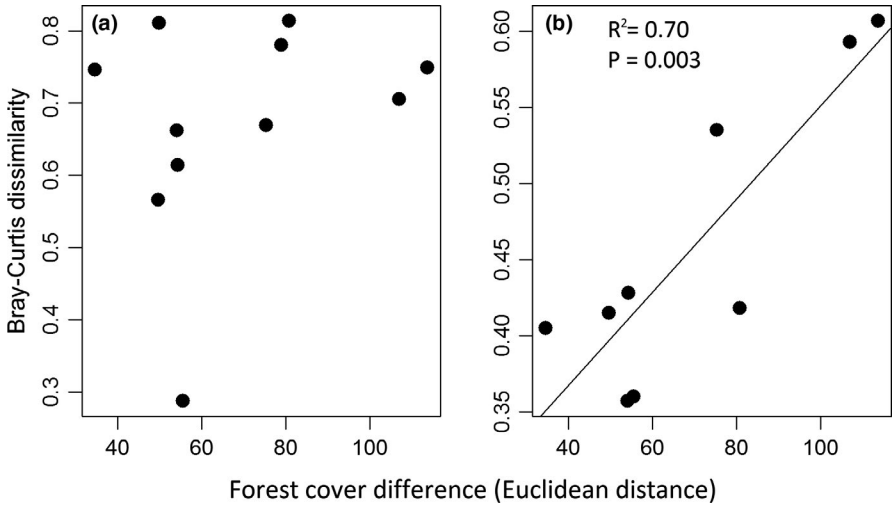

FIGURE 4 Relationships of Bray–Curtis dissimilarities of macrophyte (a) and macroinvertebrate community (b) structure, and riparian forest cover differences between two reaches with contrasting riparian land use in agricultural streams. The line shows a fitted significant linear regression model

TABLE 3 Macrophyte indicator taxa for each stream reach type, together with their indicator values (IV) and associated *p*-values

Stream reach type	Species	IV	*p*-value
Forested	*Viola palustris*	0.83	0.009
Open	*Sparganium emersum*	0.73	0.001
	Carex acuta	0.72	0.002
	Poa nemoralis	0.64	0.005
	Juncus filiformis	0.54	0.023

TABLE 4 Macroinvertebrate indicator taxa for each stream reach type, together with their indicator values (IV) and associated *p*-values

Stream reach type	Species	IV	*p*-value
Forested	*Diura bicaudata*	0.59	0.040
	Diura nanseni	0.54	0.043
Open	*Platambus maculatus*	0.75	0.043
	Orthocladius dentifer	0.66	0.008
	Psectrocladius octomaculatus	0.53	0.045

to understand if widely advocated local riparian forest buffers have benefits as a management tool in largely degraded stream catchments. One of those benefits is their potential to mitigate excessive warming of stream water during heatwaves (Bowler et al., 2012; Feld et al., 2018; Johnson & Almlöf, 2016). Our study confirms this as we found that the presence of riparian forest had a distinctly lowering

effect on stream water temperatures. This effect was particularly strong for maximum water temperatures. Another benefit is that forested riparian zones support higher biodiversity and thus provide better ecological status. Contrary to our expectations we did not observe any differences in algal accrual while macrophyte communities were expectedly different among reach types. The overall macroinvertebrate community structure showed no significant differences between the reach types, but within-streams community change was strongly related to reach-pair differences in riparian forest cover. Particularly, the relative DNA sequence abundance of sensitive EPT species was marginally higher in forested reaches.

Streams contain a hierarchy of spatially nested habitats where large-scale features (e.g. catchment geology, topography, and land use) control the characteristics of local scale habitats such as riffles (Frissell et al., 1986). Considering the constraints of catchment-scale land use, the importance of reach scale habitat factors (e.g. riparian forests) for the ecological status of degraded streams has been subject of extensive research with varying results (e.g. Lorenz & Feld, 2013; Roth et al., 1996; Storey & Cowley, 1997; Wahl et al., 2013). This ambiguity is probably rooted in differences of land use pollution. The benefit of riparian forests for local ecological conditions might be overruled by heavy pollution (Wahl et al., 2013; Walsh et al., 2007). Our results are in line with observations of studies (e.g. Johnson & Almlöf, 2016; Jones et al., 1999; Lammert & Allan, 1999) reporting higher instream habitat quality and ecological status in reaches with high riparian forest integrity despite having at least partly modified catchments. Overall, our results suggest that riparian forests are beneficial management tools for agricultural catchments at least in cases where pollution is moderate.

4.1 | Stream habitat and water temperature

The presence of riparian forests showed no clear effect on stream water quality, which was also observed in previous studies (Harding et al., 2006; Osborne & Kovacic, 1993; Turunen et al., 2019). Both the small extent of riparian forest buffers and tile drainage practices, where excessive subsurface water from fields is drained directly into streams or open ditches, are the likely reasons for the lack of any effect on water quality (Harding et al., 2006; Wahl et al., 2013). In contrast, the physical stream habitat was clearly different for forested and open reaches. The hydromorphological stream habitat status and the average substratum size were significantly higher in forested reaches. Several studies reported more silted stream beds in stream reaches that drain within agricultural fields compared to reaches that maintain riparian forests (e.g. Jones et al., 1999; Sponseller et al., 2001; Stanford et al., 2019). In comparison, mid-order agricultural streams in the same area exhibited no physical stream habitat condition differences among forested and open reaches (Turunen et al., 2019). Headwater streams are often channelised much more severely than mid-order channels in order to enhance agricultural drainage. Furthermore, the channelisation practice has typically been more extreme in stream sections that are within farm fields than those that drain in uncultivated forested areas. More extensive channelisation in open reaches is likely to be the main reason for a more homogenous and silted habitat structure rather than erosion due to land use.

The volume of LWD tended to be larger in forested compared to open reaches as was expected. Large woody debris is generally considered to have positive effects on stream biodiversity by providing habitat and inducing geomorphological changes in stream channels (Pilotto et al., 2014; Louhi et al., 2016). However, volumes of LWD were several orders of magnitude lower even in forested reaches compared to near-natural headwater streams in Finland (Turunen et al., 2017), indicating that the riparian forests are young and have been used for forestry and that the LWD has been cleared from the channels to enhance drainage.

The summer of 2018 was the hottest summer in Finland in recorded history (Finnish Meteorological Institute, https://en.ilmatieteenlaitos.fi/press-release/610918514). Water temperatures were generally lower in forested reaches (difference in means of daily mean of 0.7°C) with a very distinct difference of maximum water temperatures (2.6°C). The overall variation of water temperature was also lower for forested reaches, suggesting more stable thermal conditions. Meta-analyses and empirical studies either found decreased water temperatures when local riparian forests are present (e.g. Johnson & Almlöf, 2016; Quinn & Wright-Stow, 2008; Sponseller et al., 2001) or no significant effects (Harding et al., 2006; Turunen et al., 2019). Our results are in line with the meta-analysis of Bowler et al. (2012) who showed that riparian forest buffers have a more pronounced effect on maximum rather than mean water temperatures. The much cooler stream water temperatures we observed for forested reaches are surprising given the proximity to open reaches and the small size of the forests. Ryan et al. (2013) also reported that only 300 m of seminatural riparian vegetation resulted in up to 1°C cooling of headwater stream water during summer months. Similarly, Stanford et al. (2019) found that only 1 km of riparian tree corridor could counteract 1.5°C water temperature warming in intermittent Mediterranean streams. In mid-order channels in our study area (Turunen et al., 2019), the riparian forest did not affect stream water temperature, probably because of wider channels (less shading effect in forested reaches) and larger water volume causing higher thermal inertia (Quinn & Wright-Stow, 2008; Ryan et al., 2013).

Water temperature variation was lower in forested reaches than in open reaches suggesting that forests can stabilise thermal conditions in streams. This effect was particularly driven by the dampening impact of forests on maximum water temperatures, although forested reaches had also higher minimum temperatures, suggesting that forested reaches retain heat better during cold periods (See Figure S1). Similar findings have been observed by Malcolm et al. (2008) who reported a more moderated temperature amplitude in forested woodland stream reaches when compared with those in open moorland streams.

It is difficult to disentangle how reach scale variation of water temperature might affect species composition as temperature

variation, riparian land use, and habitat structure are correlated. However, the differences in maximum water temperatures were high and thus probably have ecological significance.

4.2 | Algal accrual and stream communities

Catchment scale land use and the resulting diffuse pollution is typically the dominating factor affecting species composition in agricultural streams (Death & Collier, 2010; Roth et al., 1996; Turunen et al., 2016; Wahl et al., 2013). However, there is evidence that reach scale riparian forests have a distinct impact on species composition and ecosystem function which improves the ecological status of agriculturally disturbed streams (Jones et al., 1999; Lammert & Allan, 1999; Turunen et al., 2019).

Contrary to our expectation of lower algal accrual in shaded forested reaches, we did not find differences between reach types. It is unlikely that nutrient limitation restricted the algal growth as concentrations of key nutrients of stream water were high. Perhaps open reach algal production did not increase because fine and instable sediments scoured and buried algal growth (Louhi et al., 2017; Turunen et al., 2018). In mid-order streams of the region, the benthic habitat structure was not different between reach types, which could explain the discrepancy to the mid-order streams where algal accrual was higher in open reaches (Turunen et al., 2019). Water turbidity was also high in both open and forested reaches which could partly limit the response of algae to shading of riparian forests.

As expected, macrophyte community structure was distinctly different between forested and open reaches. Water temperature, hydromorphological conditions, riparian forest, and canopy cover were significant correlates of macrophyte community structure. Shading by riparian forests, riparian land use and their effect on riparian microclimate (Moore et al., 2005) are likely to be the major drivers for macrophyte communities irrespective of the diffuse pollution level of a stream (Bunn et al., 1998; Turunen et al., 2019). However, the community change within a stream (measured by Bray–Curtis dissimilarity) was not correlated to the magnitude of change in riparian forest cover between the reach pairs. Although the effect of riparian forests on community structure was strong, it was similar across the streams within reach type which is contrary to the response of invertebrates (see discussion below). Similarly to mid-order streams (Turunen et al., 2019), open reaches were dominated by graminoids (grasses and sedges) and forested reaches showed a tendency to higher abundance of aquatic bryophytes. Several graminoid species were indicators for open reaches (*Carex acuta*, *Poa nemoralis*, *Juncus filiformis*), which highlights the affinity of many graminoids to well-lit environments. In general, bryophytes favour shaded stream reaches (Longton, 1988) and thus their higher occurrence in forested reaches was expected. Bryophytes are a key species in boreal streams in structuring biodiversity and influencing the ecosystem functions (Turunen et al., 2018). Thus, higher coverage of bryophytes in forested reaches is a clear ecological benefit to headwater stream ecosystems.

In line with observations from mid-order channels (Turunen et al., 2019), the overall community structure of benthic macroinvertebrates did not differ between reach types across streams. However, the Bray-Curtis dissimilarity of community structure between forested and open reaches was significantly related to the magnitude of reach-pair difference in riparian forest cover. The results suggest that riparian forest cover does have an influence on invertebrate community structure but natural between-stream variation in invertebrate assemblages causes differing community change trajectories in response to forests and thus across the streams there is no clear distinction of communities between reach types (Turunen et al., 2019). In this respect, the response of invertebrates is opposite to macrophytes where overall community structure is strongly correlated with riparian forest cover and a similar community structure is found within the reach types across the streams. It is likely that the better dispersal abilities of plants compared to benthic invertebrates (Alahuhta & Heino, 2013; Alahuhta et al., 2014) homogenises community structure across the streams within reach types. Macrophyte communities are environmentally filtered from a larger species pool to similar assemblages in similar habitats, whereas dispersal limitation result in more varying community responses in invertebrates. Community structure, while influenced by riparian forest cover, is structured within a stream rather than across them.

Certain macroinvertebrate species were associated with different reach types. The relative sequence abundance of EPT species was higher in forested reaches than in open reaches, although the difference only bordered significance. Among the EPT, the predatory stoneflies *D. nanseni* and *D. bicaudata* were identified as indicators for forested reaches whereas the chironomid midges *O. dentifer* and *P. octomaculatus* were indicators for open reaches. Across the streams, substratum size and fine sediment cover were more important correlates of invertebrate community structure than riparian canopy or forest cover, highlighting that excessive siltation of stream beds is one of the key stressors for benthic invertebrates (Piggot et al., 2015; Stanford et al., 2019; Turunen et al., 2017). Excessive sedimentation typically reduces EPT abundance and favours chironomids (Townsend et al., 2008; Turunen et al., 2017) as also observed for this study. It was surprising that the total shredder sequence abundance tended to be higher for open reaches, contrary to observations from mid-order channels (Turunen et al., 2019). Riparian forests provide abundant leaf detritus resources to leaf-shredding invertebrates (Thomas et al., 2016; Wallace et al., 1997) and this should be especially pronounced in headwater streams where instream primary production is limited by the narrowness of the stream channel and the shade of trees (Cummins et al., 1989; Vannote et al., 1980). However, it seems that at least for shredders different taxonomic groups show differing responses to the presence of riparian forests. The isopod *Asellus aquaticus*, *Tipula* sp., craneflies, and caddis flies were the dominant shredders in open reaches whereas stonefly shredders were more common in forested reaches. Both trends, however, were not significant. It is likely that inputs of fine organic matter from agricultural fields (Burrel et al., 2014) can support abundant

shredder populations in open agricultural stream reaches, whereas it is the leafy detritus, the shade, and the cooler riparian microclimate that in general benefit stoneflies in forested reaches (Collier & Smith, 2000). In addition, the finer sediment structure found in open reaches could also contribute to these differences.

The total abundance of fish was higher in forested reaches but the difference to open reaches was not statistically significant. Overall fish diversity was very low (maximum of three species per site), which is typical for boreal headwater streams (Sutela et al., 2010). However, salmonid fishes (mostly brown trout, *Salmo trutta*) were completely absent; although there is no apparent natural reason why trout should not inhabit most of the investigated streams. It is thus likely that the water quality is inadequate to support trout populations or gravel beds are silted, which greatly limits reproduction success (Sear et al., 2016). The marginally higher total abundance of fishes in forested reaches could be a result of fish seeking cooler water and shade during summer heatwaves, a behaviour that is commonly reported in cold water fish that seek optimal bioenergetic conditions (e.g. Petty et al., 2012). The electrofishing was conducted during the summer heatwave, which could have induced this type of behaviour. Moreover, the better hydromorphological conditions and coarser sediment found in forested reaches favour benthic rheophilic fish species such as bullhead and stone loach.

5 | CONCLUSIONS AND IMPLICATIONS FOR MANAGEMENT

A paradigm in stream restoration ecology states that reach scale habitat enhancements are unlikely to provide sustainable improvements for the ecological status of streams if catchment scale pollution is not addressed first (Bernhardt & Palmer, 2011). Overall, riparian forest has several positive effects on the ecological status of agricultural headwater streams and could induce partial ecological recovery of such streams even if catchment-scale nutrient and sediment pollution is not addressed. In this respect, conservation of remnant riparian forests or replanting riparian trees can be supported as a management tool to improve ecological status of agricultural headwater streams, at least in cases when the diffuse pollution is moderate. However, it is apparent that catchment land use, resulting in diffuse pollution and flow alterations are the major causes for ecological degradation in many streams and patchy riparian forests cannot completely reverse the negative impacts of agriculture in these streams (Harding et al., 2006; Stanford et al., 2019). While the benefits of local forested areas on the ecological status of streams reaches were evident in our study, forests did not have an effect on water quality, highlighting that it is mostly catchment scale land use that controls water quality variation. Moreover, the wide-spread use of tile drainage poses a significant limitation for mitigation efforts of nutrient and fine sediment pollution within riparian buffer areas (e.g. Puustinen et al., 2005; Uusitalo et al., 2005).

Finally, forestation of riparian zones of headwater streams in agricultural areas could provide an essential thermal refuge for stream fishes, especially salmonids (Ryan et al., 2013), and sensitive aquatic invertebrates. As climate change scenarios predict more frequent occurrence of extensive summer heat waves (IPCC, 2018), the riparian forests could partly help to mitigate the effects of climate change on headwater stream biodiversity and ecosystem functions.

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CONFLICT OF INTEREST

Authors have no conflict of interest to declare.

DATA AVAILABILITY STATEMENT

Data used in this paper are available via the Dryad Digital Repository (https://doi.org/10.5061/dryad.9zw3r22cr). Raw sequence data are available under the NCBI SRA accession number SRP200520.

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SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section.

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