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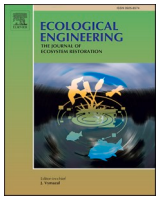

Stream restoration and ecosystem functioning in lowland streams

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ABSTRACT

Restoration has been increasingly applied over the last decades as a way to improve the ecological conditions in stream ecosystems, but documentation of the impact of restoration on ecosystem functions is sparse. Here, we applied a space-for-time approach to explore effects of stream restoration on metabolism and organic matter decomposition in lowland agricultural streams. We included stream reaches that were restored >10 years ago and compared ecosystem functioning in these streams with those in channelized and naturally meandering stream reaches from the same geographical region. Specifically, we tested the following hypotheses: 1) rates of stream metabolism (gross primary production, GPP, and ecosystem respiration, ER) and organic matter decomposition in restored reaches resemble rates in naturally meandering reaches more than rates in channelized stream reaches and 2) higher resemblance in ecosystem metabolism and organic matter decomposition between restored reaches and meandering reaches can be attributed to the improved physical habitat conditions in the restored stream reaches. Overall, we did not find that stream metabolism or organic matter decomposition differed among restored, channelized and naturally meandering stream reaches even though habitat conditions differed among the three stream types. Instead, we found a large variation in ecosystem function characteristics across all sites. When analyzing all stream types combined, we found that GPP increased with increasing plant coverage and that ER increased with increasing stream size and with the coverage of coarse substratum on the stream bottom. Organic matter decomposition, on the other hand, only slightly increased with the number of plant species and declined with increasing concentrations of nutrients. Overall, our findings suggest that physical habitat improvements in restored stream reaches can affect ecosystem functions, but also that the restoration outcome is context-dependent since many of the physical characteristics playing a role for the measured functions were only to some extent affected by the restoration and/or clouded by interference with factors operating at a larger-scale.

1. Introduction

Streams and rivers worldwide are influenced by a range of anthropogenic stressors, including water pollution, habitat degradation and flow modifications, which will all intensify in the future as a consequence of both climate change and an increasing human population (Moss et al., 2009; Vorosmarty et al., 2010). In fluvial systems, catchment-scale and local-scale stressors act in concert, leading to one of the highest rates of ecosystem-specific biodiversity losses (Strayer and Dudgeon, 2010; Reid et al., 2019). In response to the loss of biodiversity and degradation of streams, environmental conditions in stream ecosystems are restored worldwide with the aim to preserve and improve ecological conditions. These efforts are further promoted by legislation such as the European Water Framework Directive (WFD) according to which measures have to be implemented if the ecological status is not satisfactory (European Commission, 2000). Stream and river restorations often aim at improving the general habitat quality and heterogeneity at reach scale via removal of dams, re-meandering, re-profiling,

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addition of coarse inorganic or organic substrates or re-planting of riparian vegetation (Roni and Beechie, 2013). The ambition level in restoration projects vary, however, and it may not be possible to target baseline conditions when restoring streams because of e.g. land-use restrictions.

Follow-up assessments of effects of stream restoration are most often based on taxonomic and trait-based measures of community composition or on the abundance of indicator organisms that reflect the intensity of specific environmental stressors (e.g. Ernst et al., 2011, DeNicola and Stapleton, 2016, Friberg et al., 2016, Dos Reis Oliveira et al., 2020), but measures of ecosystem functions are also, to some extent, applied (e.g. Sudduth et al., 2011, Hoellein et al., 2012, Veraart et al., 2014, Dos Reis Oliveira et al., 2020). Several ecosystem functions can be used to assess the effects of restoration, but a review of the literature reveals that organic matter decomposition and ecosystem metabolism are those that have been most often studied in the context of stream bioassessment, probably because they are both important functional features of lowland streams and underpin important ecosystem services (e.g. carbon and nutrient cycling, water purification) (Ferreira et al., 2020). Generally, the outcome of these studies vary, which reflects both the width in restoration measures applied as well as the characteristics of the studied ecosystems. However, a recent review demonstrated that both metabolism and organic matter decomposition have proven effective in detecting the effects of restoration practices (Ferreira et al., 2020). Despite the low number of studies included, this suggests that these ecosystem functions may be useful indicators for the evaluation of restoration practices even though, as also pointed out by the authors, it cannot be ruled out that studies showing effectiveness are more likely to be published than studies finding lack of effectiveness.

Restoration success can be difficult to assess since clear operational targets for functional parameters may not be available to the same extent as they are for structural parameters. For instance, the WFD in Europe has provided a clear concept of how to assess improvements in biological communities set as the deviation from what would be expected under undisturbed/reference conditions ("no, or only very minor, anthropogenic alterations") with an ultimate goal of achieving at least good ecological conditions corresponding to only a minor deviation (European Commission, 2000). For functional parameters, on the other hand, different approaches have been applied. For instance, some studies evaluate success by comparing functional measures to those characterizing un-restored/degraded reaches or to those characterizing the reach before restoration measures were implemented, but this does not necessarily imply that a certain degree of movement towards the characteristics of comparable undisturbed (reference) sites has occurred. Furthermore, temporal aspects may challenge the evaluation of success as time needed for ecosystem recovery may depend on numerous factors, including both in-stream and catchment properties.

In the present study, we evaluated restoration success in middle-sized lowland streams by applying a space-for-time approach comparing the functional characteristics in three stream types, including morphologically restored stream reaches, channelized reaches, and naturally meandering reaches. Due to the high-intensity agriculture in Denmark, we were unable to identify middle-sized stream reaches in Denmark that can be characterized as reference sites due to the high levels of agriculture (Baattrup-Pedersen et al., 2009). Therefore, all stream reaches included in this study were situated in catchments dominated by agricultural land use, but this also allowed us to minimize the influence from differences in catchment characteristics that may otherwise impact the evaluation of functional effects of restoring stream morphology (e.g. dos Reis Oliveira et al. 2019). Additionally, the selected streams were situated in the same geographical region and were comparable in regime and discharge. Specifically, we explored effects of introducing meanders together with coarse inorganic substrates. We defined restoration success as the movement towards a more natural regime using the naturally meandering reaches as a benchmark. We tested the following hypotheses: 1) rates of stream metabolism (gross primary production, GPP, and ecosystem respiration, ER) and organic matter decomposition in restored reaches resemble rates in naturally meandering reaches more than rates in channelized stream reaches and 2) a higher resemblance in ecosystem metabolism and organic matter decomposition between restored reaches and meandering reaches can be attributed to the improved physical habitat conditions in the restored stream reaches.

2. Methods

2.1. Study streams

Sixteen un-shaded study streams were selected, representing three types: channelized (n = 6), natural (n = 6), and restored (n = 4). All streams were located in the same climatic conditions in West-Jutland in Denmark. The region has sandy fluvial deposits from the last Ice Age (ending about 11,000 years ago) and old moraine deposits from the previous Ice Age (ending about 130,000 years ago). With similar climate and soil type across streams, the fluvial runoff was assumed to be comparable. The specific restorations were conducted at least 14 years prior to our investigations, thereby allowing for an assessment of the long-term effects of restoration, and included two elements in all study streams: 1) re-meandering of the stream and 2) addition of coarse inorganic substrate (i.e. gravel with a grain size of 10–60 mm) to the streambed (Pedersen et al., 2006; Pedersen et al., 2014). The selected study streams were comparable in size, nutrient concentrations, discharge and catchment characteristics (land use and geology; Table 1).

2.2. Physical data

The physical characteristics of the streams were registered once per stream during August and September, overlapping with the time of functional measurements. The characterization was conducted in plots (25 × 25 cm) positioned side by side along transects within a 100 m study reach. A minimum of 120 plots were in each stream reach, and since the stream width differed among the streams, the number of transects ranged from 9 to 25. Depth, substrate cover (stone, coarse gravel, fine gravel, sand and mud), and vegetation cover (subdivided into submergent and emergent) were recorded in each plot, and the wetted width of each transect was registered according to the standard method applied in monitoring in Denmark (Pedersen et al., 2007). Plants

Table 1
Average (±SD) physical, chemical, and catchment-based parameters for the three stream types: channelized, natural, and restored. Letters indicate significant differences between stream types (ANOVA, Tukey's test, $p < 0.05$). Where there is no letter, the values are not significantly different.

	Channelized	Natural	Restored
Width (m)	3.99 ± 1.67	4.51 ± 1.08	4.95 ± 1.64
Depth (m)	0.38 ± 0.18	0.48 ± 0.18	0.52 ± 0.20
Water velocity (m s^{-1})	0.18 ± 0.12	0.16 ± 0.07	0.22 ± 0.08
Discharge (m^3 s^{-1})	0.37 ± 0.50	0.35 ± 0.28	0.63 ± 0.48
Stone (%)	1.30 ± 2.01[a]	1.83 ± 3.12[a]	12.83 ± 11.51[b]
Coarse gravel (%)	5.19 ± 12.13	4.31 ± 8.74	11.71 ± 8.10
Fine gravel (%)	10.06 ± 9.37	9.53 ± 6.36	17.22 ± 4.91
Sand (%)	53.95 ± 18.14	60.99 ± 17.23	40.73 ± 5.64
Mud (%)	28.88 ± 13.83	21.21 ± 11.24	10.86 ± 4.61
Sinuosity (m m^{-1})	1.00 ± 0.00[a]	2.03 ± 0.87[b]	1.44 ± 0.29[ab]
Total catchment (km^2)	165 ± 156[a]	755 ± 301[b]	356 ± 245[a]
Agriculture (%)	73.94 ± 9.83	68.72 ± 6.58	75.79 ± 7.40
Urban (%)	8.00 ± 4.49	8.52 ± 1.94	5.79 ± 2.62
Forest (%)	9.48 ± 5.37	13.80 ± 5.15	11.71 ± 6.54
Temperature (°C)	11.0 ± 2.53	10.33 ± 1.75	8.75 ± 2.36
Alkalinity (meqv L^{-1})	1.88 ± 1.18	1.47 ± 1.37	2.01 ± 0.72
TN (mg L^{-1})	2.91 ± 1.55	1.92 ± 1.11	1.89 ± 0.65
DIN (mg L^{-1})	3.13 ± 1.80	1.99 ± 1.29	1.85 ± 0.63
TP (mg L^{-1})	0.06 ± 0.03	0.05 ± 0.03	0.06 ± 0.01
SRP (μg L^{-1})	8.72 ± 2.73	9.95 ± 4.46	9.77 ± 2.31

were divided into the two groups because the relative abundance of these can vary among streams (e.g. Riis et al., 2001; Baattrup-Pedersen and Riis, 2004). Average water velocity was quantified using a salt slug addition (NaCl) following the procedure described in White (1978). Discharge was calculated using average water velocity and average stream profile dimensions (average of all transects). Channel sinuosity was calculated according to Stølum (1996) as the relationship between stream length along its course between the up- and downstream points and the straight down-valley distance.

Catchment size and the relative proportion of the different land uses were quantified using Geographical Information System (ArcGIS). Land-use characteristics were grouped into the following categories: urban, forest, agriculture, wetland areas, extensive land-use, and other.

2.3. Chemical data

Water samples for quantification of nutrient concentrations were collected twice per stream during August and September. The samples were transported to the laboratory on ice in dark cooling boxes and frozen until analyses. Samples for dissolved inorganic nutrient concentrations (nitrate (NO_3^-), ammonium (NH_4^+), and soluble reactive phosphorus (SRP)) were filtered using Whatman GF/C glass-fiber filter, and the concentrations were measured using a flow injection analyzer (Lachat Instruments, Loveland, CO, USA). Samples for total nitrogen (TN) and total phosphorous (TP) were not filtered. Total nitrogen was measured using TOC-V_{CPH} (Shimadzu, Kyoto, Japan), and TP was measured using ammonium molybdate colorimetry following persulfate digestion.

2.4. Ecosystem metabolism

Ecosystem metabolism was measured in 9 stream reaches ($n = 3$ per stream type) for 2 to 10 days. Dissolved oxygen (DO) concentration and temperature were measured using miniDOT data loggers (Precision Measurement Engineering, CA, USA) logging every 10 min. One logger was deployed in well-mixed areas in the middle of each stream to estimate 1-station (1-st) ecosystem metabolism. Photosynthetically active radiation (PAR, μmol photons m^{-2} s^{-1}) was estimated using a model similar to the one presented in Holtgrieve et al. (2010) using longitude, latitude, altitude, slope of water body, and average stream depth. Gross primary production (GPP) and ecosystem respiration (ER) were estimated based on diel fluctuations in dissolved oxygen (DO) concentrations as g O_2 m^{-2} d^{-1}. The reaeration coefficient (k (d^{-1}), i.e. the gas exchange with the atmosphere), was estimated using a model similar to the Bayesian Metabolic Model presented in Holtgrieve et al. (2010). The model simulates diel fluctuations in DO at a daily time step as a function of GPP, ER, and k. The change in DO concentrations (mg L^{-1}) is a first-order differential equation of the form:

$$\frac{d[O2]}{dt} = GPP - ER + k$$

GPP (g O_2 L^{-1} d^{-1}) was modeled as a hyperbolic tangent function of irradiance (μmol photons m^{-2} s^{-1}):

$$GPP = P_{max} tanh\left(\frac{\alpha_{P-I} PAR}{P_{max}}\right)$$

ER was modeled using an estimated respiration rate at 20 °C (ρ20) adjusted for stream temperature at each time step:

$$ER = \rho_{20} 1.047^{Temp-20}$$

The exchange of oxygen between stream and atmosphere was calculated as the estimated reaeration coefficient (k, d^{-1}) multiplied by the difference between stream oxygen concentration and the oxygen concentration at equilibrium with the atmosphere (Holtgrieve et al., 2010).

We implemented the metabolism models using the JAGS package interfaced with the R statistical package (R Core Team, 2013) to estimate posterior distributions for the model parameters using Markov Chain Monte Carlo (MCMC). Three MCMC chains were run with 50,000 iterations and a 10,000 iteration burn thinned by 5 to yield 10,000 draws. The model convergence was evaluated by testing the MCMC chains for autocorrelation, visually examining chains to evaluate mixing and using R-hat statistics (<1.1 considered converged, Gelman and Hill, 2007).

2.5. Organic matter decomposition

Organic matter decomposition was quantified in all stream reaches ($n = 6$ in channelized and natural stream reaches and $n = 4$ restored reaches) using readily abscised beech leaves (*Fagus sylvatica)*. Five leaf bags with fine (0.5 mm) and five leaf bags with coarse (6.5 mm) mesh size were deployed in each study stream in the middle of August 2013 ($n = 10$ in total). The leaf decomposition in the fine-meshed leaf bags reflects microbial decomposition since the mesh size restricts macroinvertebrate shredders from accessing the leaf material, whereas the leaf decomposition in the coarse mesh bags reflects the total microbial- and shredder-induced leaf decomposition (Gessner and Chauvet, 2002). Each leaf bag contained 2.0 ± 0.001 g DW of leaf material. The leaf bags were deployed in well-mixed areas of the central stream channel within the 100 m reach for 34–52 d. The number of days varied between streams because some streams experienced high amounts of precipitation, which resulted in periods where a too high water level prevented collection of the leaf bags. Despite the delayed retrieval, all bags still contained leaf material at the time of collection. The leaf material from the recovered leaf bags was rinsed in tap water and dried at 60 °C to constant mass. The microbial- ($k_{microbial}$) and shredder- ($k_{shredder}$) induced decomposition rates were calculated using total deployment time and initial and final leaf mass as described by Petersen and Cummins (1974), assuming that the decomposition follows an exponential decay model.

2.6. Macroinvertebrates

Macroinvertebrate samples were collected within the 100 m reach on the same day as the leaf bags were retrieved using a surber sampler (area = 0.06 m^2, mesh size = 500 μm; $n = 3$ samples per stream). The samples were collected randomly at each reach but stratified to cover sand and gravel habitats in the main channel. All macroinvertebrates were identified to species or genus level, except for Chironomidae, Hydrophilidae, Tubificidae, Oligochaeta, Hydracarina, Ostracoda, Corixidae, Dytiscidae, Polycentropodidae, Leptoplebiidae, Hexatominae, Simuliidae, and Psychodidae (Family). Moreover, information regarding functional feeding groups was obtained for all taxonomic groups using Tachet et al. (2002). The number of shredder species and the total abundance of shredders were calculated based on this information. The total number of macroinvertebrates, Shannon's Index of diversity of all macroinvertebrates present (H'; Shannon and Weiner, 1949), and Pielou index of evenness of all macroinvertebrates present were also calculated (J; Pielou, 1975; Table 2).

2.7. Statistics

We used one way-ANOVA followed by a Tukey's HSD post hoc test ($p < 0.05$) to compare physical, chemical, catchment land-use, and biological differences among stream types (channelized, natural, and restored). Furthermore, one-way ANOVA followed by a Tukey's HSD post hoc test ($p < 0.05$) was used to compare stream metabolism and leaf decomposition between the stream types. Data was checked for normality using goodness of fit test ($p < 0.05$) and for homoscedasticity using Levene's test ($p < 0.05$). We used a Spearman rank correlation test ($p < 0.05$) to explore correlations between functional measures (i.e.

Table 2
Average (±SD) number of plant species, cover of plants (% of reach), shredder density (number m^{-2}), number of shredder species, total macroinvertebrate species, Evenness, and Shannon for the three stream types: channelized, natural, and restored streams. No significant differences were found among stream types (ANOVA, $p > 0.05$).

	Channelized	Natural	Restored
Number of plant species	16 ± 5	21 ± 7	13 ± 10
Cover of plants (%)	43.55 ± 19.45	36.31 ± 13.50	27.61 ± 24.54
Shredder density (number m^{-2})	782 ± 1346	601 ± 501	1160 ± 1438
Number of shredder species	4.5 ± 2.35	6.67 ± 2.34	6.5 ± 3.11
Number of species, total	21.5 ± 5.01	28.0 ± 5.83	25.25 ± 11.09
Evenness	0.67 ± 0.16	0.71 ± 0.07	0.71 ± 0.14
Shannon	2.02 ± 0.46	2.32 ± 0.08	2.22 ± 0.51

metabolism and leaf decomposition) and environmental variables. Moreover, we used ANCOVA ($p < 0.05$) to test if the relationships between these parameters and independent abiotic and biotic variables descriptive of the physical habitat characteristics were comparable among stream types. We used SAS for the ANCOVA and STATGRAPHICS centurion for all other statistical tests.

3. Results

3.1. Physical, chemical, and geomorphic characteristics

Most of the physical, chemical, and geomorphic characteristics did not differ significantly among the three stream types (Table 1; ANOVA, $p > 0.05$). However, the proportion of stones on the stream bottom was significantly higher in the restored stream reaches compared to the channelized and natural stream reaches (Table 1; ANOVA, $p = 0.021$, $F = 5.32$), and the sinuosity of the natural stream reaches was significantly higher than the sinuosity of the channelized reaches but similar to the sinuosity of the restored stream reaches (Table 1; ANOVA, $p = 0.023$, $F = 5.15$) (Table 1; ANOVA, $p > 0.05$). The number of plant species, total plant cover, total number of macroinvertebrate species, shredder density, number of shredder species, and diversity measures of macroinvertebrate communities (i.e. Pielou evenness and Shannon diversity) were not significantly different among the stream types (Table 2; ANOVA, $p > 0.05$).

3.2. Stream metabolism

Overall, GPP varied between 0.93 and 5.39 g O_2 m^{-2} d^{-1}, and ER varied between 2.51 and 14.53 g O_2 m^{-2} d^{-1} (Fig. 1, Table 3). GPP and ER were not significantly different among the stream types (Table 3; ANOVA, $p = 0.391$, $F = 1.18$; $p = 0.165$, $F = 2.47$; $p = 0.600$, $F = 0.56$, respectively). Although we did not find a significant difference among stream types, the highest GPP and ER were found in restored reaches when compared to the natural and channelized stream reaches (Fig. 1). Along with that, we found that the lowest P/R occurred in the restored reaches (Fig. 1).

We discovered that GPP significantly increased with increasing plant coverage, explaining as much as 55% of the variation in GPP (Table 4, Fig. 2). The relationship did not differ significantly among the three stream types (ANCOVA, $p > 0.05$). ER, on the other hand, significantly increased with both increasing stream width, which explained 68% of the variation, plant coverage, which explained 59%, and proportional coverage of coarse gravel, which explained 60%. These relationships did not differ significantly among the three stream types (ANCOVA, $p > 0.05$). In contrast, ER significantly decreased with the coverage of sand (Table 4, Fig. 2), and again the relationship did not differ significantly among the three stream types ($r = -0.85$; ANCOVA, $p > 0.05$).

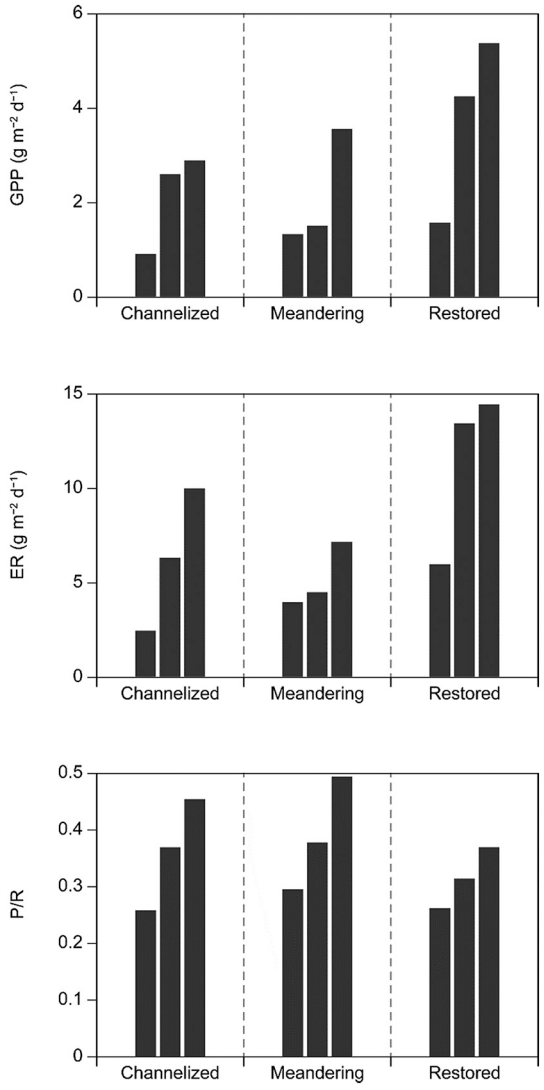

Fig. 1. GPP (g O_2 m^{-2} d^{-1}), ER (g O_2 m^{-2} d^{-1}), and P/R in channelized stream reaches, naturally meandering stream reaches, and reaches that were restored >10 years ago all situated in the same geographical region. In each category, each bar represents one stream ($n = 3$).

Table 3
Average (min-max) GPP (g O_2 m^2 d^{-1}), ER (g O_2 m^2 d^{-1}), $k_{microbial}$ (d^{-1}), and $K_{shredder}$ (d^{-1}) for the three stream types. There were no differences in the metabolism and leaf decomposition between stream types (ANOVA, Tukey's test, $p < 0.05$).

	Channelized	Natural	Restored
GPP (g O_2 m^{-2} d^{-1})	2.15 (0.93–2.91)	2.15 (1.35–3.58)	3.75 (1.59–5.39)
ER (g O_2 m^{-2} d^{-1})	6.32 (2.51–10.07)	5.26 (4.02–7.22)	11.36 (6.04–14.53)
$k_{microbial}$ (d^{-1})	0.004 (0.003–0.006)	0.005 (0.003–0.006)	0.005 (0.004–0.006)
$K_{shredder}$ (d^{-1})	0.003 (0.00–0.021)	0.001 (0.00–0.004)	0.0005 (0.00–0.002)

3.3. Organic matter decomposition

Overall, we found that $k_{microbial}$ varied between 0.003 and 0.006 d^{-1} and $k_{shredder}$ between 0 and 0.02 d^{-1} (Fig. 3, Table 2). $k_{microbial}$ and $k_{shredder}$ did not differ significantly among stream types (Table 2; ANOVA, $p = 0.650$, $F = 0.45$ and $p = 0.375$, $F = 1.06$, respectively). We

Table 4
Spearman rank correlations ($p < 0.05$) between stream metabolism and leaf decomposition and independent abiotic and biotic variables.

	Parameter	Spearman's ρ	*p*-value
GPP (g O_2 m^{-2} d^{-1})	Plant cover (%)	0.68	0.042
ER (g O_2 m^{-2} d^{-1})	Stream width (m)	0.85	0.004
	Plant cover (%)	0.83	0.005
	Coarse gravel (%)	0.71	0.031
	Sand (%)	−0.85	0.004
$k_{microbial}$ (d^{-1})	Number of plant species	0.67	0.004
	TN	−0.54	0.032
	TP	−0.51	0.043
$K_{shredder}$ (d^{-1})	Abundance of large-bodied shredders	0.58	0.030

also found that $k_{microbial}$ significantly increased with increasing number of plant species, explaining 25% of the variation,and with decreasing concentrations of TN and TP, explaining 31% and 26% of the variation, respectively (Table 4, Fig. 4). $k_{shredder}$ significantly increased with increasing abundance of large-bodied shredders, explaining 34% of the variation (Table 4, Fig. 5), and, again, the relationship did not differ significantly among the three stream types (ANCOVA, $p > 0.05$).

4. Discussion

4.1. Ecosystem metabolism

Our study showed that central functional stream characteristics (GPP and ER) were comparable in natural, restored, and channelized streams, and we were therefore unable to confirm our first hypothesis that stream metabolism is affected by morphological restoration in lowland streams. This finding indicates that morphological improvements (more coarse substrates and a higher degree of sinuosity) were less important than numerous other biotic and abiotic factors for the organic carbon production and consumption at the stream reach level. Thus, we only observed that ER increased in response to increasing coverage of coarse substrates on the stream bottom, whereas the other functional measures were unrelated to morphological habitat improvements. Instead, our results indicated that local stream characteristics (e.g. plant biomass within the channel) as well as processes acting at catchment level (e.g. nutrient input) overruled improved morphological channel characteristics. It can be argued that this finding is not surprising but simply reflects that the outcome of a restoration is context-dependent and vary in

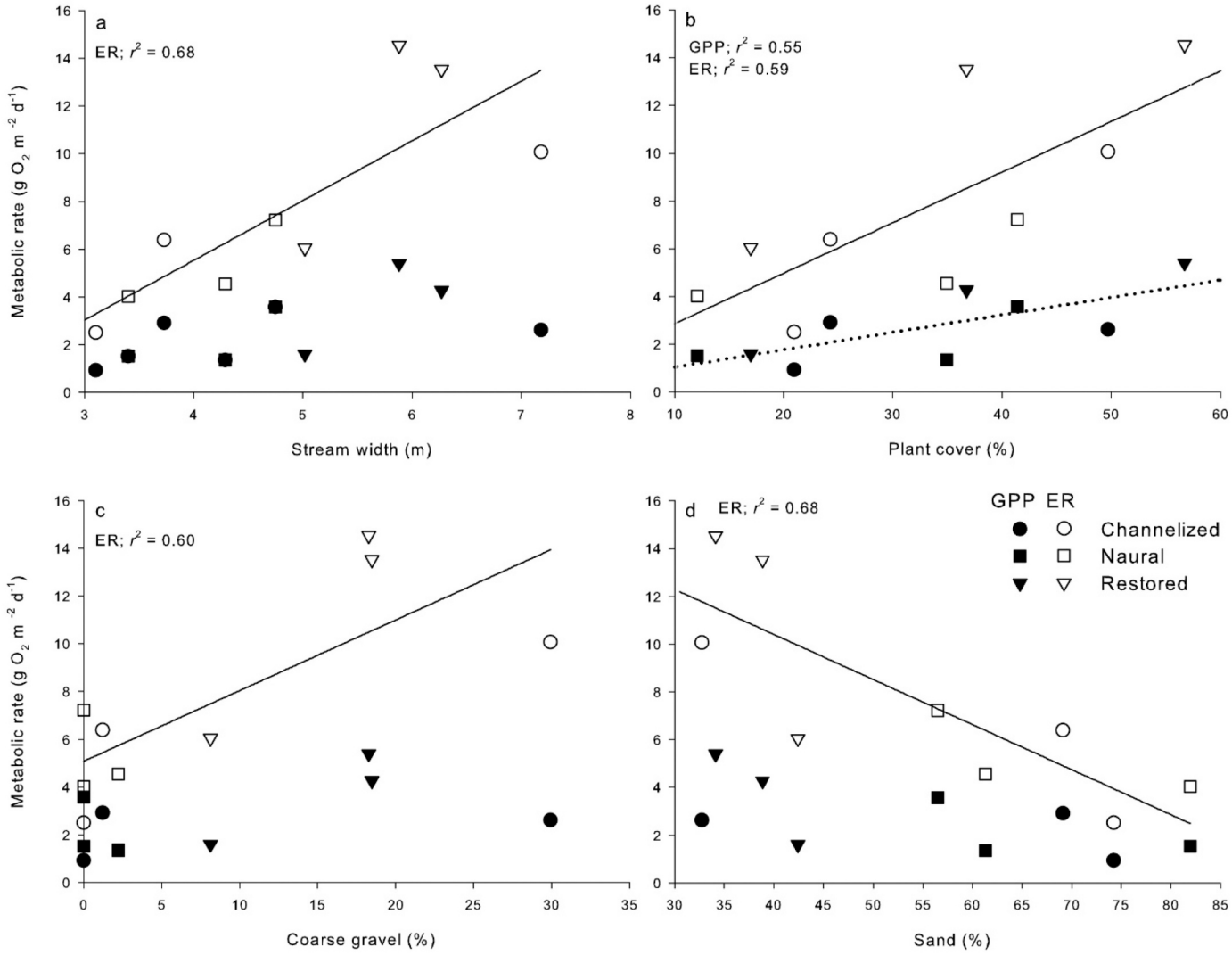

Fig. 2. GPP (g O_2 m^{-2} d^{-1}) and ER (g O_2 m^{-2} d^{-1}) as functions of a) stream width (m), b) plant cover (%), c) coarse gravel (%), and d) sand (%) for the three stream types. Linear regressions for GPP (●●●●●) and ER (—) were fitted to the data. Different symbols represent different stream types. Spearman's ρ and *p*-values are presented in Table 3.

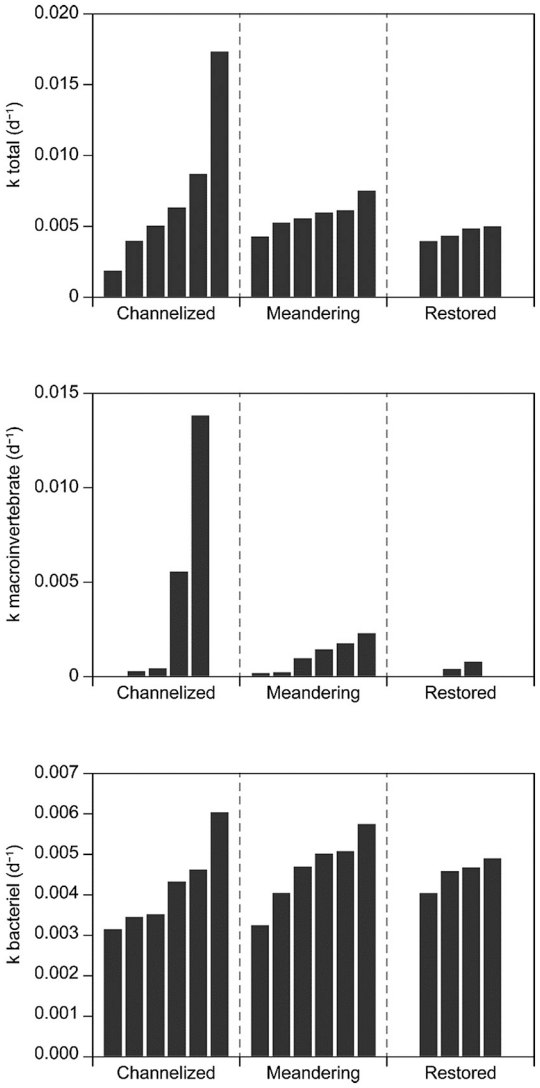

Fig. 3. $k_{microbial}$ (d^{-1}) and $k_{shredder}$ (d^{-1}) in channelized stream reaches, naturally meandering stream reaches, and reaches that were restored >10 years ago all situated in the same geographical region. In each category, each bar represents one stream ($n = 5$).

magnitude and sign, depending on the environmental settings under which they are observed. For example, in cases where restoration has stimulated plant growth within the stream channel, restoration can be associated with increased GPP (Kupilas et al., 2017), but this may not be the case if the restoration involved increased canopy cover, which will reduce GPP because of diminished light availability (Reisinger et al., 2019). Differences in factors that may influence metabolism operating at larger spatial scales can also to some extent determine restoration outcome. For example, Hoellein et al. (2012) found that habitat improvements were associated with higher rates of ecosystem function in the three streams they studied, but also that factors operating at larger spatial scales played a role. If nutrient or sediment input continues to be high, benefits of restoration can be difficult to detect despite local habitat improvements (e.g. Bohn and Kershner, 2002; Walsh et al., 2005; Ramchunder et al., 2012). For instance, suspended sediment coming from agricultural land may limit primary productivity by reducing the amount of light reaching the benthic algae community, even in open canopy streams (e.g. McTammany et al., 2007).

In line with our second hypothesis, we found that changes in stream metabolism can, to some extent, be attributed to improved habitat conditions even though a number of additional local and regional factors

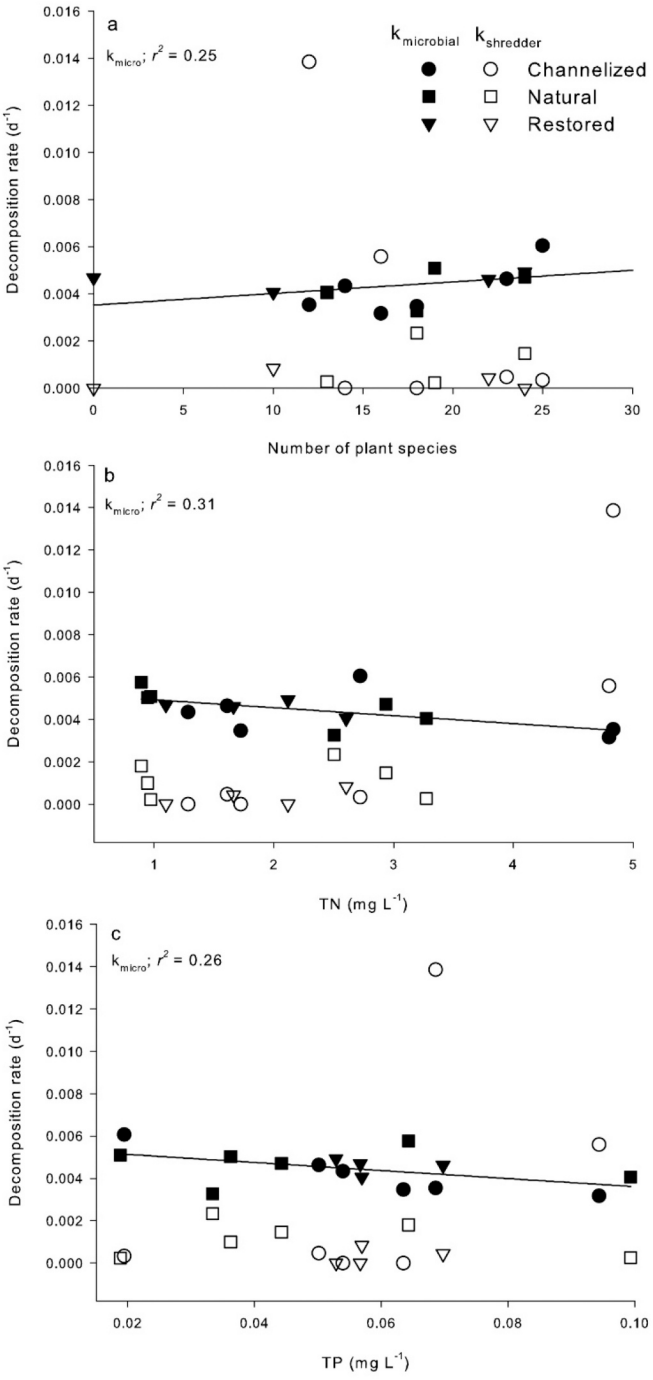

Fig. 4. $k_{microbial}$ (d^{-1}) and $k_{shredder}$ (d^{-1}) as a function of a) number of plant species, b) TN (mg L^{-1}), and c) TP (mg L^{-1}). Stream types are displayed with different symbols. Linear regressions reflect the correlations between $k_{microbial}$ and the independent variables. Spearman's ρ and *p*-values are presented in Table 3.

also seemed to play a role that was unrelated to stream restoration measures (more coarse substrates and a higher degree of sinuosity). Thus, despite a high degree of variability within and among stream types, average GPP and ER were elevated by a factor of approximately two in some of the restored stream reaches compared to measured rates in natural and channelized reaches demonstrating that habitat improvements can affect stream functions. This might reflect a higher proportional coverage of cobbles and gravel and a lower coverage of sand in the restored streams (average 24% and 41%, respectively) compared to natural and channelized streams (average 6% and 51%,

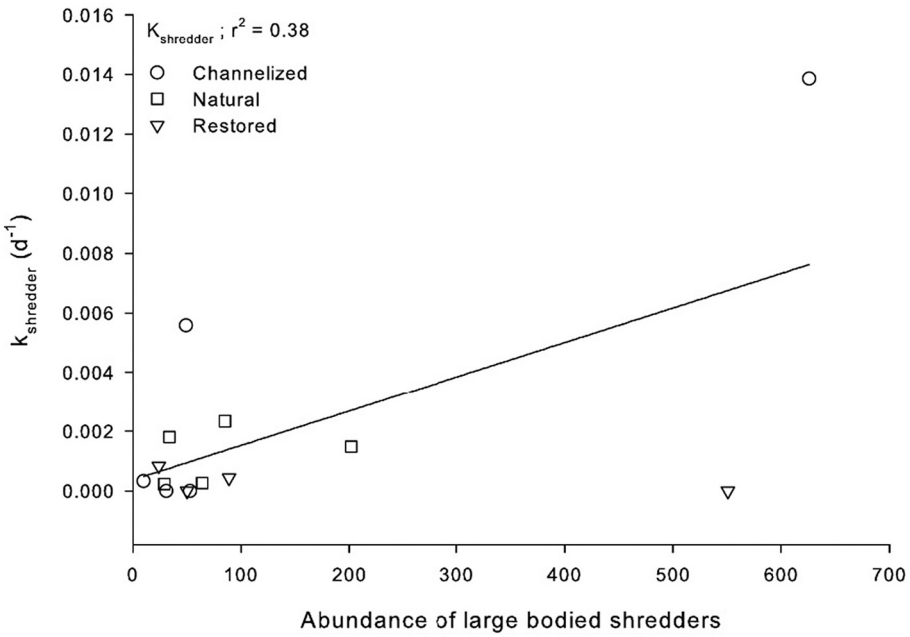

Fig. 5. $K_{shredder}$ as a function of the abundance of large-bodied invertebrate shredders. Stream types are displayed with different symbols. Linear regressions reflect the correlations between $k_{shredder}$ and the abundance of large-bodied invertebrate shredders. Spearman's ρ and p-values are presented in Table 3.

respectively) in line with our second hypothesis. A larger proportion of coarse substrate types can support a higher biomass of benthic microorganisms, particularly algae compared to sand, because of reduced scouring and reallocation of material (Atkinson et al., 2008). This can stimulate ecosystem metabolism at the reach scale (Biggs et al., 1999) and explain the observed positive correlation between ER and the coverage of coarse gravel and the negative correlation between ER and the coverage of sand.

Besides the above mentioned direct effect of benthic microorganisms on ER, the presence of coarse substrates can also have stimulated organic matter retention due to altered flow patterns within the stream channel (Sand-Jensen and Mebus, 1996) and with that ER due to enhanced heterotrophic activity in the reaches. In line with that, Flores et al. (2011) showed that after two years of restoration with addition of large wood, the retention of organic material increased 2 to 70 times because of the presence of areas in the stream with very low water velocities. Similarly, Koljonen et al. (2012) found that the retention of leaves at low discharges increased by adding moss, boulder or wood either alone or in combination into channelized streams. Furthermore, the increase in ER with total plant coverage, can also link to higher amount of accumulated fine particulate organic matter at the base of the macrophyte beds because of reduced water velocities (Sand-Jensen and Mebus, 1996), and with that enhanced ER (e.g., Acuña et al., 2011; Alnoee et al., 2016), and also to the epiphytic biofilm canstimulate in-stream processes (Levi et al., 2015).

4.2. Organic matter decomposition

Organic matter decomposition varied considerably among the investigated stream reaches, but no significant differences were observed between the stream types, which again contrasts our first hypothesis. Similar to this, Lepori et al. (2005) found that addition of coarse inorganic substrates did not affect organic matter decomposition in forest streams, which turned out to be similar to that in un-restored streams, whereas Frainer et al. (2017) found that restoration of habitat heterogeneity had the potential to increase decomposition rates in formerly channelized reaches flowing through boreal forest landscapes towards values more characteristic of undisturbed riffle habitats in reference reaches that were not previously disturbed by human intervention. Again, these contrasting responses emphasize the need for balancing the expectations of a restoration outcome with the environmental settings of the site intervened, including also factors operating a larger spatial scales. For example, the negative relationship between stream water nutrients and microbial decomposition observed in our study, which contrasts the expectation that N and P in the stream water will increase organic matter decomposition (Grattan and Suberkropp, 2001; Connolly and Pearson, 2013; Ferreira et al., 2014), likely reflects that the amount of nutrients in the stream water exceeded the levels of importance for decomposition due to high agricultural activity in the catchment. Thus, even though microbes both assimilate and release nutrients as part of the decomposition process, thereby constituting an important link in the food chain that potentially generates strong relationships between decomposition rates and water chemistry (the microbial loop), high nutrient loadings may lead to a decoupling of the microbial loop (Withers and Jarvie, 2008), and such a decoupling may explain our observation.

$k_{microbial}$ was positively correlated with the number of plant species across all study streams, which suggests that the richness of macrophyte species plays a role for $k_{microbial.}$ This may indicate that higher macrophyte richness may support higher microbial diversity at reach scale, which was supported by Levi et al. (2017) who found higher microbial diversity on morphologically complex macrophyte species compared to simpler macrophyte species. Zak et al. (2003) also showed that increasing plant diversity increased the microbial biomass, microbial respiration, fungal abundance, and microbial-induced N mineralization rates in soil. They suggested that the observed positive effects of increased plant diversity on microbial communities and associated functional parameters were driven mainly by enhanced diversity of plant substrates, which increased the microbial niche separation and thereby improved the utilization of the available carbon resources (e.g., Tilman et al., 1996; Cardinale, 2011).

$k_{shredder}$ significantly increased with increasing abundance of macroinvertebrate shredders, which is in accordance with previous studies showing that variation in the abundance of shredders is the main explanation of variation in litter decomposition rates (Graça, 2001). The large-bodied freshwater shrimp *Gammarus pulex*, a widespread species even in heavily degraded agricultural streams in Denmark, dominated the shredder guild in all study streams. *G. pulex* favors leaf material as

food resource, but it has a high feeding plasticity (Friberg and Jacobsen, 1994) and may exploit both coarse and fine particulate organic matter, smaller animals, and even biofilm, and it may utilize both macrophyte patches, riffle sequences, and depositional areas as habitats, providing it with fundamental competitive advantages in highly disturbed environments (Marchant, 1981). *G. pulex* may even maintain unaltered rates of organic matter decomposition in streams influenced by pesticide pollution (Rasmussen et al., 2012). Viewed in this light, it is not surprising that decomposition rates were unaffected by habitat improvements in restored reaches, even though higher decomposition rates might have been expected due to a higher, although not significant, shredder species richness (Jonsson et al., 2001).

4.3. Perspectives

To optimize the use of functional parameters for evaluating effects of stream restoration efforts, we propose that ecosystem functions in low-impacted stream ecosystems are characterized at various spatial and temporal scales to allow for more robust comparisons between natural and restored ecosystems. Even though we were unable to support our hypotheses in the conducted study, we still believe that ecosystem functions are central for evaluating restoration success since they embrace key processes eventually influencing a number of ecosystem services. However, benchmarks for evaluating success should be defined more precisely when planning restorative interventions in streams, in particular since local measurements of stream ecosystem functions are affected by processes operating at larger scales that may interfere with local habitat improvements. Furthermore, research including the publication of both positive and negative results following restoration work, is needed to evaluate the effectiveness of various restoration measures and to identify how resources should be used to optimize restorations outcome and ultimately stream ecosystem health.

CRediT authorship contribution statement

Annette Baattrup-Pedersen: Conceptualization, Supervision, Methodology, Project administration, Writing - review & editing. **Anette Baisner Alnoe:** Methodology, Visualization, Formal analysis, Writing - original draft. **Jes J. Rasmussen:** Methodology, Writing - review & editing. **Peter S. Levi:** Methodology, Writing - review & editing. **Nikolai Friberg:** Conceptualization, Project administration, Funding acquisition, Writing – review & editing. **Tenna Riis:** Conceptualization, Supervision, Methodology, Writing - review & editing.

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.

Data availability

Data will be made available on request.

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