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Disentangling small dam impacts: macroinvertebrate metrics reveal local stressors in degraded agricultural streams

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ABSTRACT

Agricultural land use and dams present prevalent, interacting stressors on freshwater ecosystems across Europe and globally. This study assessed the efficacy of established, taxonomy-based macroinvertebrate metrics for detecting localized dam impacts within streams already heavily modified by agriculture. Community responses were compared between rare riffle habitats and the dominant, slow-flow habitat types within the catchments. Metrics were based on the relative species richness of sensitive and tolerant taxonomic groups (calculated as the number of species within taxonomic groups divided by the total number of species). Despite a lack of significant differences in measured single-event physical habitat parameters between the dammed and reference sites, the macroinvertebrate assemblages exhibited clear responses. Dam impacts were most strongly detected in riffle habitats, aligning with a priori expectations of a greater number of sensitive taxa in these habitats. The general degradation metrics effectively teased out the dam signal, which shifted toward tolerant taxa (Oligochaeta, Diptera). The responses were habitat specific; for instance, filter feeding Trichoptera increased below the dams, while riffle specialist Plecoptera decreased. These findings underscore the utility of indices of general degradation when applied strategically with targeted, habitat-specific sampling, highlighting that effective biomonitoring and conservation strategies must prioritize the assessment and protection of rare, highly valued microhabitats in multi-stressed river networks.

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Dam; stream; agriculture; aquatic macroinvertebrates; land use

Introduction

Agricultural land use and dams are pervasive pressures on freshwater ecosystems across Europe and elsewhere (Craig et al. 2017; Birk et al. 2020; Lemm et al. 2021). At the catchment scale, agricultural land use is associated with diffuse pollution from excess use of fertilizers (Grizzetti et al. 2017) and pesticides (Liess et al. 2021), hydromorphological alterations of the channel bed are associated with channelization, dredging and large inputs of fine sediment, and loss of riparian vegetation and fragmentation of stream-riparian meta-ecosystems (Baattrup-Pedersen et al. 2018). At local scales, agricultural land use often results in stream habitats that are characterized by a reduced availability of coarse substrata and heterogeneous in-stream habitats (Crisp and Gledhill 1970; Brookes 1988), along with concomitant changes in water quality and biota (Pedersen 2009; Schürings et al. 2022). Additionally, at reach scales, small dams modify flow regimes, alter river geomorphology, and reduce the longitudinal transport of sediments and allochthonous organic matter, resulting in the loss of longitudinal and lateral connectivity (e.g. Poff and Ward 1989; Ward and Stanford 1995; Vörösmarty et al. 2003; Kuriqi et al. 2021). These and other dam-induced changes in environmental conditions affect aquatic organisms through shifts in community composition and diversity loss (e.g. Poff and Ward 1989; Vinson 2001; Zarfl et al. 2015). However, while the individual impacts of agricultural land use and dams have been studied extensively, fewer studies have investigated local-scale dam impacts within river systems that already have substantial alterations associated with large-scale agricultural land use. Understanding the compound effects of these stressors, which arise from both local and

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catchment scales, is of paramount importance for effective ecological assessments, conservation and restoration planning across a large number of global river networks (Craig et al. 2017).

Stream ecological health is commonly assessed using macroinvertebrate-based indices that compare community metrics (e.g. richness, composition) to expected reference conditions (Armitage et al. 1983; Extence and Ferguson 1989; Johnson et al. 1993; Böhmer et al. 2004, Birk et al. 2012). The primary limitation of these taxonomy-based metrics is not their ability to detect general degradation, but their inherent struggle with stressor attribution (Böhmer et al. 2004; Schäfer et al. 2011). However, these metrics retain the potential to detect local-scale impacts (e.g. dams) superimposed on systems with prevailing large-scale stressors (e.g. agricultural land use), given that appropriate reference conditions (i.e. sites within agricultural catchments) are used for comparison. This conjecture is founded on the conceptual framework of hierarchy theory (Tonn 1990; Poff 1997) that implies a biotic assemblage at a site can be seen as the product of a series of filters (e.g. regional, catchment, reach, and microhabitat), where each species found at a site has to pass through these filters to potentially persist at a site. Consequently, the stream community should be the result of the structural integrity of the site and the catchment (Tonn 1990; Poff 1997; Leibold et al. 2004), for example, where the dam locally filters taxa from the taxa pool determined by large-scale agricultural land use-related impacts. Indeed, local filters can have an effect on assessment outcomes, and studies have revealed that certain human impacts on macroinvertebrate assemblages are substantially more evident in some habitats than in others (Kerans et al. 1992; Roy et al. 2003).

Numerous studies have demonstrated the severe effects of dams and agricultural land use on macroinvertebrate metrics, causing general degradation, such as decreased species richness and a shift to more disturbance-tolerant assemblages (e.g. Vinson 2001; Rumschlag et al. 2023). In turn, using metrics derived from the relative species richness of macroinvertebrate groups with differing sensitivities should provide an appropriate general indicator of impact. Species-level presence–absence data often exhibit high variability among sites, which can introduce considerable 'noise' and potentially mask the broader, persistent impact signals of general degradation (Clarke 2006). Thus, a valid approach in bioassessment is to aggregate data to higher taxonomic levels (e.g. order) to reduce this fine-scale variability while maintaining the ability to detect the underlying anthropogenic signal (Armitage et al. 1983). This approach is supported by studies that suggest lower level (e.g. order) identification can be as effective as species-level data for detecting environmental impacts, particularly general degradation, while being more cost-effective (Resh and McElravy 1993; Resh and Jackson 1993; Lenat and Resh 2001; Waite et al. 2004). The orders Ephemeroptera (E), Trichoptera (T) and Plecoptera (P) are broadly considered sensitive (EPT taxa), while Diptera and Oligochaeta are generally tolerant to many types of pollution (Armitage et al. 1983; Rolauffs et al. 2003; Berger et al. 2018). Based on these classifications, it is expected that the relative species richness of Diptera and Oligochaeta will increase near dams compared to reference streams. Conversely, responses in sensitive groups are expected to be highly variable, especially in riffle habitats. For example, filter-feeding Trichopterans, though sensitive overall, benefit from enhanced seston below dams (e.g. Parker et al. 1983; Voelz and Ward 1996). Furthermore, Plecopterans are highly habitat-specific to riffles (e.g. Carlson et al. 2013), reducing their indicator potential in dominant slow-flow habitats. It is therefore expected that in dammed streams compared to reference streams, the strongest responses will be evident in riffle habitats: tolerant taxa and Trichoptera should increase in relative species richness, while Plecoptera should decrease. These expectations regarding the efficacy of general metrics and the variation in habitat-specific responses frame the key knowledge gaps addressed by this study.

Based on hierarchy theory, this study posits two main hypotheses regarding dams as local filters within agriculturally stressed systems: (1) a dam acts as a distinct local filter on the specific community of macroinvertebrates already shaped by the prevailing agricultural landscape, resulting in a community structure different from that of comparable free-flowing agricultural sites and (2) the ability to detect this local filtering effect is habitat-dependent, meaning certain specific habitats within the agricultural catchment will more clearly show the impact of the dam than others. In the context of these hypotheses, the following work investigates two core questions, using standard metrics of general degradation to assess impacts: (1) what is the potential for taxonomy-based metrics indicative of general degradation in the detection of local-scale impacts on stream communities from dams when large-scale agricultural land use impacts are predominant? and (2) to what degree does the macroinvertebrate community reflect the impact of a dam in riffle habitats directly downstream of a dam compared to the habitat type dominating in agricultural systems (upstream of the impoundment and downstream of the riffle)? To address these questions, this study investigated local (reach scale) impacts from small dams in streams by comparing macroinvertebrate assemblage responses in the dominant habitat type often found in agricultural catchments (characterized by slow flow and fine sediment substrates) with those found in riffle habitats. The methodology used to measure general degradation was based on the relative species richness of macroinvertebrate groups classified a priori as sensitive or tolerant to anthropogenic stress.

Methods

Study area and reaches

Ten lowland streams were selected in catchments with 10%–30% agricultural land use, where riffle habitats are rare and the dominant in-stream habitat type is characterized by slow-flow, greater depth and width, and substrates composed mainly of fine sediment. The study area is situated within the hemiboreal transition zone of south-central Sweden, specifically encompassing parts of Uppsala and Stockholm counties. This region is part of the Central Swedish lowlands, a landscape characterized by fertile agricultural plains interspersed with managed forests. The selected stream reaches are distributed across a regional geographic extent, with a maximum distance of approximately 50 km between the most distal sites.

Across all the sites, the riparian zones (0–5 m from the stream edge) were characterized by a mix of grasses and shrubs, reflecting the surrounding agricultural and managed forest landscape. The narrow riparian buffers transitioned into a broader near-stream area (0–30 m) dominated by croplands, pastures, and small patches of mixed deciduous and coniferous trees.

The catchment area averaged 132 (standard deviation 91) km^2 and streams were small (width 5.9 [3.1] m), circumneutral (pH 7.6 [0.23]), and nutrient-rich (total phosphorus [TP] 44.8 [14.9] μg/L). Five of the ten streams had a dam (impact sites), and five streams had no dam (reference sites). The five streams with a dam had small (<3 m height) dams with small impoundments. The study sites in both dammed and reference streams were located at least 3 km from other dams. For all ten streams, a reach with a riffle habitat was selected. For the five streams with a dam, the riffle reaches were directly downstream of the dam. For six of these streams (3 dammed and 3 reference) reaches of the dominant habitat type were selected downstream and upstream of each riffle reach (Figure 1). Among the three streams with a dam that included an upstream and downstream reach of the dominant habitat type, the upstream reaches were directly upstream of the impoundment.

Environmental variables

Catchment land use/cover data were obtained from the Corine land cover database (http://sia.eionet.europa.eu/CLC2000). The land use within the catchments was delineated according to topographic maps with a scale of 1:100,000 (Swedish Geodata; roadmap from Lantmäteriet), and the delineations were digitised using ArcGIS 9 (ESRI, Redland, CA, USA; http://www.esri.com/).

Within each river, the sampling units comprised a 100 m reach. In each reach, flow and substratum categories were recorded in summer as percentages. River bottom substrata were characterized as percent fine sediment (<0.063 mm), sand (≤0.063 to <2 mm), gravel (≥2 to ≤63 mm), cobble (>6.3 to ≤20 cm), stone (>20 to ≤400 cm) and boulder (>400 cm). The flow classes were classified as percent slow current <0.2 m/s, moderate current >0.2–0.4 m/s and fast current >0.4 m/s. In the middle of each of the upstream and downstream reaches, and the riffles in the four streams where only riffle habitats were sampled, a water sample was collected for chemical analysis. Water samples for chemical analyses were collected and analyzed within 24 h for nutrients (inorganic N, TP) and pH according to international and European standards (Fölster et al. 2014).

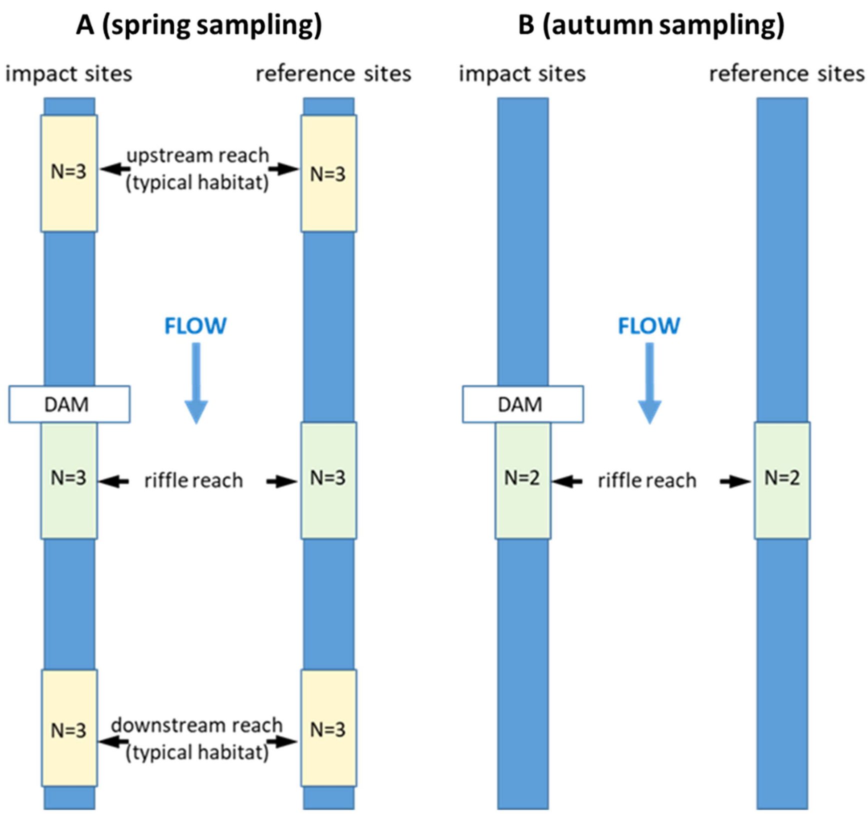

Figure 1. Illustration of the study reaches for the ten selected streams. Three impact (dam) streams and three reference streams had upstream, riffle and downstream sites (see A). Two impact (dam) streams and two reference streams had only riffle sites (see B).

Macroinvertebrate assemblages

Macroinvertebrate samples were collected from ten streams in total. The sampling timing varied depending on the sites included in the assessment: spring sampling (May) occurred in six streams encompassing upstream, downstream (dominant habitat type), and riffle reaches (Figure 1A), while autumn sampling (October) occurred in four streams where only riffle habitats were assessed (Figure 1B). The sampling protocols utilized a standard kick net with a 0.5 mm mesh size and were standardized according to European and Swedish guidelines (Fölster et al. 2014). In all riffle habitats, sampling occurred in the middle of each designated 100-m reach. Three individual kick samples were taken by disturbing the bottom substratum for 60 seconds along a 1 m stretch and consolidated into one composite sample per site. For the slow-flow habitat reaches, two collection methods were employed: three standardized sweeps of the vegetated stream edge and three rake samples collected from the mid-channel (using a long-handled rake with an attached net of the same dimensions and mesh size as the kick net). Both edge and mid-channel samples were consolidated into separate composite samples for taxonomic identification. After identification, lists of taxon presence/absence data were combined into one representative sample per site prior to data analysis. All samples were preserved immediately in 96% ethanol (70% final concentration).

Taxonomic identification methods differed by sampling season. The autumn-collected samples were sorted and identified using microscopy to the lowest possible taxonomic unit, usually the species level. Spring-collected samples were processed using DNA metabarcoding procedures based on the protocol outlined by Buchner et al. (2021). The DNA procedure involved homogenizing bulk samples without prior sorting using a laboratory-grade blender (25,000 rpm, 3 min), after being pre-cooled to −20 °C. The blender was thoroughly cleaned between samples using ddH2O and a DIY-DS solution (0.6% bleach, 1% NaOH, 1% Alconox and 90 mM sodium bicarbonate). The homogenized samples were stored at -20 °C until DNA extraction. DNA was extracted from 55 µL aliquots after centrifugation (14,000 × g for 5 min) to pellet the tissue, and the pellet was broken up by 30 s of bead-beating in a FastPrep Bead Beater (MP

Biomedicals, Eschwege, Germany). Subsequent automated processing was completed on a Biomek FX liquid handling workstation (Beckman Coulter, Brea, CA, USA). Duplicate extractions were performed for each sample, followed by two-step PCR with unique-twin indexing. All samples achieved high sequencing coverage (>200 reads per sample) on MiSeq or HiSeq platforms (using fwhF2+fwhR2n or BF3+BR2 primers). Data analysis was performed using JAMP, BOLDigger and TaxonTableTools software platforms. Only species detected in both replicate samples and meeting a minimum abundance threshold of 0.01% were retained for the final analyses.

The primary metric used was relative species richness, which was calculated as the number of species within defined taxonomic groups divided by the total number of species at that site. The taxonomic groups used in this analysis included the orders Coleoptera, Diptera, Ephemeroptera, Trichoptera, Odonata, and Plecoptera; classes Bivalvia, Gastropoda, and Hirudinea; subphylum Crustacea; and subclass Oligochaeta.

Statistical analyses

Environmental gradients of sites

Principal component analysis (PCA) was performed on centered and standardized environmental variables to analyze correlated trends within the data and identify potential differences in habitat characteristics between the dammed and reference sites. The analysis was conducted using Canoco 5 (ter Braak and Šmilauer 2012), which reduces the number of dimensions in the data via linear combinations of the environmental variables (Johnson and Wichern 1988). The variables included in the analysis comprised mean width and depth, percentage coverage of six substratum size classes, and percentages of three categories of flow. The number of meaningful PCs was determined by examining the eigenvalues of the initial axes.

ANOSIM (analysis of similarities) was used to evaluate the dual-scale influence of dams as local filters on macroinvertebrate communities (differences in relative species richness within groups) within agriculturally stressed systems. By analyzing all habitats collectively, this study assessed the dams' capacity to act as a primary determinant of community structure relative to larger agricultural impacts. Subsequent habitat-specific analyses (upstream, riffle and downstream) were conducted to identify which environments exhibited the highest sensitivity to this local filtering effect, thereby determining the degree to which dam-induced alterations are habitat-dependent. ANOSIM is based on comparing distances between groups with distances within groups, which are converted to ranks. ANOSIM generates a value of R that is scaled between −1 and +1, a value of zero representing the null hypothesis. Generally, R lies between zero and +1, where a large positive R (up to 1) signifies dissimilarity between groups. Values smaller than zero indicate greater dissimilarity among replicate units within samples than occurs between samples. The significance was computed by permutation of group membership, with 10,000 replicates. SIMPER (similarity percentage) was used to assess which taxonomic groups were primarily responsible for differences between assemblages based on relative species richness (Clarke 1993). For both analyses, the compositional dissimilarity between samples was quantified using the Bray–Curtis index.

Non-metric multidimensional scaling (NMDS) was used to visualize the distance (degree of dissimilarity) between assemblages by plotting more similar assemblages closer together in a 2-dimensional space. NMDS ordinations were run on a Bray-Curtis dissimilarity matrix based on the percentage of taxa within orders of benthic invertebrates.

NMDS, ANOSIM and SIMPER analyses were done using the software package PAST, version 4.15 (Hammer et al. 2001). In addition, *t*-tests were used to compare assemblages (NMDS axis scores) in the dam and reference streams separately for each habitat unit (upstream, riffle and downstream). T-tests were performed in JMP 17.0.0 (SAS Institute Inc. JMP 2022).

Results

Environmental variables

Riffle habitats clearly separated from upstream and downstream habitats along the first PC axis (eigenvalue 0.549). The upstream and downstream habitats were correlated with higher proportions of fine sediment, greater mean depth and width, and lower velocity of flow (<0.2 m/s), while riffle habitats were related to larger substrate sizes, higher substrate diversities and higher flow velocities (Figure 2). The second PC axis (eigenvalue = 0.154) indicated a gradient in substrate size (Figure 2); however, no patterns emerged in terms of dam versus reference sites or upstream versus downstream.

Macroinvertebrate assemblages

When all habitats were analyzed together, ANOSIM indicated significant differences in assemblages between dammed and reference streams (R = 0.12, p=0.035). As anticipated, SIMPER indicated that the mean relative number of species in the tolerant groups Oligochaeta and Diptera had the highest contribution to the differences in assemblages between the dammed and reference sites (28%), with a higher relative number of species in the dammed streams compared to reference streams (Table 1). Additionally, as predicted, the sensitive groups Plecoptera and Ephemeroptera had similar contributions (27.6%), with a higher relative number of species observed in the reference streams compared to dammed streams (Table 1).

When the habitat types were analyzed separately, ANOSIM revealed near significant differences in assemblages downstream of dams and in reference streams without dams but not between upstream assemblages and reference streams (downstream: R = 0.44, p=0.09; riffles: R = 0.22, p=0.08; upstream: R = −0.33, p=1). The R-values indicated that the dissimilarity between the dammed and reference sites was greatest in the downstream dominant habitat sites, followed by the riffle habitats. For upstream assemblages, the negative R-value indicated a greater dissimilarity among replicate units within dammed and reference sites than occurred between dammed and reference sites.

For downstream dominant habitat sites, SIMPER indicated that the mean relative number of species in the sensitive groups Plecoptera and Ephemeroptera had the highest contribution to differences in assemblages between dammed and reference sites (39.9%), with a higher relative number of species in reference streams compared to dammed streams. This was followed by the tolerant groups Oligochaeta and Diptera (25.6%), with a higher relative number of species in the dammed streams compared to reference streams (Table 2). For the riffle habitats, Trichoptera was the group that contributed the most to the dissimilarity between the dammed and reference streams (14.9%), with higher relative number of species in the dammed compared to reference streams. The groups Plecoptera, Oligochaeta, Diptera and Ephemeroptera followed Trichoptera, with similar contributions to dissimilarity between dammed and reference streams (14.2%–13.4%), with patterns between dammed and reference streams comparable to those observed in riffle habitats (Table 2). Although ANOSIM revealed no differences in assemblages

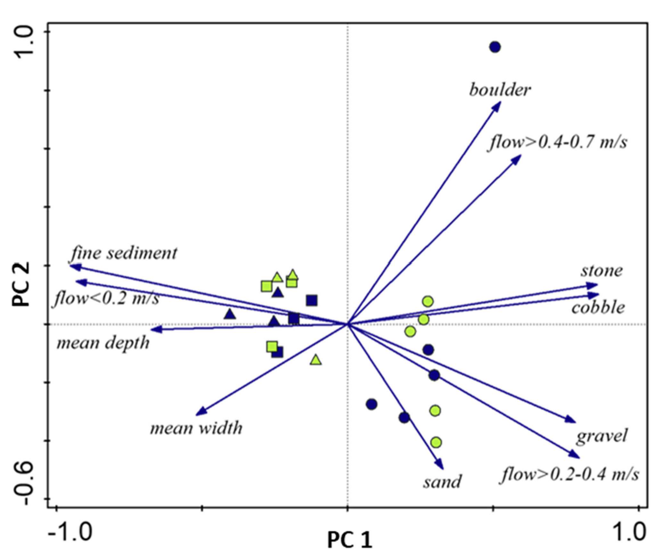

Figure 2. Principal component analysis (PCA) of the 11 environmental variables and the sites of the ten study streams. Green colored symbols = reference sites and blue colored symbols = dam sites. Squares = downstream sites, circles = riffle sites, and triangles = upstream sites. Eigenvalue of axis 1 = 0.549; axis 2 = 0.154.

Table 1. Summary of ranked SIMPER taxon groups by the relative number of species when habitat types were analyzed together. Average dissimilarity between dam and reference is based on the Bray–Curtis dissimilarity.

Taxon group	Ave. Dissim.	Contrib. %	Cumulative %	Dam mean	Reference mean
Oligochaeta	3.991	14.02	14.02	14.5	10.9
Diptera	3.97	13.95	27.97	28.4	22.4
Plecoptera	3.965	13.93	41.9	1.13	8.13
Ephemeroptera	3.9	13.7	55.6	12.5	16.1
Trichoptera	3.07	10.79	66.39	20.6	17.1
Odonata	2.716	9.543	75.93	6.77	7.66
Coleoptera	2.291	8.05	83.98	3.69	5.94
Gastropoda	1.877	6.595	90.58	2.4	3.9
Hirudinea	1.322	4.646	95.23	3.15	2.05
Crustacea	0.846	2.973	98.2	5.13	4.52
Bivalvia	0.5128	1.802	100	0.672	0.486

Table 2. Summary of ranked SIMPER taxon groups by the relative number of species when habitat types were analyzed separately. Average dissimilarity between dam and reference is based on the Bray–Curtis dissimilarity. In the last column '*p*-value' is in relation to students *t*-test of the difference between dam and reference means for each taxon group. NS = non significant (p>0.15), NA = not applicable.

Section	Taxon group	Ave. Dissim.	Contrib. %	Cumulative %	Dam mean	Reference mean	*p*-Value
Downstream	Plecoptera	4.946	22.89	22.89	1.67	11.4	0.0788
	Ephemeroptera	3.682	17.04	39.93	13.6	17.8	NS
	Oligochaeta	2.978	13.78	53.71	15.1	9.33	0.1385
	Diptera	2.558	11.84	65.55	28	23.2	NS
	Gastropoda	1.924	8.902	74.45	3.54	4.98	NS
	Trichoptera	1.835	8.491	82.94	18.7	16.8	NS
	Coleoptera	1.133	5.242	88.18	3.06	2.49	NS
	Odonata	1.088	5.035	93.22	9.34	7.47	NS
	Hirudinea	1.081	5	98.22	2.74	2.49	NS
	Crustacea	0.3849	1.781	100	4.13	3.94	NS
	Bivalvia	NA	NA	NA	0	0	NA
Riffle	Trichoptera	4.901	14.94	14.94	24.3	16.3	0.0940
	Plecoptera	4.666	14.22	29.16	0.426	9.23	0.0962
	Oligochaeta	4.646	14.16	43.32	13.7	10.7	NS
	Diptera	4.47	13.62	56.94	32.4	23.7	0.0382
	Ephemeroptera	4.41	13.44	70.38	8.45	15.4	0.0968
	Coleoptera	2.735	8.335	78.72	4.58	8.7	0.1373
	Odonata	1.964	5.984	84.7	1.68	4.8	0.1079
	Gastropoda	1.597	4.866	89.57	2.1	2.72	NS
	Hirudinea	1.311	3.994	93.56	2.53	1.05	NS
	Crustacea	1.197	3.648	97.21	6.06	4.72	NS
	Bivalvia	0.9152	2.789	100	1.48	1.07	NS
Upstream	Diptera	3.374	16.64	16.64	22.1	19.4	NS
	Ephemeroptera	3.36	16.57	33.21	18	15.6	NS
	Oligochaeta	3.254	16.05	49.26	15.3	12.8	NS
	Gastropoda	2.1	10.36	59.61	1.75	4.78	NS
	Coleoptera	1.988	9.805	69.42	2.84	4.78	NS
	Plecoptera	1.808	8.914	78.33	1.75	3.03	NS
	Trichoptera	1.452	7.16	85.49	16.4	18.9	NS
	Hirudinea	1.166	5.752	91.24	4.59	3.27	NS
	Odonata	1.154	5.691	96.94	12.7	12.6	NS
	Crustacea	0.6214	3.065	100	4.59	4.78	NS
	Bivalvia	NA	NA	NA	0	0	NA

T-tests confirmed that the sensitivity of macroinvertebrate communities to dams as local filters is habitat-dependent in that the NMDS axis 1 score (variance explained = 59.9%) differed in riffles (p=0.02), and differences were nearly significant in downstream reaches (p=0.10), compared to their relative reference reaches (Figures 3 and 4), while no significant differences were indicated in upstream sites. No significant differences were observed in the NMDS axis 2 scores (29.3% explained). Linear regression indicated that the NMDS axis 1 score were negatively correlated with the PCA axis 1 score (p=0.03, R^2 =0.22), and the negative correlation with PCA axis 2 was nearly significant (p=0.06, R^2 = 0.16).

between streams with dams and no dams in upstream assemblages, SIMPER indicated that contributions were highest in Diptera, Ephemeroptera and Oligochaeta (16.6%–16.1%), all with a mean relative number of species higher in dammed streams compared to reference streams (Table 2).

Discussion

This study sought to answer two primary questions within streams characterized as heavily modified by widespread agricultural land use: (1) what is the potential for taxonomy-based metrics indicative of general

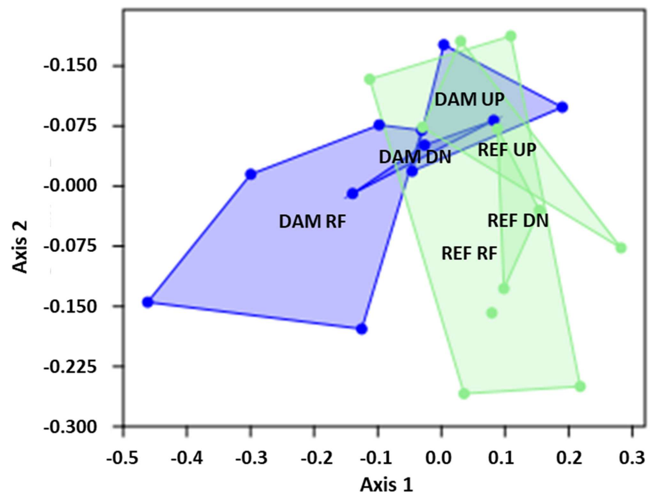

Figure 3. Ordination results from non-metric multidimensional scaling (NMDS). Reference sites are shaded in green and dam sites are shaded in blue. DAM = dam sites, REF = reference sites, DN = downstream, RF = riffles, UP = upstream. The stress value was 0.144.

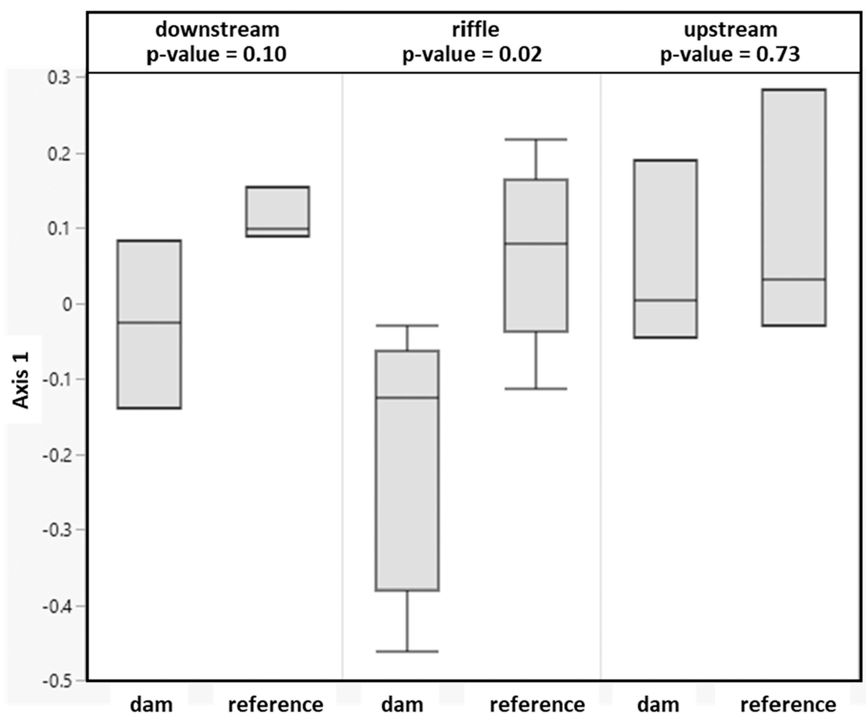

Figure 4. Downstream, riffle and upstream mean values of scores of the first axis from non-metric multidimensional scaling (NMDS) and *p*-values testing differences in means between dam and reference sites using Students *t*-test.

degradation in the detection of local-scale impacts on stream communities from dams? and (2) to what degree does the macroinvertebrate community structure reflect the impact of a dam in riffle habitats compared to the habitat type dominating agricultural systems (characterized by slow-flow and fine sediment substrates)? A key challenge in this assessment was that physical habitat differences (such as substrate composition, flow and water quality) between the dammed and reference sites were not obvious. This initial lack of clear physical distinction might suggest that these small dams do not have a significant effect on the immediate stream environment (e.g. Poff and Ward 1989; Vinson 2001). However, the findings of this study provide clear evidence that general degradation metrics can successfully detect reach-scale small dam impacts and that specific habitats, particularly riffles, serve as more sensitive indicators of these local, superimposed impacts, despite the lack of apparent physical habitat differences.

Stream health assessments often rely on comparing macroinvertebrate indices between reference and presumed disturbed conditions (Armitage et al. 1983; Extence and Ferguson 1989; Birk et al. 2012; Böhmer et al. 2004), but are often limited in their ability to attribute causality to specific stressors (Böhmer et al. 2004; Schäfer et al. 2011). Based on hierarchy theory (Tonn 1990; Poff 1997), this study hypothesized that general degradation metrics could detect local dam effects if appropriate agriculturally impacted reference sites were used, as the dam acts as an additional local filter on the regional taxa pool. The results of this study confirmed this potential. When all the habitats were analyzed together, ANOSIM indicated significant differences in assemblages between the dammed and reference streams. The observed shifts of a higher relative number of species in the tolerant groups (Oligochaeta, Diptera) and a lower number in the sensitive groups (Plecoptera, Ephemeroptera) demonstrate that the general indicator metrics successfully teased out the local dam effect from the prevailing agricultural signal.

The ordination of macroinvertebrate assemblages confirmed that dam impacts varied significantly by habitat type, directly addressing the second research question. The impacts were most evident in the riffle habitats, followed by the downstream habitats, while differences in the upstream habitats were not apparent. This differential sensitivity has important implications for biomonitoring design. If different habitats vary in sensitivity to specific stressors, sampling could be targeted to account for these differences, resulting in greater ability to detect biological changes and lower costs. The significant detection of impacts on riffle habitats and downstream dominant habitats below dams suggests that monitoring efforts should focus on these habitat types to assess dam effects in agriculturally disturbed catchments (Tiemann et al. 2004; Gerth and Herlihy 2006; Sullivan and Manning 2018). For upstream habitats, ANOSIM indicated high within-site variability, suggesting that the dominant agricultural signal or microhabitat complexity masked the dam effect in these slow-flow, fine-sediment environments. This result aligns with previous studies indicating that anthropogenic impacts are significantly more detectable in high-gradient habitats, such as riffles, compared to deeper or less turbulent environments (Kerans et al. 1992; Roy et al. 2003).

However, interpreting these results requires acknowledging that replication varies by habitat, with five site pairs for riffles compared to only three for upstream and downstream sites. This limited sample size for the latter habitats increased the likelihood of Type II errors. Though several *t*-tests showed *p*-values suggestive of trends (e.g. downstream NMDS $p<0.10$), failing the $p<0.05$ threshold, these trends are biologically meaningful, align with *a priori* expectations and agree with previous research on dam impacts on flow and seston dynamics. Consequently, while significant results were robustly detected in the higher-replicated riffle habitats, the consistent trends in the lower-replicated sites provide supporting evidence for a generalized dam impact across different habitats. Nevertheless, future research with consistently greater spatial replication is necessary to statistically confirm these patterns across a wider range of streams.

Expectations regarding specific taxonomic shifts were largely met, providing insight into the mechanisms underpinning dam impacts. As expected, dammed streams generally supported a higher relative number of species in the tolerant groups than in the sensitive groups. The results indicated lower mean relative species numbers of Ephemeroptera and Plecoptera (a highly riffle-specific group; Carlson et al. 2013) in dammed riffle and downstream sites. Diptera and Oligochaeta, which are generally considered tolerant groups (Armitage et al. 1983; Berger et al. 2018), were higher in dammed streams. A key insight came from Trichoptera, where many species are filter feeders known to benefit from enhanced seston supply below dams (Parker et al. 1983; Voelz and Ward 1996). Post-hoc analyses showed higher numbers of Trichoptera species in riffle habitats below the dams, especially *Hydropsyche*, *Limnephilus* and *Polycentropus* genera, and that the trait 'passive filter feeders' was significantly higher below the dams ($p=0.004$). The specific biological responses observed are attributed to chronic dam-induced stressors, such as temporal variability in the flow regime and altered seston transport, which were not captured by the single-event measurements of physical parameters (e.g. flow, substrate composition) that otherwise did not differ significantly between sites. This outcome underscores the limitations of snapshot sampling in detecting ecologically relevant physicochemical differences in highly dynamic systems. To verify these proposed mechanisms of biotic response, future research should incorporate repeat, high-frequency sampling across seasons and include direct measurement of relevant, but often unmeasured variables, such as food resources for benthic macroinvertebrates (e.g. seston quality and quantity and biofilms).

Findings from this study have direct implications for management and future research concerning dams in agriculturally dominated landscapes, where the global prevalence of these stressors highlights the importance of understanding their interactive, cumulative effects (Craig et al. 2017). The results demonstrated that general degradation indices are effective when applied strategically. To maximize detection power, monitoring programs should focus sampling on the most responsive habitat type (e.g. riffles) or expand to include multiple habitat types (riffles and downstream). The results of this study are highly relevant because they demonstrate that even in systems heavily modified by agriculture, localized dam impacts manifest strongly in specific, sensitive habitats (e.g. riffles). This finding provides critical insight because riffle habitats are inherently rare in low-gradient, lowland agricultural stream systems, yet they support a disproportionately high diversity of specialized and disturbance-sensitive macroinvertebrate taxa that contribute significantly to overall stream beta diversity. The scarcity of these critical habitats in degraded streams emphasizes their vital contribution to maintaining the local species pool. This study underscores that effective conservation strategies cannot rely solely on broad catchment metrics but must employ targeted habitat assessments that identify and protect these rare, high-value microhabitats.

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Author contributions

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