Reach-scale stream restoration in agricultural streams of southern Minnesota alters structural and functional responses of macroinvertebrates

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Abstract: Recent studies suggest that stream restoration at the reach scale may not increase stream biodiversity, raising concerns about the utility of this conservation practice. We examined whether reach-scale restoration in disturbed agricultural streams was associated with changes in macroinvertebrate community structure (total macroinvertebrate taxon richness, total macroinvertebrate density, Ephemeroptera, Plecoptera, Trichoptera [EPT] taxon richness, % abundance of EPT taxa) or secondary production (macroinvertebrate biomass over time). We collected macroinvertebrate samples over the course of 1 y from restored and unrestored reaches of 3 streams in southern Minnesota and used generalized least-square (GLS) models to assess whether measures of community structure were related to reach type, stream site, or sampling month. After accounting for effects of stream site and time, we found no significant difference in total taxon richness or % abundance of EPT taxa between restored and unrestored reaches. However, the number of EPT taxa and macroinvertebrate density were significantly higher in restored than in unrestored reaches. We compared secondary production estimates among study reaches based on 95th-percentile confidence intervals generated via bootstrapping. In each study stream, secondary production was significantly (2–3×) higher in the restored than in the unrestored reach. Higher productivity in the restored reaches was largely a result of the disproportionate success of a few dominant, tolerant taxa. Our findings suggest that reach-scale restoration may have ecological effects that are not detected by measures of total taxon richness alone.

Key words: secondary production, biodiversity, richness, EPT, habitat heterogeneity, impaired waters, biomonitoring, dominant taxa

Throughout much of the globe, human activities have resulted in drastic and pervasive alterations to many of the defining characteristics of running waters, including their habitat structure, hydrology, and supplies of nutrients and organic matter (Allan 2004). Scientists now recognize that the extent to which highly disturbed streams can provide ecological services may depend on whether these systems can be managed or designed de nouveau to maintain key ecological functions (Palmer et al. 2004, Hobbs et al. 2011). Thus, attempts to restore or rehabilitate degraded streams have become widespread (Bernhardt et al. 2005).

The goals of many small-scale stream-restoration projects are to stabilize stream channels by reducing local erosion and sediment deposition and to enhance biodiversity by increasing structural heterogeneity of in-stream and riparian habitat (Roni et al. 2008). Often, such 'restoration' activities are not intended to return streams to an historical or undisturbed condition, but rather to alter a degraded (i.e., physically unstable, habitat-limited) system by enhancing channel stability and habitat availability. Typical restoration activities at the stream-reach scale include adding rock and wood structures to the stream chan-

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nel, revegetating the riparian zone, and remeandering straightened channels (Roni et al. 2008).

A fundamental and possibly erroneous assumption of reach-scale stream restoration is that 'if you build it, they will come', i.e., that provision of physical-habitat structure will enable biotic recovery in streams that have undergone hydrologic and geomorphic disturbances and associated biodiversity losses (Palmer et al. 1997, Hilderbrand et al. 2005). A few studies have lent support to this assumption. For example, a study evaluating the experimental addition of wood to degraded agricultural streams in Australia showed local increases in macroinvertebrate richness following addition of wood (Lester et al. 2007). However, a review of the available stream-restoration literature conducted in 2010 indicated that macroinvertebrate biodiversity was not typically enhanced by the restoration of in-stream habitat, at least over time scales of <10 or 20 y (Palmer et al. 2010). Studies published since that review continued to indicate that stream restoration efforts, including the addition of wood, often have no measurable effect on macroinvertebrate richness (e.g., Louhi et al. 2011, Testa et al. 2011).

The failure of reach-scale restoration to improve biodiversity may stem from the over-riding influence of larger-scale factors, such as patterns of land use throughout the watershed, that limit the occurrence of sensitive species in disturbed systems (Palmer et al. 2010). However, even if larger-scale restorations are undertaken, no guarantee exists that ecosystem structure can be made to resemble a prior state, first, because ecosystems are naturally dynamic over time, and second, because human activities have created novel ecological settings to which historical communities may not be well adapted (Hilderbrand et al. 2005, Hobbs et al. 2011). Thus, returning biodiversity to approximately historical levels may not be a sufficient measure by which to gauge the ecological recovery or enhancement of disturbed systems.

In theory, ecosystem function could be enhanced more readily than biodiversity in disturbed systems because multiple species may have similar functional roles (Palmer et al. 1997, Hilderbrand et al. 2005). Measures of ecosystem function also may provide a more comprehensive understanding of biotic condition than biodiversity measures alone (Bunn and Davies 2000). For example, secondary production integrates several measures of biological success beyond species richness, including density, biomass, growth rate, fecundity, survivorship, and life span (Benke 1993). Secondary production can be a sensitive indicator of a variety of human disturbance effects (Sallenave and Day 1991, Lugthart and Wallace 1992, Wallace and Webster 1996, Carlisle and Clements 2003, Shieh et al. 2003). In resource-limited systems, increases in secondary production may reflect improvements in availability of habitat or food (French McCay and Rowe 2003). Higher values of secondary production can be interpreted as a proxy for greater foodweb support, i.e., for resources available to higher trophic levels of conservation concern, such as fish, amphibians, reptiles, or birds (e.g., French McCay and Rowe 2003, Wong et al. 2011).

In southern Minnesota, as throughout the midwestern USA, landscape disturbances associated with agriculture include elimination of most wetlands, conversion of perennial plants to annual crops, installation of artificial drainage networks, and use of fertilizers and pesticides (Galatowitsch and van der Valk 1994, Lenhart et al. 2012). These changes have altered stream water quality and hydrology, and have caused widespread degradation of aquatic life (MPCA 2009). Over the last 2 decades, a diverse collection of volunteer organizations, academic institutions, and local, state, and national agencies have undertaken numerous restoration projects, generally at the stream-reach scale, to improve water quality in the region (Brezonik et al. 1999, MPCA 2009).

Secondary production has been used to gauge recovery of stream ecosystem structure and function after reach-scale restoration in low-order, forested systems (Wallace et al. 1995, Entrekin et al. 2009), but to our knowledge, the response of secondary production to restoration has not been evaluated for streams in highly modified agricultural regions. The goal of our study was to evaluate the response of macroinvertebrate community structure and secondary production to reach-scale restoration in 3 agricultural streams in southern Minnesota by collecting macroinvertebrates over the course of 1 y (excluding winter months) from restored and unrestored reaches of each stream. The structural metrics we evaluated were total macroinvertebrate taxon richness and total number and % abundance of Ephemeroptera, Plecoptera, and Trichoptera (EPT) taxa. We used EPT metrics because of their demonstrated potential to serve as sensitive indicators of ecosystem condition (Barbour et al. 1999), and because we wanted to investigate whether reach-scale restoration might have effects on community structure beyond those detected by total taxon richness alone. Our specific objectives were to compare: 1) macroinvertebrate community structure, 2) secondary production, 3) contributions of specific taxa to secondary production, and 4) habitat conditions between restored and unrestored reaches.

METHODS

Study area

Prior to European settlement, land cover in southern Minnesota was primarily prairie interspersed with thousands of poorly drained wetlands known as prairie potholes (Galatowitsch and van der Valk 1994). The region is underlain by the Des Moines Lobe till, a dense, blue-gray, fine-grained subsoil covered with rich, black, silt–clay topsoil (Lenhart et al. 2012). Today, >80% of the region is farmed intensively as row crops (corn and soybeans) or animals (hogs and cattle) (NRCS 1997). A vast network of surface ditches and subsurface drain tiles installed for more than a century has eliminated most wetlands from the landscape by increasing flow to the drainage network (Galatowitsch and van der Valk 1994, Brooks et al. 2003). These dramatic changes in land use and hydrology have resulted in many water-quality concerns for streams and rivers, including high loads of nutrients, sediment, bacteria, and pesticides, and the degradation of in-stream and riparian habitat and aquatic life (Magner et al. 2004, MPCA 2009, 2014).

Study sites

We examined the effects of reach-scale restoration projects implemented by the Minnesota Pollution Control Agency (MPCA) in 3 streams in southern Minnesota: Buffalo Creek, Elm Creek, and Rush River (Fig. 1). Catchments of all 3 streams are similar in size (~100–300 km^2), are dominated by similar underlying geology and land use (i.e., corn–soy agriculture), and are drained by networks of subsurface drain tiles. Each stream has been listed by the MPCA as impaired for ≥1 of the following stressors: turbidity, fecal coliform, low dissolved O_2, and poor fish or macroinvertebrate Index of Biological Integrity (IBI) scores (MPCA 2014). Before restoration, property adjacent to a site in each stream was endangered by severe bank erosion caused by increased toe-slope shear of the stream channel.

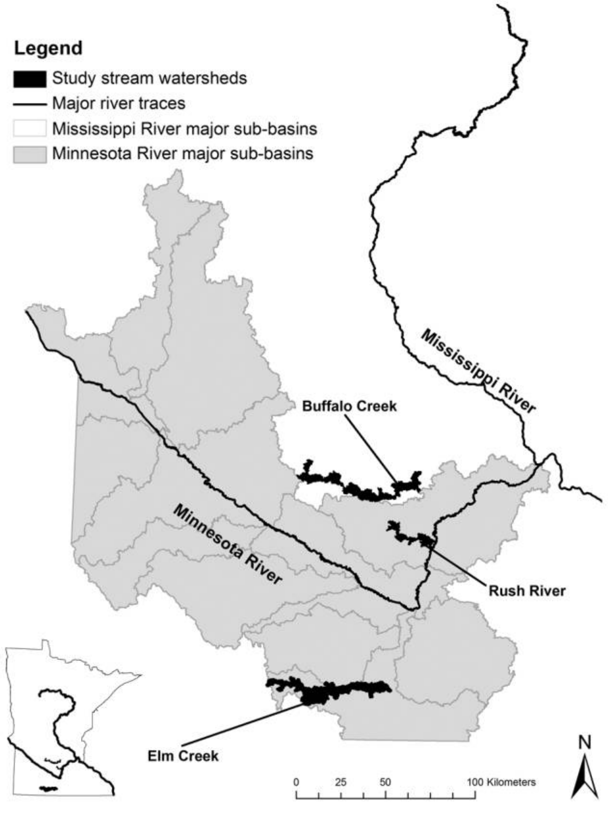

Figure 1. Map of study region, indicating watershed areas of study streams.

Restoration activities in each stream included placement of boulder weirs and large woody debris (root wads and cut logs) in the channel to redirect flow from erosion-sensitive areas and toward the thalweg. Stream banks were revegetated with low grasses and shrubs, and silt fencing was installed along the edges of the stream where bare soil was present. Last, soil was added below steep banks to create tiered floodplain benches, with the intention of decreasing stream power and channel shear stress at high flows, thereby preventing banks/bluffs from collapsing directly into the main channel. The primary goal of these efforts was to stabilize the stream channel by preventing continued bank erosion and land loss. A secondary goal was to increase the availability and heterogeneity of in-stream habitat and food resources by increasing the availability of overhanging vegetation and boulder and wood surfaces that could be colonized by macroinvertebrates or used as cover by fish. Managers hoped that the addition of rock, wood, and vegetation to the stream channel and banks also would indirectly improve conditions for fish and macroinvertebrates by reducing localized sediment deposition, increasing retention of organic matter, and exposing gravel substrates (as a result of scouring by redirected flow). Restoration activities were similar in all 3 streams, but they were implemented in different years along variable lengths of stream channel: in 2001 along ~100 m of stream channel at Rush River, in 2006 along ~750 m of stream channel at Elm Creek, and in 2008 along ~100 m of stream channel at Buffalo Creek.

We established 2 study reaches in each stream: a 100-m reach of restored channel and a 100-m reach of unrestored channel. Unrestored reaches were 100 m upstream from restored reaches. At Elm Creek, where restoration was done along a longer section of stream channel, we used a 100-m section at the upstream end of the restoration as the restored study reach.

In-stream and riparian habitat

We measured a suite of in-stream and riparian habitat variables at 10 transects in each study reach in August 2010 (Table 1). Transects were spaced 10 m apart and consisted of 0.3 × 0.3-m quadrats at 4 points spaced equally across the stream channel and a 5th point in the thalweg. In each quadrat, we measured water depth and depth of fines, and visually estimated the dominant substrate type (boulder, cobble, gravel, sand, silt, clay, or detritus), % embeddedness of coarse substrates, and % coarse substrates covered by algae. At each transect, we measured the vertical length of bare soil on each bank to estimate the amount of bank erosion, and we visually estimated the amount of contiguous undisturbed land within 100 m of the stream channel to estimate the riparian-buffer width. We used a spherical crown densiometer to measure overhead canopy cover

Table 1. Means for in-stream and riparian habitat variables collected from 3 stream sites in August 2010.

	Buffalo Creek		Elm Creek		Rush River	
Habitat	Unrestored	Restored	Unrestored	Restored	Unrestored	Restored
Water depth (m)	0.54	0.50	0.58	0.82	0.44	0.58
Thalweg depth (m)	0.69	0.67	0.75	0.69	0.68	0.88
Depth of fines (cm)	13	12	10	10	6	6
% embedded	86	64	63	40	24	28
% algae	1	2	1	2	24	28
% boulder	4	8	0	2	16	10
% cobble	8	20	12	14	20	30
% gravel	8	24	52	56	10	16
% sand	70	48	30	24	54	44
% silt	10	0	6	4	0	0
Bank erosion (m)	2.0	2.6	1.6	2.4	0.5	0.7
Riparian buffer width (m)	19	56	0	0	94	66
% canopy cover	64.2	63.7	6.7	0	24.7	12.7

from the center of the stream and the right and left banks at each transect. We measured stream water temperature with Hobo® data loggers (Onset®, Bourne, Massachusetts) set to record temperatures every 30 min throughout the study period at each site.

We derived % boulder, % cobble, % gravel, % sand, and % silt from mean values calculated across the visual estimates made in all quadrats in a reach. Mean values for depth, thalweg depth, % embeddedness, depth of fines, % algae, bank erosion, riparian buffer width, and % canopy cover were calculated across all measurements taken in all 10 transects at each study reach.

Macroinvertebrates

We collected macroinvertebrates from all study reaches on 19–21 April, 25–26 May, 8–9 July, 10–12 August, 8–10 September, and 1–5 November 2010. We sampled unrestored and restored reaches in individual streams on the same day. During each sampling visit, we examined each reach for 5 types of macroinvertebrate habitat: 1) riffles, 2) undercut banks and overhanging vegetation, 3) submerged or emergent macrophytes, 4) snags and woody debris, and 5) debris dams/leaf packs. We used a D-frame kick net (mesh size = 500 μm) to collect 1 subsample from each available habitat type (for a total of 5 subsamples). Habitats with nonuniform surfaces (such as branches of wood snags) made truly quantitative sampling difficult. However, we sought to standardize sampling area and effort as much as possible to generate semiquantitative samples. We placed the D-net on the habitat surface (for riffles and woody debris) or held the net immediately downstream of and at the same depth as the habitat (for overhanging vegetation, submerged/emergent macrophytes, and debris dams) and thoroughly disturbed (i.e., churning and cleaning by hand) a 0.09-m^2 area of the habitat type immediately upstream of the net opening. Sampling area was visually estimated and sampled by the same person for all samples collected during this study. All surfaces included within the sampling area (i.e., individual pieces of gravel and cobble, wood surfaces, individual leaves in debris dams, individual leaves of vegetation) were scrubbed by hand until all visible material had been removed and captured in the net. If all habitat types were not present, or if they could not be accessed because of high-flow conditions, we took additional samples from the most abundant habitat types in order of abundance, until we had collected a total of 5 subsamples. We preserved subsamples individually by transferring all debris collected in the net to a 0.5-L plastic sampling jar and adding 70% ethanol. In the laboratory, we spread each subsample evenly onto trays and sorted all organisms with the aid of a dissecting microscope. We identified all sorted organisms to the lowest possible taxonomic level (typically genus) using standard keys (e.g., Merritt et al. 2008), and measured individuals to the nearest 1 mm.

We estimated macroinvertebrate biomass with length–mass regressions published by Benke et al. (1999). We based estimates of secondary production for each study reach on macroinvertebrate data pooled from all habitat subsamples collected during each site visit. We used the size-frequency method with a correction for cohort production interval to estimate production of common taxa with the size–frequency method (Benke and Huryn 2006). We estimated production of rare taxa based on published production to biomass ratios (Krueger and Waters 1983, Benke 1993, France 1993, Stagliano and Whiles 2002) (Appendix S1). We used the instantaneous growth (IGR) method to estimate nontanypodine chironomid production. We estimated growth with temperature and size-specific growth rates published by Walther et al. (2006). The IGR method requires an estimate of mean daily temperature during the interval between sampling events. We estimated mean daily temperature from data recorded every ½ h by Hobo temperature loggers at each study reach.

Statistical analyses

We calculated total macroinvertebrate taxon richness, EPT taxon richness, % abundance of EPT taxa (% EPT taxa), and total macroinvertebrate density for each study reach in each month by pooling data from all habitat subsamples collected during each visit. Thus, we derived 6 repeated-measure estimates (estimates collected over time) of total richness, EPT taxon richness, % EPT taxa, and density for each study reach. All measures were standardized to the total area sampled during each visit.

We used generalized least-square models (GLS; Zuur et al. 2009) to assess whether structural metrics (total richness, EPT taxon richness, % EPT taxa, density) were related to site, treatment, or month, while allowing for heterogeneity in the variance structure of the data set. GLS is a method of linear regression designed to deal with repeated measures data and allows model errors to have unequal variance or to be correlated across observations (Zuur et al. 2009).

We used restricted maximum likelihood (REML) on models containing the full set of explanatory variables (site, treatment, and month) to evaluate several possible residual variance and correlation structures for each macroinvertebrate metric. We used Akaike's Information Criterion (AIC) to select the optimal residual variance structure (i.e., the variance structure that resulted in homogeneity of the normalized residuals; see Zuur et al. 2009 for a detailed description). We subsequently conducted a likelihood ratio (L-ratio) test, using maximum likelihood estimation (Zuur et al. 2009), to identify whether each fixed variable of interest (site, treatment, and month) was significantly related to macroinvertebrate metrics. We dropped each explanatory variable in turn (backward selection) from GLS models for each macroinvertebrate metric, and conducted an L-ratio test to compare the resulting reduced models with the full model containing all 3 explanatory variables. A significant L-ratio result ($p < 0.05$) indicated that the dropped variable was significantly related to the macroinvertebrate metric of interest. Our data set was not large enough for us to evaluate effects of interaction terms (e.g., site × treatment) on macroinvertebrate metrics. Upon identifying a model with the best covariance structure and significant fixed terms, we refit the model using restricted maximum likelihood (REML) estimation (Zuur et al. 2009) to produce the final model for each metric.

Secondary production calculations produced a single value for each study reach. Thus, we could not use standard parametric statistical techniques to test for differences in secondary production among reaches. Instead, we estimated uncertainty associated with secondary production estimates by bootstrapping (Efron 2003, Benke and Huryn 2006). Bootstrapping creates replicate samples from a single sample by randomly resampling from the original sample with replacement (Efron 2003, Manly 2007). We created 1000 bootstrap replicate samples for each original sampling event at each study reach. We used these replicates to generate 1000 estimates of secondary production for each study reach. We calculated 95% confidence intervals for biomass and secondary production at each reach with the percentile method (Carpenter and Bithell 2000).

We defined the dominant taxa contributing to total secondary production as those taxa that individually contributed ≥1% of total secondary production in each study reach. We used 95%th-percentile confidence intervals generated via bootstrapping to compare the productivity of dominant taxa between reach types.

We evaluated the effect of treatment on in-stream and riparian habitat variables with linear mixed effects (LME) models that accounted for differences among study streams as a random effect (a random intercept model; Zuur et al. 2009). This analysis was equivalent to a split-plot design with streams as blocks for treatment effects. The units of replication were the individual transects within reaches. We chose LME models over the more detailed GLS models used to model macroinvertebrate metrics because modeling site and treatment effects on each habitat variable would have created an excessively large number of results to interpret, and we were primarily interested in habitat differences between treatments rather than among sites.

All data analyses were done in R (version 3.0.1; R Project for Statistical Computing, Vienna, Austria) with the *gls* and *lme* functions (nlme package; Pinheiro et al. 2013).

RESULTS

Total richness, EPT richness, % EPT taxa, and density

We collected a total of 121 unique taxa in 52 families across all 3 streams (Appendix S1). We identified 102 taxa to genus and 19 to family. These taxa included 62 Diptera, 19 Ephemeroptera, 13 Coleoptera, 11 Trichoptera, 6 Plecoptera, 4 Hemiptera, 3 Odonata, 1 Amphipoda, and 1 Collembola.

Total richness was related to stream site (L-ratio = 14.71, df = 13, $p < 0.001$) and month (L-ratio = 24.50, df = 10, $p < 0.001$), but not treatment (L-ratio = 1.51, df = 14, $p = 0.219$). The final GLS model for total richness indicated that Elm Creek and Rush River had 11.60 and 10.53 fewer taxa on average, respectively, than Buffalo Creek (Table 2, Fig. 2A).

The model also indicated that 14 to 15 more taxa were found in July, August, and September than in April, and 5 more taxa were found in May than in April.

EPT taxon richness was related to stream (*L*-ratio = 11.76, df = 8, $p = 0.002$), treatment (*L*-ratio = 5.73, df = 9, $p = 0.017$), and month (*L*-ratio = 32.42, df = 5, $p < 0.0001$). On average, restored reaches yielded 1.94 more EPT taxa than unrestored reaches (Table 2; Fig. 2B). Approximately 3 more EPT taxa were found at Buffalo Creek than at Elm Creek and Rush River. EPT taxon richness was higher during the peak growing season (July, August, September) than in spring (April, May) or autumn (November).

Percent EPT taxa was related to site (*L*-ratio = 22.13, df = 8, $p < 0.0001$), and month (*L*-ratio = 49.47, df = 5, $p < 0.0001$), but not treatment (*L*-ratio = 0.45, df = 9, $p = 0.500$). Percent EPT taxa was ~18 points lower at Rush Creek than at Buffalo Creek (Table 2, Fig. 2C). Percent EPT taxa was highest in July and lowest in April (Table 2).

Table 2. Final general least-square models showing mean (±1 SE) change in each structural metric (total taxon richness, Ephemeroptera, Plecoptera, Trichoptera [EPT] taxon richness, % EPT taxa, total density) for significant fixed variables (site, treatment [restored, unrestored], or month, depending on the model). Variance functions for total richness and density allowed different variance per month. EPT taxon richness and % EPT taxa did not exhibit significant heterogeneity by month, and models for these metrics do not include a variance function. In all models, significant changes in mean metric values across stream site are shown relative to Buffalo Creek, changes related to treatment effect are shown relative to unrestored reaches, and changes related to month are shown relative to samples collected in April. *L*-ratio = log-likelihood ratio.

Structural metric	*L*-ratio	Coefficients	Mean	*t*	*p*
Total richness	−98.41	Intercept	27.21 ± 2.24	12.12	0.00
		Site (Elm Creek)	−11.60 ± 1.25	−9.26	0.00
		Site (Rush River)	−10.53 ± 1.25	−8.40	0.00
		Month (May)	5.17 ± 2.20	2.35	0.03
		Month (July)	14.00 ± 3.47	4.04	0.00
		Month (August)	15.00 ± 5.54	2.71	0.01
		Month (September)	15.33 ± 3.26	4.71	0.00
		Month (November)	1.00 ± 5.55	0.18	0.86
EPT taxon richness	−73.57	Intercept	5.41 ± 1.35	4.01	0.00
		Site (Elm Creek)	−3.00 ± 1.10	−2.72	0.01
		Site (Rush River)	−3.17 ± 1.10	−2.87	0.01
		Treatment (restored)	1.94 ± 0.90	2.16	0.04
		Month (May)	2.50 ± 1.56	1.60	0.12
		Month (July)	7.50 ± 1.56	4.81	0.00
		Month (August)	6.83 ± 1.56	4.38	0.00
		Month (September)	6.83 ± 1.56	4.38	0.00
		Month (November)	2.50 ± 1.56	1.60	0.12
% EPT taxa	−144.99	Intercept	8.61 ± 5.34	1.61	0.12
		Site (Elm Creek)	3.20 ± 4.62	0.69	0.49
		Site (Rush River)	−17.60 ± 4.62	−3.81	0.00
		Month (May)	20.45 ± 6.54	3.13	0.00
		Month (July)	53.53 ± 6.54	8.19	0.00
		Month (Aug)	31.29 ± 6.54	4.79	0.00
		Month (September)	20.98 ± 6.54	3.21	0.00
		Month (November)	41.80 ± 6.54	6.40	0.00
Density	−238.30	Intercept	1440.23 ± 406.85	3.54	0.00
		Treatment (Restored)	258.11 ± 128.23	2.01	0.05
		Month (May)	−1058.27 ± 408.12	−2.59	0.01
		Month (July)	545.09 ± 985.18	0.55	0.58
		Month (August)	−327.95 ± 457.77	−0.72	0.48
		Month (September)	71.72 ± 522.79	0.14	0.89
		Month (November)	−928.99 ± 496.61	−1.87	0.07

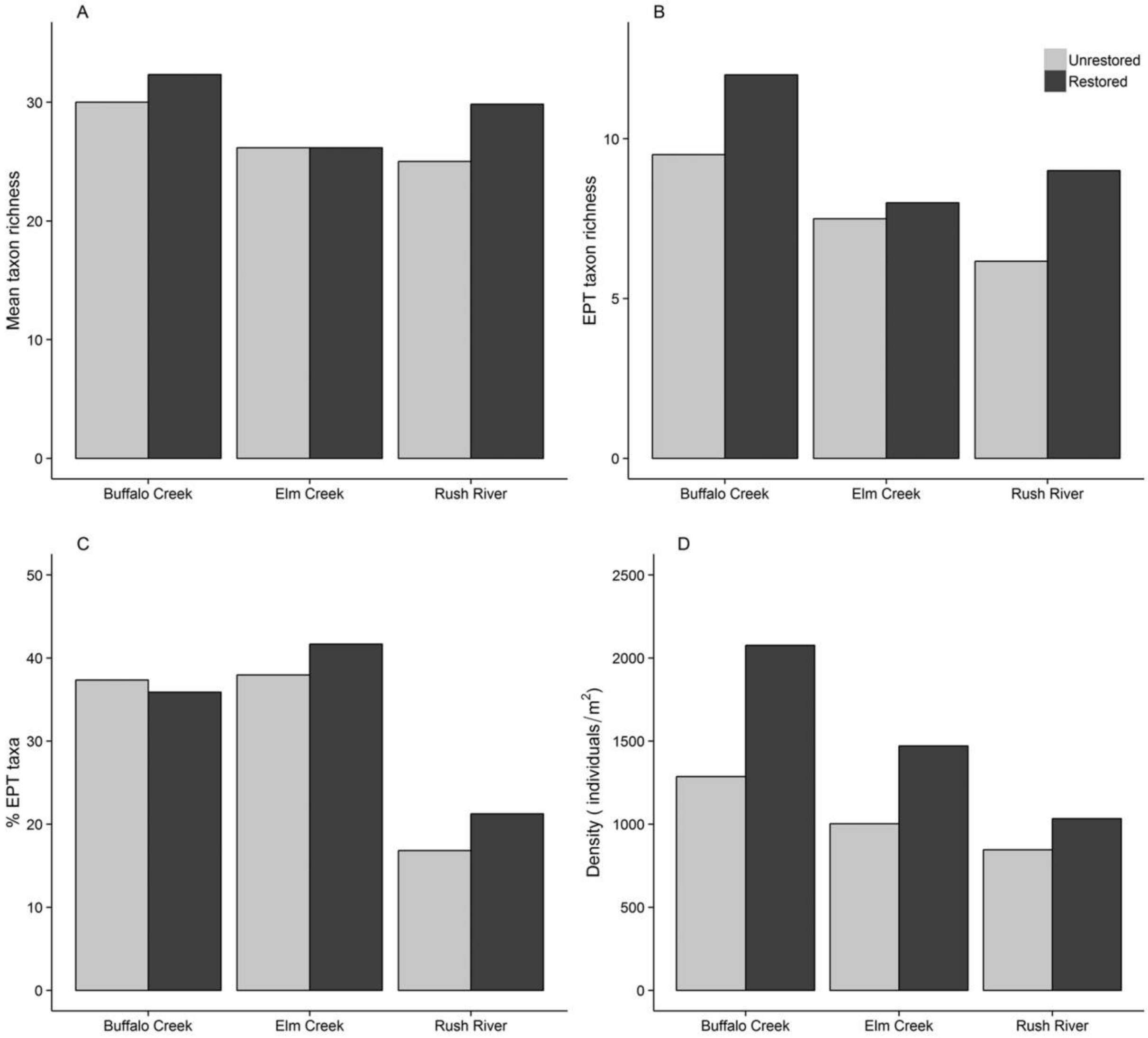

Figure 2. Mean total taxon richness (A), Ephemeroptera, Plecoptera, Trichoptera (EPT) taxon richness (B), % EPT taxa (C), and total density (D) at unrestored and restored reaches of 3 study streams in 2010.

Density was affected by treatment (L-ratio = 5.82, df = 14, p = 0.016) and month (L-ratio = 26.01, df = 10, p < 0.0001), but not site (L-ratio = 5.50, df = 13, p = 0.064). On average, density was 258 individuals/m^2 higher in restored than in unrestored reaches (Table 2, Fig. 2D). Density was lower in May and November than in other months.

Secondary production

Secondary production estimates ranged from 0.9 g m^{-2} y^{-1} at the unrestored reach of Rush River to 10.2 g m^{-2} y^{-1} at the restored reach of Buffalo Creek. In each study stream, secondary production was ~2 to 3× higher at the restored than at the unrestored reach (Fig. 3). Confidence intervals generated by bootstrapping indicated that secondary production was significantly higher in the restored reach of each stream than in the respective unrestored reach.

Secondary production was dominated by similar groups of taxa in all study reaches. At Buffalo Creek, 8 taxa (*Simuliidae*, *Hydropsyche*, *Cheumatopsyche*, *Ceratopsyche*, *Nectopsyche*, *Tricorythodes*, *Polypedilum*, *Heptagenia*) accounted for 77% and 90% of total secondary production in the unrestored and the restored reach, respectively (Fig. 4A; see Appendices S1, S2 for individual taxa). Five of these taxa were significantly more (and in some cases, many times more) productive at the restored than the unrestored reach. At Elm Creek, 11 taxa (*Cheumatopsyche*, *Simuliidae*, *Nectopsyche*, *Tipula*, *Heptagenia*, *Hydropsyche*, *Pseudocloeon*, *Taeniopteryx*, *Ceratopsyche*, *Polypedilum*, *Stenelmis*) accounted for 92% of total secondary production at the restored reach (Fig. 4B). A similar group of taxa dominated secondary production at the unrestored reach, with 7 taxa (*Nectopsyche*, *Simuliidae*, *Pseudocloeon*, *Heptagenia*, *Taeniopteryx*, *Cheu-*

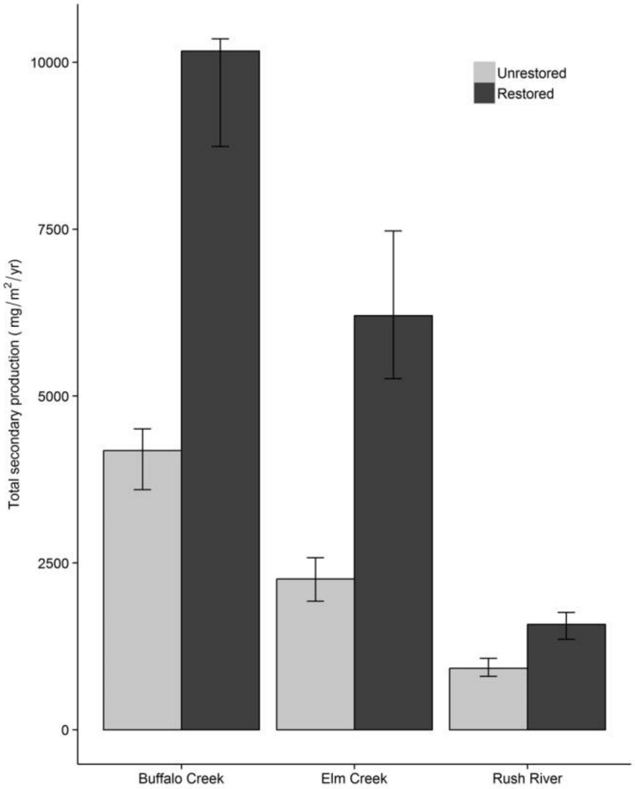

Figure 3. Mean (95% CI, generated by bootstrapping) total secondary production of macroinvertebrates (mg m^{-2} y^{-1}) at unrestored and restored reaches of all 3 study streams in 2010.

matopsyche, *Polypedilum*) accounting for 74% of total secondary production. Most of the dominant taxa at Elm Creek were significantly more productive in the restored reach than the unrestored reach. At Rush River, 11 taxa (*Simuliidae*, *Tricorythodes*, *Orthocladius*, *Polypedilum*, *Nectopsyche*, *Atherix*, *Tipula*, *Stenelmis*, *Rheotanytarsus*, *Cricotopus*, *Chironomus*) accounted for 77% of total secondary production in the restored reach (Fig. 4C). A similar group of 10 taxa (*Simuliidae*, *Tricorythodes*, *Orthocladius*, *Polypedilum*, *Baetis*, *Dicrotendipes*, *Atherix*, *Lepidostoma*, *Pycnopsyche*, *Rheotanytarsus*) accounted for 70% of total secondary production at the unrestored reach. Several dominant taxa were significantly more productive at the restored than at the unrestored reach (e.g., *Simuliidae*, *Tricorythodes*, *Orthocladius*).

In-stream and riparian habitat

Differences in habitat variables between unrestored and restored reaches depended on stream site (Table 1). However, % sand, % embeddedness, and bank erosion differed between restored and unrestored reaches independently of site effects. Percent sand (L-ratio = –2.37, df = 3, $p = 0.038$) and % embeddedness (L-ratio = –275.07, df = 3, $p = 0.003$) were significantly lower, whereas bank erosion (L-ratio = –81.64, df = 3, $p = 0.013$) was significantly higher at restored than at unrestored reaches. Treatment was not related to any other in-stream or riparian-habitat variables measured.

DISCUSSION

Stream restoration had no effect on total richness in our study reaches. This finding is consistent with those of other studies (reviewed by Palmer et al. 2010). Thus, typical stream restoration activities conducted at the reach scale do not appear to improve stream biodiversity. However, the relationship between reach-scale restoration and ecosystem structure and function in agricultural streams may require a more nuanced interpretation because restored reaches yielded higher estimates of macroinvertebrate density and EPT taxon richness than unrestored reaches. Moreover, secondary production was significantly higher in restored than unrestored reaches within streams.

Higher macroinvertebrate density, EPT taxon richness, and secondary production in restored reaches could be interpreted as signs of partial recovery by macroinvertebrates in these reaches. EPT taxa are considered sensitive to a wide array of environmental stressors at multiple scales including land cover, substrate quality, and water quality, and have been widely used as a measure of stream biotic condition (e.g., Richards et al. 1993, Sponseller et al. 2001). A significantly higher number of EPT taxa in restored than in unrestored reaches suggests that conditions in the restored reach may have improved relative to the conditions elsewhere in the study streams (but we note that the absolute value of the difference in EPT taxon richness between reach types was small). Higher macroinvertebrate density and secondary production per area of habitat in restored reaches suggests that the stability or quality of habitat or resource availability (or both) may have improved for macroinvertebrates after restoration.

Physical differences in the quality and quantity of coarse substrates between restored and unrestored reaches suggests possible improvements in riffle habitats for macroinvertebrates associated with restoration. Coarse substrates (predominantly found in riffle habitats) had lower embeddedness in restored than in unrestored reaches (i.e., less total surface area of these substrates was covered by fine sediments). Reduced embeddedness of coarse substrates could improve the suitability of this habitat for some taxa because of increased substrate stability, reduced negative respiratory effects associated with deposition of fine sediments, and increased availability of food sources associated with coarse substrates, such as epilithic biofilms (Wood and Armitage 1997).

Contribution of specific taxa to secondary production

Higher productivity in restored reaches was mostly the result of the disproportionate success of a small number of dominant taxa (e.g., hydropsychid caddisflies and black flies). Many of these dominant taxa are considered mod-

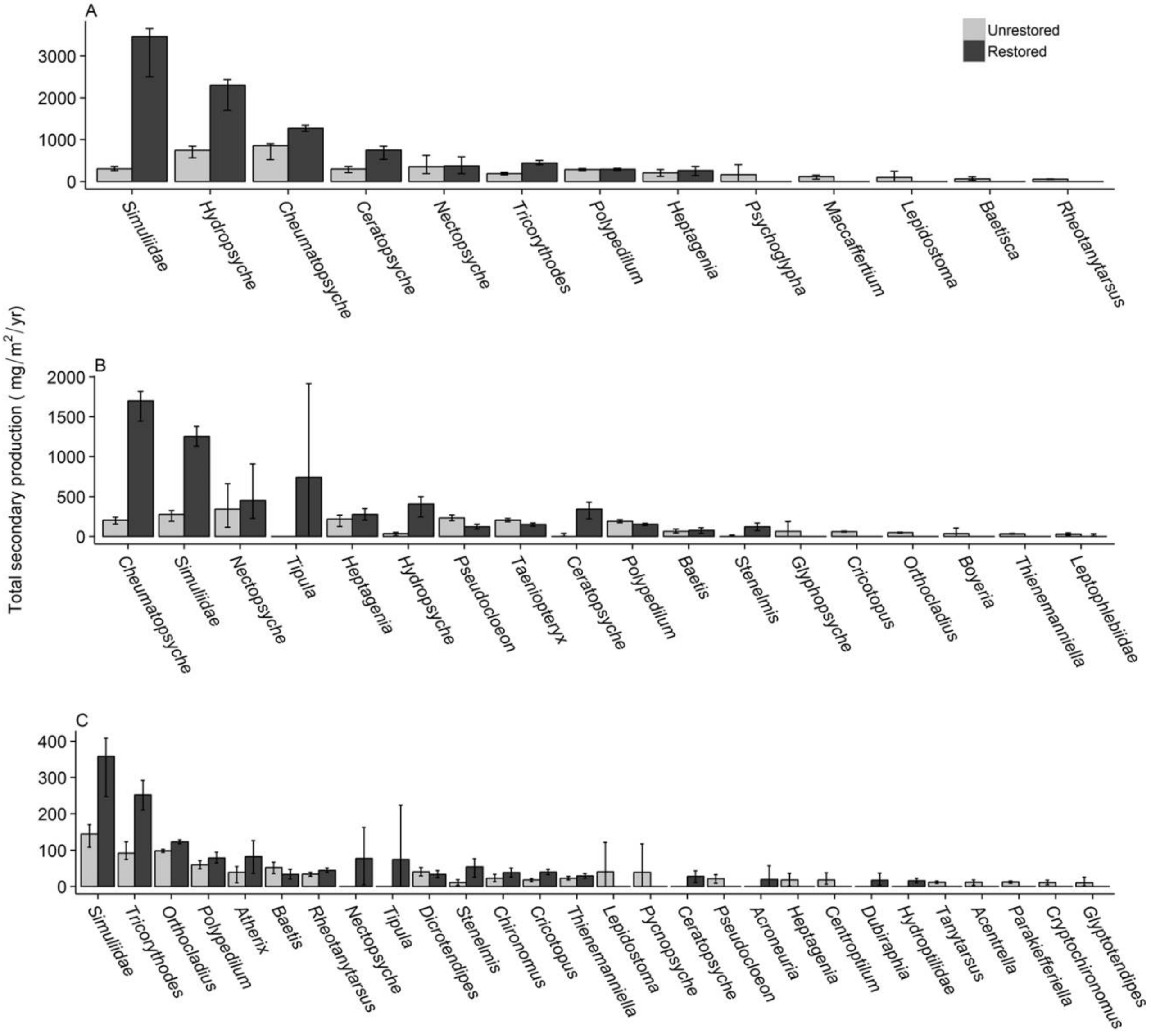

Figure 4. Mean (95% CI, generated by bootstrapping) contribution of each taxon to secondary production at unrestored and restored reaches of Buffalo Creek (A), Elm Creek (B), and Rush River (C) in 2010. Only taxa contributing at least 1% of total secondary production in each study reach are shown.

erately to highly tolerant of pollution, especially high levels of suspended sediments (Merritt et al. 2008, Jackson et al. 2010). Thus, although some of our findings point to possible restoration-related changes in habitat or resource quality for macroinvertebrates, such changes may have disproportionately benefitted a small number of taxa that are not of particular conservation concern. Nevertheless, higher secondary production of these taxa in the restored reaches could provide an important subsidy to higher-level consumers in the streams and across the freshwater–terrestrial ecosystem boundary. Further study is needed to quantify whether the production of these taxa is a limiting resource for higher trophic levels, such as birds, bats, amphibians, or fish in the streams we studied.

Comparison to other agricultural streams

Secondary production estimates for the study streams, especially in unrestored reaches, were low compared to other similarly sized agricultural streams. In a recent synthesis of available secondary production studies, Finlay (2011) indicated that streams draining watershed areas comparable in size ($\sim$100 km^2) to those of our study sites and dominated by agricultural land use generally yielded macroinvertebrate secondary production estimates >10 g m^{-2} y^{-1}. However, secondary production estimates for our sites were all $\leq$10 g m^{-2} y^{-1}. Relatively low secondary production at the study sites may reflect stressful environmental conditions for macroinvertebrates, including flashy stream hydrology and high loads of sediment, nutrients, and pesticides. High levels of suspended particulates in the study streams also could be suppressing in-stream primary production, thereby limiting the amount of autochthonous food sources available to support secondary production.

Alternatively, our sampling approach may have resulted in artificially low estimates of total secondary production. We did not collect samples in winter (December through March) because of snow and ice cover on the streams. We assumed that macroinvertebrate production during winter would be small compared to production during spring, summer, and autumn. This assumption may have resulted in failure to adequately account for the production of taxa, such as *Taeniopteryx*, that are bioenergetically active primarily during winter and early spring, and may have led to underestimation of total secondary production. Our comparatively low secondary production estimates also may have resulted, in part, from the exclusion of meiofauna. We collected macroinvertebrate samples with nets with 500-μm mesh, so our production estimates included only individuals ≥1 mm in length. The contribution of smaller individuals to total secondary production may depend on the physical characteristics of the stream, but can be quite high (15–50%) in some systems (Stead et al. 2005). Additional study is needed to quantify the contribution of meiofauna to total secondary production in our study streams.

Further study also is needed to evaluate whether the rates of secondary production we documented are representative of longer-term trends at these stream sites. For example, our secondary production estimates may have depended in part on hydrologic conditions in the study streams during our sampling period. For example, precipitation totals in 2010, the year we sampled macroinvertebrates, were near or above record highs for many locations throughout Minnesota, and much of the precipitation occurred as heavy rainfall associated with severe weather. The resulting high-flow conditions could have flushed macroinvertebrates from the study reaches, thereby reducing their density and survivorship. Another question related to temporal trends at the study sites is how the length of time since restoration might affect macroinvertebrate or physical-habitat metrics. Restoration efforts at the study streams were implemented in different years (2001, 2006, and 2008). Time elapsed since restoration did not appear to be related to the difference in secondary production among restored and unrestored reaches, but with only 3 study locations sampled during 1 y, we cannot say definitively whether such a relationship may exist for the study streams.

Conclusions

Our findings highlight the potential benefits of using multiple structural and functional indicators of stream condition. The lack of association between reach-scale restoration and total richness may stem, as Palmer et al. (2010) suggested, from watershed- and basin-scale disturbances that limit the pool of species available to colonize restored streams in highly disturbed ecosystems. However, the higher values of EPT richness and secondary production we observed in restored reaches indicate that reach-scale restoration may affect macroinvertebrate assemblages and ecosystem function in ways not captured by total taxon richness alone.

Nevertheless, we did observe differences in macroinvertebrate community structure and function that were related to reach-scale restoration, even though the primary purpose of restoration was not habitat improvement per se. Restoration materials (e.g., boulder weirs, root wads, and cut logs) were added to the study streams primarily to stabilize stream banks and prevent stream-bank soil loss. Resource managers hoped that these additions would, directly or indirectly, also improve conditions for aquatic life, and our findings indicate that such improvements may have occurred for some taxa. However, an important research question is whether restorations specifically aimed at improving habitat or resource conditions for particular target species or groups of taxa would have larger or different effects on macroinvertebrate community structure and function beyond those observed in our study.

Conservation and recovery of biodiversity at local, regional, and global scales is undoubtedly one of the most critical needs faced by resource managers. However, gauging the effect of management activities based on changes in biodiversity alone may fail to identify other potentially consequential changes in ecosystem structure and function. Given that altered stream ecosystems may never recover the biological composition that characterized them in the past, monitoring changes in ecosystem functions, such as secondary production, may enable more informed conservation decisions.

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