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Contrasting Responses among Aquatic Organism Groups to Changes in Geomorphic Complexity Along a Gradient of Stream Habitat Restoration: Implications for Restoration Planning and Assessment

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Abstract: Many stream restoration projects aim to increase geomorphic complexity, assuming that this increases habitat heterogeneity and, thus, biodiversity. However, empirical data supporting these linkages remain scant. Previous assessments of stream restoration suffer from incomplete quantification of habitat complexity, or a narrow focus on only one organism group and/or one restoration measure, limiting learning. Based on a comprehensive quantification of geomorphic complexity in 20 stream reaches in northern Sweden, ranging from streams channelized for timber floating to restored and reference reaches, we investigated responses of macroinvertebrates, diatoms, and macrophytes to multiple geomorphic metrics. Sediment size heterogeneity, which was generally improved in restored sites, favored macroinvertebrate and diatom diversity and macroinvertebrate abundance. In contrast, macrophyte diversity responded to increased variation along the longitudinal stream profile (e.g., step-pools), which was not consistently improved by the restoration. Our analyses highlight the value of learning across multiple restoration projects, both in identifying which aspects of restoration have succeeded, and pinpointing other measures that might be targeted during adaptive management or future restoration. Given our results, a combination of restoration measures targeting not only sediment size heterogeneity, but also features such as step-pools and instream wood, is most likely to benefit benthic biota in streams.

1. Introduction

Researchers and restoration practitioners expect greater habitat complexity to favor higher species diversity and abundance [1–5]. This expectation arises from basic ecological theory, which posits that habitats that are structurally more complex provide a greater range of niches and reduce the likelihood of competitive exclusion, together facilitating species co-existence [1,6]. Variation in habitat complexity might also mediate the effects of disturbance and predation through the provision

of refugia [6,7]. Furthermore, structurally complex habitats might support more food resources. For example, the presence of more complex habitat structures in streams might support a greater accumulation of biofilm, by increasing the surface area of benthic substrates, and enhance retention of particulate matter [8–12]. Indeed, the likely importance of complex habitat structures for benthic organisms in streams has long been recognized [13–15], especially for macroinvertebrates [16,17]. Consequently, structural features or (hydro)geomorphic complexity have become a central focus in river management and restoration [18–22]. However, the ecological outcomes of most restorations of geomorphic complexity in streams have been disappointing, with weak or even negative effects on benthic biodiversity [20,23–25]; see [26].

Optimization of restoration rests, firstly, on a clear identification of program goals, which most often focus on improvements in the diversity and abundance of particular organism groups, followed by an identification of which measures are most likely to achieve these goals [27]. Unfortunately, this process is hindered by our limited understanding of relationships between different aspects of geomorphic complexity and the responses of particular organism groups, and even species within groups. Indeed, most previous restoration assessments have focused on a narrow range of biotic metrics calculated for only one organism group, most often macroinvertebrates or fish [25], although multiple group assessments are becoming more common [28–31]. Since different organism groups differ in their niche requirements, degree of ecological specialization, and the spatial scale over which they operate [12,32–34], it is unlikely that a single restoration measure will be equally effective for all groups. For example, rehabilitation of microhabitat diversity (e.g., in sediment size distributions) at small scales may be most beneficial for macroinvertebrates [17], while for primary producers, such as macrophytes and benthic algae, availability of a high variety of stable substrates in both shallower and deeper water habitats for rooting and attachment may be of particular importance [34,35]. Accordingly, evaluation of a project based on a single organism group could be misleading and result in uniform management and conservation practices inappropriate for other organism groups [25,36].

An effective means of generating learning that can assist in setting priorities in future restoration projects is the analysis of habitat complexity–biodiversity relationships from previous restoration programs [27]. Unfortunately, a thorough quantification of shifts in geomorphic complexity is often not included in follow-up evaluations of restoration success, with previous assessments rarely including more than one measurement per project [20]. Even where such measurements are included, assessments of the effects of restoration on geomorphic complexity is typically based on the average among categories, i.e., restored vs. control (unrestored) vs. pristine [12]. However, restoration undertaken at different sites will vary in the level of geomorphic complexity achieved, due to differences in the potential complexity of a given site, which is likely to be constrained by larger scale, natural gradients in geology and topography, etc. [22]. Accordingly, any assessment of shifts in complexity requires quantifying variability around the trend [22]. Measurements of variation, such as the coefficient of variation (CV) of stream depths and the CV of flow [37] or CV of width [28], or ranges in sediment grain sizes [38], are better descriptors of the geomorphic complexity experienced by instream organisms than the means of these parameters. Commendably, some larger assessment programs have started using geomorphic complexity metrics to quantify the effects of restoration on habitats [39], but even these collapse all hydrogeomorphic parameters into an average, potentially missing key organism responses to changes in specific aspects of habitat complexity.

Five spatial dimensions of geomorphic complexity have been recognized [22]—sediment grain size distribution, longitudinal profile, cross-section, planform, and instream wood (Figure 1). Instream biota respond to aspects of all five dimensions, including substrate type (e.g., wood vs. boulders vs. fines), sediment size variation, stream depth, and step-pool formation [16,40–42]. For example, the addition of boulders or instream wood (1) increases the range of substrate sizes available for different species of instream plants and diatoms to attach to, (2) enhances stream bed stability, and (3) provides refugia from high flow for macrophytes and benthic macroinvertebrates [6,34,35,43].
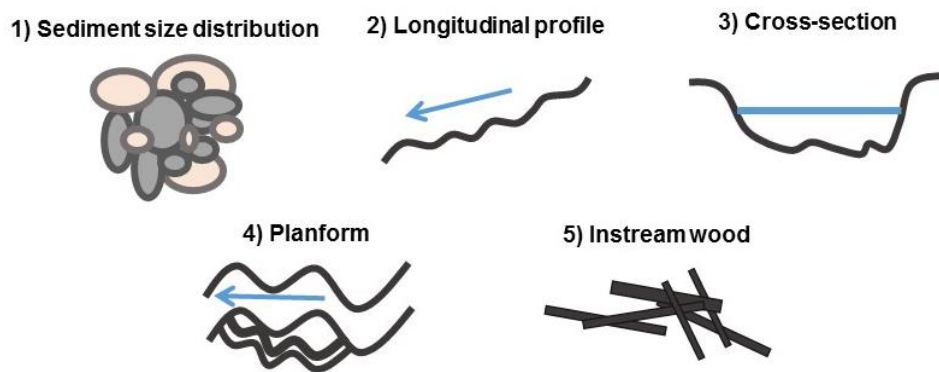
Figure 1. Graphical descriptions of the five dimensions of geomorphic complexity used to get a holistic view of the effect of restoration across a gradient of restored and potential complexity. Eight sediment size distribution (1) metrics were calculated from data collected using a "pebble count" of 300 sediment grains. Longitudinal profile (2) captures how the stream looks as it flows downstream from the side (profile view of a stream shown here); seven metrics were calculated that describe the complexity of the longitudinal profile. The two cross-section (3) metrics describe the complexity of the stream as if one took a slice of a bread loaf, e.g., measuring the complexity of the stream bottom compared to bankfull width. The six planform (4) metrics describe the complexity of the stream as seen from above. Six metrics of instream wood (5) describe the complexity of naturally recruited and restored wood in the stream. Of these 29 metrics, 14 were used in the final analysis.

The addition of large boulders, wood, and coarse gravel, which created spawning beds for fish, during restoration, can increase sediment size variation and enhance retentivity (entrapment of organic matter), potentially restoring niche space and food resources for different species and feeding guilds [12,44,45]. Additionally, introduction of larger substrates can increase roughness and decrease flow velocity which, in turn, can lead to flow attenuation and overbank flows. If restoration increases channel–floodplain connectivity through removal of cobble/boulder levees, channel width increases and channel depth decreases, which increases niche space for aquatic and riparian plants [46,47]. Step-pools are increasingly being used during restoration to reduce the magnitude and frequency of peak discharges, duration and volume of flow, and deal with reduced sediment supplies [40], all of which have implications for instream habitat quality and quantity at the reach scale. Furthermore, step-pools as well as large boulders provide variation in water depth in the stream channel, with implications for light attenuation and, therefore, light availability for benthic organisms.

In northern Sweden, the forestry industry physically modified most streams and rivers from the 1850s up to the 1960s, to facilitate timber floating. Beginning in the 1980s, restoration projects have aimed at increasing geomorphic complexity on these channelized streams [46,48]. Early on, restoration efforts focused on improving instream habitat for local fish populations, although the most recent restorations have broader ecosystem goals, and have involved more restoration measures and effort, including replacing large boulders, instream wood, and gravel spawning beds [46]. In the most recent restorations, the additional effort aimed to push the geomorphic complexity to levels beyond those of older best-practice techniques [22]. This provides an excellent opportunity for quantifying responses of different organisms to the actual gradient of geomorphic complexity achieved among sites, and to identify cases where increases in geomorphic complexity did and did not succeed in altering community composition and/or enhancing biodiversity.

Here, we address three of the shortcomings that we suggest have hindered learning from previous assessments of restoration outcomes; namely, the generally narrow focus on just one geomorphic complexity metric, responses of a single organism group, and/or a focus on differences between dichotomous restoration categories that obscure variation in the level of complexity achieved. We do this by evaluating the effects of restoration of instream geomorphic complexity using (1) multiple geomorphic complexity metrics to evaluate responses of (2) multiple organism groups (3) along

a gradient of restoration effort, to learn more about which geomorphic complexity metrics most strongly regulate the responses of different organism groups. We measured the responses of three organism groups—macroinvertebrates, diatoms, and macrophytes—to restoration of geomorphic complexity across 13 stream reaches, which differed in restoration effort (number of restoration measures applied). We also included channelized and unchannelized near-natural reference reaches, to assemble an extended gradient of geomorphic complexity for 20 streams in the study. We expected that the quantification of multiple metrics of geomorphic complexity will allow better explanation of variation in the responses of biota along the restoration complexity gradient, compared with using categories of restoration status. Furthermore, we expected that responses of the different organism groups to restoration would contrast according to taxon-specific habitat requirements associated with geomorphic complexity. Specifically, we hypothesized that macroinvertebrates are more likely to respond to variation in microhabitats, i.e., variation in smaller sediment sizes [17] that can provide refuge from predators and flow and other disturbances, and facilitate trapping of fine particulate organic matter [12]. We expected that macrophytes would respond to metrics that measure the reach-scale complexity, e.g., variation in stream depth and width [30], given the preferences of several species for edge habitats and other shallow water areas where sun exposure reaches the river bed and flow velocities are slow [49]. Such habitat types are often very restricted in channelized systems. Diatoms are a relatively understudied organism group when it comes to stream restoration [30], but we hypothesized that they would likely respond to metrics that reflect sediment size distribution (related to stability of sediments and scouring by fine sediments, [35]) and light, e.g., variation in depths.

2. Methods

2.1. Study Area

The study reaches are all classified as "boreal rivers" within the Fennoscandian shield [50], which includes the northern half of Sweden, all of Finland, and the westernmost part of European Russia [51]. The landscape has a low relief (~200–600 m above sea level) and is the product of repeated glaciations, with large glacial legacy sediment (boulders and cobbles) dominate even some low-gradient (<1%) reaches [22]. Managed boreal forests, dominated by *Pinus sylvestris*, *Picea abies*, and *Betula pubescens* with an understory of dwarf shrubs, characterize the upland landscape. *Betula* spp., *Alnus incana*, *Salix* spp., or *Juniperus communis* make up the riparian overstory and diverse graminoid and forb communities border the streams.

The streams are comprised of slow-flowing reaches interspersed with relatively short rapids (pool-riffle, plane-bed, and cascade). Rapids were typically the target of channelization efforts because these were common places for floated logs to jam up. Explosives were used to destroy big boulders, coarse sediment was moved to the sides, channels were straightened and narrowed, and side channels were closed [48]. Much of the finer sediment was transported downstream after channelization increased and homogenized flow velocities [22,48], and sediment recruitment is limited in this system [52]. Each study reach was 60 m long. We grouped our study reaches into five categories according to their restoration status: those that were (1) control sites comprising unrestored reaches channelized during the timber floating era (*n* = 4); (2) previously channelized reaches restored in the 1980s using "best-practice" methods that returned cobbles and boulders to the main channel from levees on the channel margins (25-year-old, *n* = 3); (3) previously channelized reaches restored in the 2000s with best-practice methods, often with an additional measure targeting the opening of closed side channels (10-year-old, *n* = 5); (4) reaches that were first restored by best-practice methods in the 2000s and again in 2010 by adding large boulders (>1 m), coarse gravel (~10 mm diameter) for spawning beds, and instream wood (enhanced restoration, [53]; called "demonstration" restoration in [22], *n* = 5); and finally (5) unchannelized reference reaches never subjected to channelization or restoration (called "unimpacted" in [22], *n* = 3). Unchannelized reference reaches had steeper channel slopes than all other reach types [22]; this is an inevitable consequence of the challenge of timber

floating steep reaches with more boulders or exposed bedrock, with such reaches typically excluded from modification during the channelization era.

2.2. Geomorphic Complexity Metrics

Data collected at each reach consisted of topographic surveys, measurements of sediment size distribution, instream wood surveys, and observations of valley characteristics. Using a Trimble S3 total station, topographic surveys of the longitudinal profile of the morphologic bankfull edges on both sides, including any islands, and the thalweg (lowest point in the stream) and three cross-sections (10, 30, and 50 m downstream from the top of the reach) were conducted. A 300-particle "pebble count" was conducted using a random walk along equally spaced transects throughout the reach, where the intermediate axis of each sediment grain was measured; a single observer was used for all of the pebble counts to eliminate inter-observer error [54]. For all instream wood (with any part of log within the bankfull edge) with a diameter >0.05 m and length >1 m, the diameter, length, and longitudinal distance of the midpoint from the top of the reach were recorded. Additionally, whether the log had signs of being chewed by beaver or cut by people (using saws) was determined.

We calculated 29 metrics, in total, from the field data collected, and reduced them to 14, following [22], by removing collinear variables ($\varrho > 0.7$) *within* each of the five dimensions of complexity, keeping those that correlated most with the first two axes of a principal components analysis (PCA) that included all of the 29 metrics (see Table 1 for a list of the 14 metrics). In our study, we further reduced the 14 metrics from [22] to 12 by removing variables that were collinear *among* the five dimensions ($\varrho > 0.7$). The two variables we removed were the longitudinal profile variable "Thalweg Sinuosity" and the planform variable, the coefficient of variation of stream widths "Width CV". These were correlated with each other ($\varrho = 0.69$), and were both correlated with the sediment grain size variable "Sediment Heterogeneity" (SedHetX in our study, "Het2" in [22]; $\varrho > 0.7$; see Appendix A for full correlation matrix).

2.3. Site Characteristics

In addition to the geomorphic complexity metrics, we also retrieved information on catchment area, latitude, longitude, and average channel depth and slope from [22]. We further measured distance from stream edge to nearest logging activities in the field. Based on 50 m digital elevation models in the ArcHydro package of ArcMap 10, we determined elevation above sea level, calculated drainage areas, and quantified the distance from the stream reach to the nearest upstream lake, which has been associated with the propensity of ice formation in these streams [55]. Additionally, we quantified leaf area index (LAI) as a measure of canopy closure and shading, using three hemispherical photos taken from the center of the stream reach with a digital camera (Nikon Coolpix 4500, Nikon, Tokyo, Japan) equipped with a fisheye lens (FC-E8, Nikon, Tokyo, Japan) and analyzed using Gap Light Analyzer v. 2 software (Millbrook, New York, NY, USA). Finally, we collected stream water samples from each reach in August 2011 and 2012, which were frozen for later analysis of water quality parameters, including concentrations of total N, NH_4^+, $NO_2^- + NO_3^-$, ultraviolet absorbance (which correlates with water color and dissolved organic carbon, DOC; [56]) at the certified laboratories of the Department of Aquatic Sciences and Assessment, Swedish University of Agricultural Sciences, Uppsala (see [12] for details). We used an average value for each site between the two years for our subsequent statistical analyses.

Table 1. Descriptions of the 14 geomorphic complexity metrics retained after tests of collinearity of the 29 original metrics in Polvi et al. [22]. Names of complexity metrics and their codes (abbreviations) were changed from the original paper to be more accessible to a wider audience. The original codes are shown in parentheses below our codes to enable comparison with [22].

Complexity Dimension	Complexity Metric	Code (Polvi et al. 2014)	Technical Description	Ecological Description	Change with Increased Complexity
Sediment size	Sediment heterogeneity extremes	SedHetX (Het1&Het2)	Spread in lower portion of sediment size distribution—highly correlated in this study with spread in higher portion of sediment size distribution (Het2), thus renamed to reflect both extremes	Lower values = higher variation in smaller or larger sediment sizes	−
	Sediment sorting	SedSD (Sort)	Standard deviation of sediment size distribution	Higher values = more variation in sediment sizes	+
	Sediment peakedness	SedPeak (Kurt)	Measure of peakedness (kurtosis) of sediment size distribution	Lower values = larger spread in sediment sizes	−
	Sediment skewness	SedSkew (Skew)	Measure of asymmetry of sediment distribution	Higher values = a larger spread in either larger or smaller sediment sizes	+
Longitudinal profile	Longitudinal depth variation	LongR2 (LP_R2)	Goodness of fit of linear regression to longitudinal thalweg depth profile	Higher values = more step-pools as opposed to consistent rapids	−
	Longitudinal roughness	LongRuff (Rough)	Proportionally weighted deviations in stream bed elevation from that predicted by mean slope	Higher values = more roughness elements or bed form variably	+
	Longitudinal sinuosity	LongSin (Th_P)	Ratio of the curvilinear length of the thalweg to the straight-line distance	Higher values = more complex (sinuous) path of thalweg	+
Cross-section	Cross-section topographic ratio	XSTopo (XS_CT)	Ratio of topographic distance to straight line distance of cross-section	Higher values = more changes in elevation of the channel bed along the cross-section	+
	Depth CV	DepthCV (XS_CV_d)	Coefficient of variation of depths at bankfull at a given cross-section	Higher values = more variation in elevation of the channel bed along the cross-section	+
Planform	Width CV	WidthCV (W_cv)	Coefficient of variation of stream widths	Higher values = larger variation in width	+
	Bank length ratio	BankRatio (Bratio)	Ratio of total bank length to reach length	Higher values = more bends, backwaters and irregularities of the stream edge at bankfull	+
Instream wood	Total wood volume	WoodTot (W_V_tot)	Sum of volume (length * mid-diameter) of instream wood	Higher values = more wood in the stream that affects water flow and substrate for organisms	+
	Percent volume beaver-chewed wood	WoodBeav (W_V_beav)	Percentage of instream wood exhibiting beaver chew by volume	Percent of total wood attributed to beaver activity, more is better	+
	Percent volume sawed wood	WoodSaw (W_V_saw)	Percentage of instream wood exhibiting saw marks by volume	Percent of total wood attributed to restoration efforts or historic forestry, more is better	+

2.4. Biotic Sampling

2.4.1. Macroinvertebrates

We sampled benthic macroinvertebrates between 10 and 14 September 2012 using a Surber sampler. We collected five samples from each reach, ca. 10–15 m apart over the 60 m reach, always from within riffle habitats with a predominantly mixed gravel-cobble substrate. At each sampling point, we agitated the substrate manually to a depth of ~10 cm within a 0.1 m² quadrat for 1 min, with dislodged macroinvertebrates retained in a downstream 0.5 mm net (GB Nets, Cornwall, UK).

We pooled the five subsamples and preserved them in 70% ethanol for later sorting and identification. During sorting, we quantitatively subsampled the pooled samples for each site, with subsamples representing 1/20 of the total sample, progressively sorted until we had picked 400 individuals. We then calculated total richness and abundance for the entire sample based on the percentage of the total sample sorted. We identified the benthic macroinvertebrates to the lowest possible taxonomic level, in most cases, to species or genus, but identified some groups to a higher taxonomic level, e.g., Simuliidae (identified to family) and Chironomidae (identified to subfamily). We used species richness, abundance, and Shannon diversity index in our analyses of biodiversity.

2.4.2. Diatoms and Other Periphyton

We collected benthic algae between 13 and 24 August 2012, according to the European/Swedish standard method (SS–EN 14407; CEN 2004), by scraping biofilm from the upper surface of five cobbles using a toothbrush and metal blade, and then pooling them into one composite sample. To enable a quantitative evaluation of our diatom metrics per unit substrate area, we quantified the scraped area of the cobbles. We measured the surface areas by wrapping aluminum foil around the sampled surface of each cobble, covering the scraped area, and then removing, cutting the foil into stars so that they could be flattened. We scanned the foil "stars" and determined the area using the software ImageJ v. 1.46r (National Institutes of Health, North Bethesda, MD, USA). We stored the periphyton samples in light-blocking bottles preserved with Lugol's iodine solution for transport to the laboratory. Each periphyton sample was divided into two subsamples, one for a quantitative analysis of algal biovolume, and the second for a detailed diatom species analysis.

For the analysis of biovolume, we counted at least 1000 benthic algal units (cells in most cases, colonies or filaments for some taxa) per sample at $100\times$ and $400\times$ magnification under an inverted microscope in a 2 mL Utermöhl chamber. We calculated biovolumes ($\mu m^3/cm^2$) for four broad algal groups—diatoms, green algae, blue green algae, and other algae (mainly red algae) following best-fitting geometric models [57]. Here, we present biovolume results for diatoms, as the other groups did not show any clear responses in our analyses.

For the diatom biodiversity analysis, we treated the samples with H_2O_2, embedded the cleaned frustules in Naphrax, and counted according to the European/Swedish standard method (SS–EN 14407; CEN 2004). We assigned taxa belonging to the *Achnanthidium minutissimum* (Kützing) Czarnecki complex to one of three size groups by mean cell width according to the Swedish standard (SEPA 2007). From the taxonomic data, we calculated two commonly used diatom indexes, the indice de polluo-sensibilité spécifique (IPS—or the specific pollution sensitivity index [58]) and the ACID index [59], as well as Shannon diversity index. We used species richness, biovolume, and Shannon diversity index in our analyses of biodiversity.

2.4.3. Macrophytes

We recorded percent cover of macrophytes (vascular plants and bryophytes combined) from 30 randomized plots (0.25 × 0.25 m), stratified along five transects spaced 10 m apart at each site between 4 and 23 July 2011. We placed plots in only those areas of the streambed that remained wetted at mean water level. We identified vascular plants to species in plots, and bryophytes to the lowest taxonomic level, generally genus, in the laboratory from specimens collected from five cobbles per reach (one per transect) during 13–24 August 2012. We sampled cobbles based on bryophyte presence

in riffles within the main channel at a standard depth of 20–30 cm under the water surface. We also determined the scraped area of the cobbles by the same method as for diatoms. Using a dissecting microscope, we cleaned bryophytes of rocks, dirt, and algae, and sorted them into different petri dishes for each species. We measured the relative abundance of each species sampled by estimating how much each species covered of the petri dish, using abundance categories based on Daubenmire cover classes (Daubenmire 1959). We used these abundance measurements to calculate the Shannon diversity index, whereas we used the abundance of bryophytes in the 30 plots for the analysis of total abundance of macrophytes.

2.5. Data Analysis

We performed all statistical analyses in R [60], unless stated otherwise. To visualize the complexity gradient for the reaches we sampled, we reanalyzed the principle components analysis (PCA) from [22], because we used only 20 of their original 22 sites. Using the set of 14 metrics from [22], we ran a PCA to determine the location of reaches in complexity metric space. We then plotted complexity metrics as vectors on the PCA biplot to show magnitude and direction of each complexity metric, thus showing the relationship of these metrics to the different restoration statuses. We performed and plotted the PCA using the *factoextra* package [61].

Prior to analyzing relationships between geomorphic complexity and diversity, we first tested for differences among the categories of restoration status, as has been standard in previous restoration assessments. We used linear mixed-effect models (LMM) in the *lme4* package [62] to test the effect of "restoration status" (five categories: channelized, old basic restoration, new basic restoration, enhanced restoration, reference) for all complexity metrics, site characteristics (e.g., N of stream water, drainage area, distance to lake), as well as species richness, Shannon index, and abundance of the three organism groups. Since the enhanced restoration sites were located about 1 km downstream of the 10-year-old sites, we included stream identity as a random factor to control for within stream variation (also done in [12] for these study streams). We tested the significance of the fixed factor (restoration status) by likelihood ratio tests of the models with and without restoration status included. To detect differences in the complexity metrics and site characteristics among the restoration statuses, we performed pairwise comparisons among the least-square means using *lsmeans* package [63]. This is equivalent to Tukey's honest significant difference test, but for LMMs. We tested all metrics for normality and transformed them using either log or power transformations, if needed, to meet this assumption for data analysis.

To better determine the relative importance of the different continuous metrics of geomorphic complexity influencing species richness, diversity, and abundance of each of the organism groups measured, we ran multiple regression analyses using the *step* procedure in the *lmerTest* package [64]. *lmerTest* performs backward elimination of non-significant effects, starting from the random effects based on a likelihood ratio test. The random effect of stream identity did not explain variation in any of the models, thus, we used ordinary least squares (OLS) multiple regression analysis (lm) with the *step* procedure, which is based on the AIC value (Akaike's information criterion). We then plotted the most important metric explaining the variation in species richness, diversity, or abundance as determined by the multiple regression analysis.

To assess how geomorphic complexity relates to the community composition of our three different organism groups, we first used nonmetric multidimensional scaling ordination (NMDS) to summarize patterns in the community composition of each organism group. We then used the *metaMDS* function in the *vegan* package [65] to perform the NMDS ordination. Prior to analysis, we log ($x + 1$) transformed abundance data for macroinvertebrate species and arcsine square root-transformed diatom biovolume to reduce the influence of numerically dominant species and to better approximate multivariate normality. We used Bray–Curtis distances to project the species composition data onto ordination space. We converted macrophyte abundance data to presence-absence because protocols for measuring abundance of bryophytes and vascular plants at the species level differed. Since they were presence–absence data, we used Raup–Crick distances to project macrophyte composition data

in the NMDS, as they are often more robust to changes in α diversity for presence-absence data [66]. To determine which continuous geomorphic complexity metrics correlated most with the community composition of the three organism groups, we used the function *envfit* in the *vegan* package [65] to provide correlation coefficients and *p*-values for each of the metrics with the composition data. We used biplots to show the relationships of species composition with the complexity metrics.

To determine the statistical differences of our restoration statuses in NMDS space, we conducted permutational multivariate analyses of variance (PERMANOVA) for each organism group using the *adonis* function in the *vegan* package [65]. When significant differences were found, we used *pairwise.adonis* [67] to determine which restoration statuses were most associated with differences among groups. Finally, we used SIMPER (similarity percentage) in PAST [68] as a simple method for assessing which taxa are primarily responsible for differences between groups of samples [69].

3. Results

3.1. Geomorphic Complexity

Our PCA analysis of geomorphic complexity metrics explained 30.2% of the variation on axis 1% and 13.8% of the variation on axis 2 (Figure 2). PCA1 describes a gradient of increasing geomorphic complexity of the stream channel, while PCA2 is associated with large-scale, landscape factors that constrain the potential complexity of a local stream reach. Groupings of our sample reaches according to restoration status are also evident in the ordination space. Unchannelized reference reaches generally lacked complexity in the longitudinal depth profile (abbreviated as LongR2), whereas variability in other metrics created a gradient of higher complexity with increasing restoration effort (Figure 2). These metrics were a sediment size heterogeneity metric, SedHetX; a planform metric, the CV of channel widths (WidthCV); two longitudinal profile metrics, thalweg sinuosity (ThalSin) and longitudinal roughness (LongRuf) that describe the variation in the stream depth along the longitudinal profile; and finally, the total volume of instream wood (WoodTot; Figure 2). As mentioned in the methods, it was also clear that thalweg sinuosity and width CV were intercorrelated and were both negatively correlated with the grain size metric SedHetX (Figure 2, Appendix A).

Many of the differences in geomorphic complexity found among the different restoration statuses of the streams depended on the extra restoration effort undertaken in enhanced-restored sites, while best-practice-restored sites typically had some intermediate level of complexity between channelized and enhanced-restored sites (Table 2, Figure 2). Enhanced-restored sites had a greater overall variation in sediment sizes (SedSD) than channelized sites (Table 2; $\chi^2 = 9.48$, $p = 0.050$). The enhanced-restored sites were more complex than the channelized sites for two longitudinal profile metrics, longitudinal roughness (LongRuf; Table 2; $\chi^2 = 18.57$, $p = 0.001$), and thalweg sinuosity (ThalSin; Table 2; $\chi^2 = 13.36$, $p = 0.010$). The CV of stream widths was more complex for enhanced-restored sites than for sites restored 25 years ago (WidthCV; Table 2; $\chi^2 = 12.83$, $p = 0.012$), and the total volume of instream wood was greater at enhanced-restored sites than channelized sites (WoodTot; Table 2; $\chi^2 = 17.37$, $p = 0.002$). Unchannelized references and enhanced-restored sites both had a wider distribution of sediment sizes (SedHetX) than channelized sites (Table 2; $\chi^2 = 14.92$, $p = 0.005$). Unchannelized reference sites drove the differences for the longitudinal profile metrics, with significantly less variation in the stream depth along the longitudinal profile (LongR2) occurring at unchannelized reference sites than either enhanced or 10-year-old restored sites (Table 2; $\chi^2 = 11.44$, $p = 0.034$). Note that the underlying reasons for the similarity of LongR2 between unchannelized and channelized streams differed; shallow cascade steps characterized some of the unchannelized sites whereas plane beds characterized the channelized sites. Both these cases resulted in low variation in depth along the longitudinal profile. In contrast, a series of larger step-pools (usually not channel-spanning) in the restored sites increased the variation in stream depth along the longitudinal profile (LongR2), particularly in the enhanced and 10-year-old restored sites. By contrast, the channelized sites drove the differences found among restoration statuses in the skewness of the sediment size distribution (SedSkew; Table 2; $\chi^2 = 10.49$, $p = 0.033$). No other geomorphic complexity metrics differed among stream categories (all others $\chi^2 < 8.66$, $p > 0.05$; Table 2).
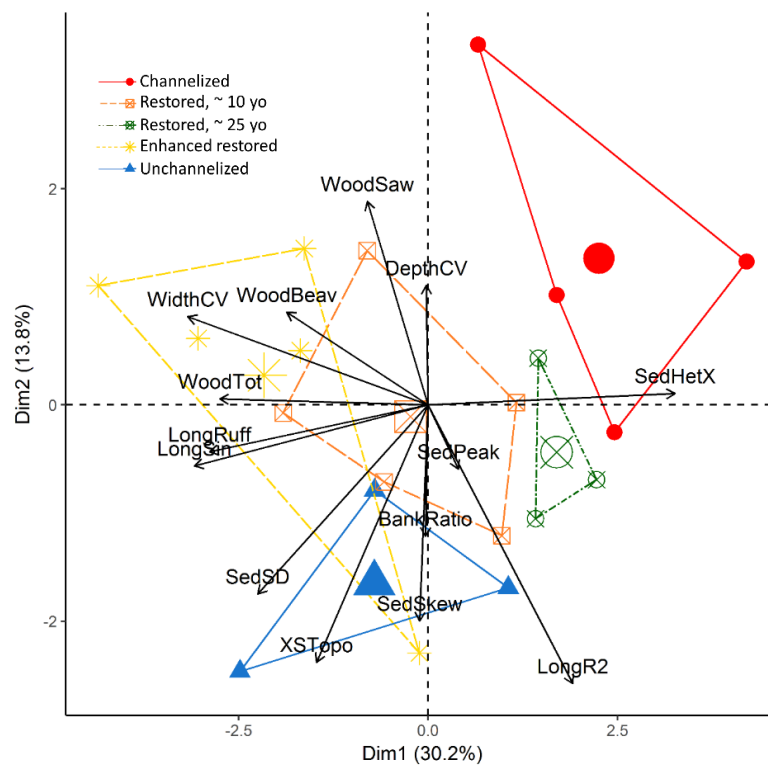
Figure 2. First two dimensions (Dim) of the PCA ordination of a reduced set of complexity metrics (14) with the percent of the variation they described in parentheses. Each point represents a single reach and different symbols show the restoration status of a given reach. We have delineated the extent of the range in variation for each status with different line patterns and colors that match the color of the points. The oversized symbol marks the average position of the sites of a given status in ordination space. Arrows show strength and direction of geomorphic complexity metrics as they relate to the sites.

3.2. Other Stream Reach Characteristics

As with the geomorphic complexity metrics, unchannelized reference streams generally drove differences seen in site characteristics (Appendix B). For channel slope, unchannelized reaches were steeper than both channelized reaches and reaches restored 10 years ago (χ^2 = 16.59, *p* = 0.002; Appendix B). LAI was at least 60% higher in unchannelized reaches than in channelized reaches and the younger restored reaches (χ^2 = 19.70, *p* = 0.001; Appendix B). Reaches restored 25 years ago did not have higher LAIs than 10-year-old reaches, but had higher LAIs than enhanced-restored or channelized reaches (Appendix B). DOC, as measured by absorbance, of the stream water was 52% higher in unchannelized streams than in enhanced-restored streams (χ^2 = 12.12, *p* = 0.016; Appendix B). The only site characteristic that did not connect to differences driven by unchannelized reference sites was the concentration of ammonium (NH_4^+); NH_4^+ concentrations in 25-year-old restored sites were twice as strong as NH_4^+ in channelized reaches (χ^2 = 12.22, *p* = 0.016; Appendix B). All other measured site characteristics did not differ among restoration categories (all χ^2 < 8.93, all *p* > 0.05; Appendix B).

3.3. Diversity and Community Composition of Three Organism Groups

3.3.1. Macroinvertebrates

There was no significant difference among restoration statuses in the diversity or abundance of macroinvertebrates (χ^2 < 1.869, all *p* > 0.760; Appendix C). In contrast, several aspects of macroinvertebrate diversity varied with different geomorphic complexity metrics.

Table 2. Differences in geomorphic complexity among restoration statuses based on results of linear mixed-effect models (LMM). Differences among the restoration statuses were determined using pairwise comparisons among the least-square means, and equivalent test to Tukey's honest significant difference test, but for LMMs. Means and standard errors are reported; letters denote significant pairwise differences, values that share <u>a</u> letter are not different from each other.

Complexity Dimension	Complexity Metrics	Code	Change with ↑ Complexity	Reference Unchannelized	Control Channelized	Enhanced 2-Year-Old	Best-Practice 10-Year-Old	Best-Practice 5-Year-Old	χ^2	p
Sediment size	Sediment heterogeneity	SedHetX	−	0.059 ± 0.041 [b]	0.302 ± 0.032 [a]	0.078 ± 0.036 [b]	0.164 ± 0.054 [a,b]	0.200 ± 0.071 [a,b]	14.92	**0.005**
	Sediment sorting (m)	SedSD	+	266.08 ± 87.95 [a,b]	139.00 ± 27.88 [a]	280.30 ± 28.79 [b]	219.00 ± 17.54 [a,b]	173.63 ± 26.13 [a,b]	9.479	**0.050**
	Sediment peakedness	SedPeak	−	1.042 ± 0.021	1.090 ± 0.052	1.138 ± 0.054	1.500 ± 0.206	1.194 ± 0.017	8.663	0.070
	Sediment skewness	SedSkew	+	0.392 ± 0.008 [a,b]	0.316 ± 0.070 [b]	0.387 ± 0.027 [a,b]	0.477 ± 0.0341 [a]	0.408 ± 0.016 [a,b]	10.49	**0.033**
Longitudinal profile	Longitudinal depth variation *	LongR2	−	0.947 0.014 [a]	0.705 0.202 [a,b]	0.750 0.070 [b]	0.696 0.110 [b]	0.924 0.018 [a,b]	10.44	**0.034**
	Longitudinal roughness (m) [†]	LongRuff	+	0.106 ± 0.013 [a,b]	0.059 ± 0.013 [b]	0.142 ± 0.005 [a]	0.098 ± 0.018 [a,b]	0.068 ± 0.004 [b]	18.57	**0.001**
	Longitudinal sinuosity	LongSin	+	1.063 ± 0.012 [a,b]	1.026 ± 0.004 [b]	1.063 ± 0.011 [a]	1.043 ± 0.010 [a,b]	1.023 ± 0.009 [b]	13.36	**0.010**
Cross-section	Cross-section topographic ratio	XSTopo	+	1.192 ± 0.030	1.097 ± 0.030	1.158 ± 0.030	1.187 ± 0.034	1.107 ± 0.035	4.613	0.329
	Depth CV	DepthCV	+	0.511 ± 0.049	0.575 ± 0.051	0.567 ± 0.036	0.621 ± 0.045	0.523 ± 0.096	2.316	0.678
Planform	Width CV	WidthCV	+	0.169 ± 0.030 [a,b]	0.123 ± 0.010 [a,b]	0.199 ± 0.034 [a]	0.146 ± 0.024 [a,b]	0.081 ± 0.004 [b]	12.83	**0.012**
	Bank length ratio	BankRatio	+	1.399 ± 0.290	1.037 ± 0.013	1.121 ± 0.040	1.073 ± 0.025	1.041 ± 0.018	6.488	0.166
Instream wood	Total wood volume (m³) [†]	WoodTot	+	0.823 ± 0.415 [a,b]	0.088 ± 0.081 [b]	1.790 ± 0.414 [a]	0.604 ± 0.245 [a,b]	0.873 ± 0.170 [a,b]	17.37	**0.002**
	Percent beaver wood (%)	WoodBeav	+	0.000 ± 0.000	13.70 ± 13.70	24.72 ± 15.30	14.88 ± 14.88	0.000 ± 0.000	2.668	0.615
	Percent sawed wood (%)	WoodSaw	+	5.97 ± 5.97	25.38 ± 24.87	31.13 ± 16.37	18.23 ± 17.09	15.09 ± 14.85	1.321	0.858
	N			3	4	5	5	3		

Notes: * power-transformed variable, [†] $\log_{10}$-transformed variable.

Macroinvertebrate species richness increased with sediment heterogeneity (SedHetX; Table 3; Figure 3a) and percentage of instream wood attributed to beavers (WoodBeav), but decreased with increasing total instream wood volume (WoodTot; Table 3). The Shannon index, on the other hand, was negatively related to a larger scale geomorphic variable, namely, the formation of steps and pools as described by the variation in the stream depth along the longitudinal profile (LongR2; Table 3; Figure 3d), but positively to the percentage of instream wood attributed to beavers (Table 3). Macroinvertebrate abundance was explained by four different complexity metrics. Macroinvertebrate abundance was related positively to sediment size heterogeneity (SedHetX; Table 3; Figure 3g), as well as the changes in elevation of the channel bed along the cross-section (XSTopo) and percentage of saw-cut instream wood (WoodSaw; Table 3), but was negatively related to a different microhabitat descriptor, the standard deviation of sediment sizes (SedSD).

Benthic macroinvertebrate community composition did not differ according to restoration statuses (PERMANOVA; $F_{(4,19)} = 1.22$, $p = 0.188$; Figure 4a). However, different aspects of geomorphic complexity were still important for describing patterns in community composition (Figure 4a). Sediment heterogeneity (SedHetX), longitudinal depth variation (LongR2), and the percentage of saw-cut instream wood (WoodSaw) were all significantly correlated with the first and second axes of the NMDS ordination (Figure 4a, $\alpha < 0.1$). Another sediment size variable, the standard deviation of sediment sizes (SedSD), was correlated with the third NMDS axis ($\alpha < 0.05$). Twenty-two taxa contributed to 50% of the dissimilarity among the restoration status (SIMPER analyses, Appendix D). The five most important species contributing to restoration status-associated dissimilarity included *Pisidium* spp., *Hydropsyche siltalai*, *Ephemerella* spp., *Elmis aenea*, and *Heptagenia sulphurea* (Appendix D). *Pisidium* spp. and *Hydropsyche siltalai* accounted for a combined 6.3% of the cumulative dissimilarity among restoration statuses and are both of the functional feeding group "collector-filterer". They occurred in the highest abundance at all three types of restored sites (Appendix D). *Ephemerella* spp. are collector-gatherers that accounted for 2.8% of the dissimilarity among restoration statuses and occurred in the highest abundance at channelized sites (Appendix D). *Elmis aenea* and *Heptagenia sulphurea* accounted for 2.7% and 2.5% of the cumulative dissimilarity, respectively, among restoration statuses, and both belong to the functional feeding group "scraper". *E. aenea* had the highest abundance in reference sites, while *H. sulphurea* occurred in the highest abundance at all three types of restored sites (Appendix D).

3.3.2. Diatoms

Restoration status did not affect the diversity or abundance of diatoms ($\chi^2 < 5.528$, all $p > 0.237$, Appendix C), rather, a combination of geomorphic complexity variables was able to explain the variation in diatom diversity indices. Diatom species richness related to only one geomorphic complexity metric; it increased with increasing heterogeneity of sediment sizes (SedHetX; Table 3; Figure 3b). One complexity metric also described the Shannon index for diatoms, with increasing diatom diversity coupled to decreasing asymmetry of the sediment size distribution (SedSkew; Table 3; Figure 3e). Diatom biovolume decreased with higher heterogeneity of sediment sizes (SedHetX; Table 3; Figure 3h) and the CV of stream depths along the cross-sections (DepthCV); and increased with the total volume of instream wood (WoodTot; Table 3).

Diatom assemblages at channelized sites differed from most restoration categories, except for some overlap with enhanced-restored sites, with this result near significance at the 5% level (PERMANOVA; $F_{(4,19)} = 1.357$, $p = 0.052$). Furthermore, the diatom community at best-practice sites restored 25 years ago was different from all other categories except unchannelized reference sites ($\alpha = 0.1$; Table 4; Figure 4b). Supporting the differences in community composition of diatoms between restoration status and similar to NMDS results for the macroinvertebrates, the heterogeneity of sediment grain sizes (SedHetX) and the variation in the stream depth along the longitudinal profile (LongR2), both correlated with the first and second axes of the NMDS ordination (Figure 4b, $\alpha < 0.05$). No other geomorphic complexity metrics correlated with the NMDS ordination. Eighteen taxa contributed to 50% of the dissimilarity among sites (SIMPER, Appendix E).

Table 3. Summary of the multiple linear regression analyses used to explain patterns of species richness, Shannon diversity index, and abundance of macroinvertebrates, diatoms, and macrophytes along 20 stream reaches with varying geomorphic complexity. We report standard partial regression coefficients for each explanatory variable with the *F*-value, *p*-value, and adjusted R^2 for the full model. Significant *p*-values are in bold (α = 0.05) or in bold italics (α = 0.10). We show only significant contributors to the models. We explain abbreviations for the geomorphic complexity metrics in Table 1. Please note that we have inverted the signs of the relationships with Het2 and LP_R2 here to make interpretation easier, because these metrics become more negative with increased complexity.

| Taxa | Metric | Sediment Size Distribution | | | Longitudinal Profile | | Cross-Section | | Planform | Instream Wood | | | Statistic | | | |
		SedHetX	SedSD	SedSkew	LongR2 *	LongRuff †	XSTopo	DepthCV	BankRatio	WoodTot †	WoodBeav	WoodSaw	F	R^2	p	df
Macroinvertebrates	Species richness †	0.45								−0.48	0.47		3.47	0.28	**0.041**	3.16
	Shannon index				−0.51						0.40		2.65	0.15	*0.099*	2.17
	Abundance †	0.65	−0.40				0.30					0.44	5.77	0.50	**0.005**	4.15
Diatoms	Species richness †	0.48											5.33	0.19	**0.033**	1.18
	Shannon index			−0.46									4.78	0.21	**0.042**	1.18
	Biovolume ‡	−0.71						−0.44		0.57			4.69	0.37	**0.016**	3.16
Macrophytes	Species richness	−0.39		−0.42	0.68		0.63						11.94	0.70	**<0.001**	4.15
	Shannon index		0.73		1.12	0.70			0.41			−0.60	5.28	0.53	**0.006**	5.14
	Percent cover †		−0.46				0.56						3.45	0.20	*0.055*	2.17

Notes: * power-transformed variable, † log$_{10}$-transformed variable, ‡ rank-transformed variable, average of bryophyte and vascular plant indices.
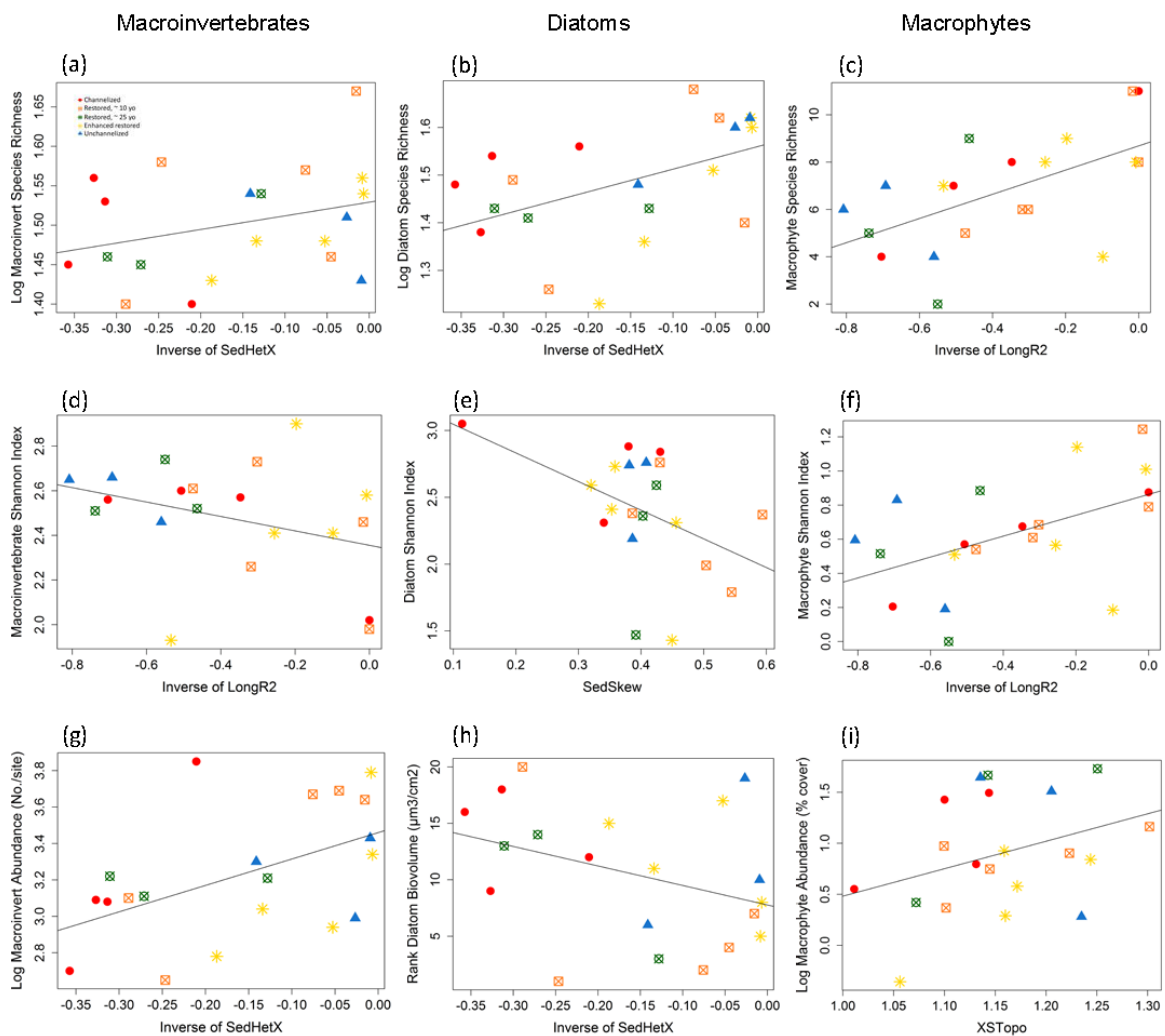
Figure 3. Linear regressions of the most important geomorphic complexity metrics explaining variation in species richness (top row), Shannon diversity index (middle row), and abundance (bottom row) of macroinvertebrates (left column), diatoms (middle column), and macrophytes (right column). Geomorphic complexity always increases from left to right on the x-axis; because SedHetX and LongR2 become more complex at lower values, these values are inverted here to make interpretation easier. Different symbols and colors represent each restoration status. LongR2 was power transformed before analysis, other axes describe transformations of data (typically log). See Table 1 for explanations of complexity codes.

The five most important species contributing to the dissimilarity among statuses were *Achnanthidium minutissimum* group 2 (mean width 2.2–2.8 μm) that accounted for 5.8% of the difference among restoration status, *Tabellaria flocculosa* that accounted for 4.7% of the difference, *Brachysira brebissonii* for 4.4%, *Eunotia incisa* var. *incise* for 3.5%, and *Fragilaria gracilis* that accounted for 3.3% of the difference among restoration status. The proportion of taxa identified as *A. minutissimum* group 2 was lowest in the channelized sites, whereas the proportion of *T. flocculosa* was lowest in reference and the 25-year-old sites. *B. brebissonii* had the lowest proportions at enhanced-restored and 10-year-old sites. *E. incisa* var. *incise* had the highest proportion at reference sites, while *F. gracilis* had the lowest proportion at the 25-year-old sites (Appendix E).
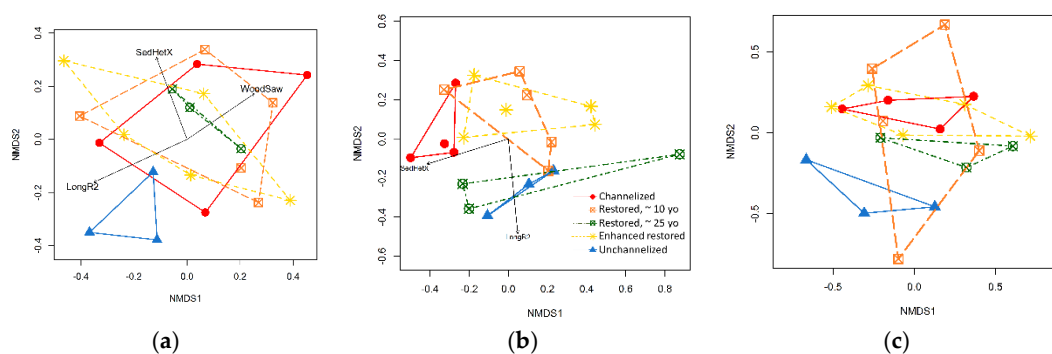
Figure 4. Axes 1 and 2 of NMDS ordinations for assemblages of macroinvertebrates (**a**), diatoms (**b**), and macrophytes (**c**) for all sites (*n* = 20). Analyses were based on Bray–Curtis dissimilarity index on transformed abundance data for macroinvertebrates and diatoms, and Raup–Crick dissimilarity index on presence–absence data for macrophytes. Each point represents the community composition of a different site. We have delineated the extent of the range in variation for each status with different line colors that match the color of the points. Arrows show strength and direction of significant correlations of geomorphic complexity variables with the ordination space (LongR^2 = variation in longitudinal profile, SedHetX = variation in smaller and larger—extreme—sediment sizes, WoodSaw = volume of instream wood cut by a saw). There were no significant correlations of geomorphic complexity with macrophytes.

3.3.3. Macrophytes

Macrophyte cover was the only variable that differed among the restoration statuses; enhanced-restored sites had 46% less cover of macrophytes than the 10-year-old sites (Appendix C; χ^2 = 13.02, *p* = 0.011). However, neither macrophyte species richness nor Shannon index differed overall among restoration status (Appendix C; χ^2 < 2.369, *p* > 0.668).

The species richness model included four geomorphic complexity metrics (Table 3). Species richness of macrophytes decreased with increasing heterogeneity of sediment sizes (SedHetX) and with less asymmetry of the sediment size distribution (SedSkew), but increased with more variation in the reach-scale variation in stream depth along the longitudinal profile (LongR2; Figure 3c) and with changes in elevation of the channel bed along the cross-section (XSTopo). Shannon diversity of macrophytes was positively related to four of the five complexity metrics in the multiple regression equation explaining its variation (Table 3): The standard deviation in sediment sizes (SedSD), two metrics that describe variation in the reach-scale complexity, namely, stream depth along the longitudinal profile (LongR2, Figure 3f, and LongRuff), and the number of small bends and irregularities of the stream edge (BankRatio). The volume of saw-cut wood (WoodSaw) was the only significant variable that was negatively associated (Table 3). The equation describing variation in macrophyte abundance (percent cover) was less complicated and did not include reach-scale metrics (Table 3), with a negative relationship with the overall standard deviation in sediment sizes (SedSD) and a positive relationship with changes in elevation of the channel bed along the cross-section (XSTopo, Figure 3i).

Table 4. Results of PERMANOVA for pairwise comparisons to test for differences in diatom community composition among streams that were unchannelized (U), channelized (Chan), restored using enhanced (E) techniques 2 years ago, restored using best-practice techniques about 10 years ago (10yo) or about 25 years ago (25yo). Significant *p*-values are in bold ($\alpha = 0.05$) or in bold italics ($\alpha = 0.10$).

	Diatoms			
Status	**U**	**Chan**	**E**	**10yo**
Chan	**0.034**			
E	0.272	0.127		
10yo	0.292	*0.060*	0.924	
25yo	0.400	*0.055*	*0.053*	*0.094*

Macrophyte community composition did not differ among the restoration status categories (PERMANOVA; $F_{(4,19)} = 0.969$, $p = 0.537$; Figure 4c). Surprisingly, the community composition of macrophytes did not correlate with any of our geomorphic complexity metrics (Figure 4c), as we hypothesized that reach-scale factors would affect macrophytes. Seven taxa contributed to just over 50% of the dissimilarity among sites (SIMPER, Appendix F). The five most important species contributing to any minor difference among statuswere *Schistidium* spp., *Utricularia intermedia, Myriophyllum alterniflorum, Fontinalis dalecarlica,* and *Sparganium natans* (Appendix F). *Schistidium* spp. are short turf mosses that accounted for 8.6% of the variation among restoration statuses; they did not occur at any of the 25-year-old restoration sites. *U. intermedia* is a submerged, insectivorous vascular plant that accounted for 8.3% of the variation among restoration statuses and did not occur at the reference sites. *M. alterniflorum* is a submerged vascular plant that accounted for 7.9% of the variation among restoration statuses, and occurred at a higher frequency at the 25-year-old restored sites. *F. dalecarlica* is a moss with long floating stems (streamer). It accounted for 7.7% of the variation among restoration statuses and did not occur at any of the enhanced-restoration sites, but all the reference sites. Finally, *S. natans* is a submerged vascular plant that accounted for 7.6% of the variation among restoration status. It occurred most often in reference sites, and least often in the 25-year-old sites (Appendix F).

4. Discussion

Our analyses of the responses of three organism groups to multiple geomorphic complexity metrics along a gradient of restoration effort demonstrate the potential for learning from previous restoration programs to aid goal setting and refinement in future restoration projects. Our three organism groups responded to geomorphic complexity in different ways, seemingly reflecting their taxon-specific habitat preferences at the spatial scale captured by our geomorphic complexity metrics. In some cases, these responses were in line with the restoration effort, whereby restoration succeeded in altering aspects of geomorphic complexity likely to have positive outcomes for some biota. For example, restoration generally increased sediment heterogeneity, which is associated with positive outcomes for macroinvertebrates and diatoms, indicating the value of focusing on this parameter in future restoration projects. In other cases, exemplified by the relationship between macrophytes and depth variation, the relationship between geomorphic complexity and biodiversity did not track restoration effort, pointing towards the types of additional restoration measures which might be undertaken, in future, to benefit a wider range of organism groups. Since our analyses were based on multiple individual restoration projects, we can make some generalizable recommendations for restoration practice. In common with the investigation of [70]—this issue—our results highlight the benefit of designing restoration evaluation programs that move beyond the assessment of before/after changes or comparison among restoration categories to take a more holistic perspective.

4.1. Macroinvertebrates

As hypothesized, macroinvertebrate species richness and abundance responded positively to metrics that described the heterogeneity in microhabitats, i.e., variation in smaller sediment sizes and instream wood attributed to beavers. Unexpectedly, we also saw negative associations with the spatial arrangement of those sediments, namely, the variation in depths along the longitudinal profile. Community composition of macroinvertebrates also varied with these three metrics. The positive relationship between benthic macroinvertebrate richness and abundance and variation in sediment size heterogeneity is encouraging, given the pervasiveness of restoration projects targeting the configuration of instream habitats. Such relationships have not always been apparent in previous restoration assessments [25,38,71], but our findings are similar to those of [17], analyzing the outcomes of multiple restoration projects at a European scale. Verdonschot et al. [17] found that positive macroinvertebrate responses to restoration were most likely to occur in projects that successfully addressed the diversity and patchiness of microhabitats, specifically, with changes in the cover of cobbles, sand, and especially coarse particulate organic matter in restored sections. In our assessment, the specific metric most strongly associated with macroinvertebrate responses was variation in extreme grain sizes. Variation of extreme sediment grain sizes is likely important for specific life stages of macroinvertebrates (e.g., larger grain sizes are potentially important for adult insects needing to oviposit on stable, partially exposed substrates [72]), as well as for providing refugia from high flood events [6,7]. Greater variation in grain size is also likely to contribute to greater variation in near-bed flow dynamics, and may enhance entrapment of different sizes of organic particulate detritus and favor greater variability in autotrophic resources, opening up niche space and feeding opportunities for a wider variety of species [10,12]. Indeed, a previous European-scale assessment based on analysis of stable isotopes found evidence that the breadth of resources consumed by macroinvertebrates increased following restoration [73].

Kail et al. [30] pointed out the importance of sediment size for invertebrates, as opposed to other dimensions of geomorphic complexity, and found that a variety of instream restoration measures, such as placement of large wood or creation of riffles, had a higher mean response ratio for macroinvertebrates compared to planform measures, such as remeandering or river widening. We also did not find any planform measures that affected macroinvertebrates, and agree with [30] that instream measures appear most capable of rapidly increasing substrate diversity, which in turn may increase macroinvertebrate diversity if source populations are able to reach the restored reaches. In contrast, planform measures, such as widening and remeandering primarily elongate the river reach and promote future, long-term recruitment of sediments, but do not necessarily increase substrate diversity, at least in the short term [30].

The negative relationship between the longitudinal variation in depth and macroinvertebrate Shannon diversity appeared driven by the most recently restored sites, which were characterized by the most variation in stream depths in this complexity dimension. This might reflect a time-lag in recovery of macroinvertebrates following the physical disturbance associated with restoration activities, e.g., inputs of large substrate, disturbance of microhabitats including macrophytes [26,30]. Even though the enhanced restoration sites had the most wood, the negative relationship between *total* volume of instream wood and macroinvertebrate richness likely reflects disturbance from recent enhanced-restoration activities.

Interestingly, higher percentages of beaver-chewed wood seemed to favor macroinvertebrate richness and diversity, whereas saw-cut wood favored increased macroinvertebrate abundance. Earlier studies found that beavers reduce taxonomic richness of macroinvertebrates [74] or have no effect [75], though a recent meta-analysis found an overall positive effect of beaver dams on macroinvertebrate diversity [76]. The wood in our reaches was not associated with dam building but rather was associated either with recent beaver tree felling, or was saw-cut wood left over from conifers felled during the timber-floating era [77]. Beaver-chewed wood was more likely to be visible on the surface of the substrates, whilst the saw cut timber had long-since sunk to the bottom of the streams, and was at least

partially buried in the substrates. It is likely that positive relationships between macroinvertebrates and beaver and old timber-floated wood result from the effects of both wood types altering stream hydraulics and habitat formation, changing habitat configurations and even generating new types of habitats. These effects are also likely to favor greater macroinvertebrate taxonomic richness and diversity [78], as well as favor accumulation of organic matter, important as a basal resource for many macroinvertebrates [79].

Our multivariate analyses did not detect marked, consistent differences in community composition among restoration status, which is partly attributable to the low replication of each category. Nevertheless, abundances of some key organisms tended to differ among status, and these responses are worthy of further investigation in future research. Restoration overall tended to favor filter feeders, *Pisidium* spp. and *Hydropsyche siltalai*, suggesting that aspects of the environment at the channelized sites may be too harsh for these species. Channelized systems lack larger rock and wood structures which might moderate water currents during high flow events, which might disturb the construction of filtering nets in the case of *H. siltalai*. Pilotto et al. [26] also found that *Pisidium* spp., in particular, were favored by the enhanced restored sites, with this effect having strengthened with time since restoration. In all the restored sites, but especially the enhanced restored sites, species of shredders and scrapers were more abundant. The abundance of shredders and scrapers suggests that these sites are more favorable for species that feed on coarse organic matter or graze algae and other organic matter that is attached to rocks and plants, and may relate to the increased retention of organic matter in restored sites [12,45,80]. Frainer et al. [12] found, in their analysis of detritivore species, that species with flow and substrate preferences favored by restoration had strong shredding feeding traits associated with more efficient leaf consumption. Furthermore, scrapers also increased in Finnish streams after a similar type of restoration [81]. Of the 22 species that made up 50% of the cumulative dissimilarity among restoration statuses, more than half of them were either very rare or extremely abundant at reference sites. This underscores the difference in community composition between reference and channelized sites, or previously channelized (and then restored) sites seen in the NMDS plot that likely represents differences in natural potential complexity.

4.2. Diatoms

Our hypothesis that diatoms would respond to metrics that affect sediment size distribution (related to stability of sediments and scouring by fine sediments [35]) was supported by the finding that sediment size heterogeneity was positively related to diatom species richness. This likely relates to both potential for scouring (presence of fines) as well as flow conditions, because addition of large boulders increases roughness which increases variation in flow velocities [46]. The negative association between variation in depths along the cross-section and diatom biovolume might reflect the increase in channel length consisting of sites with more deeper, depositional areas which are also darker (especially in the DOC rich waters of northern Sweden), and thus offer worse growing conditions for diatoms overall. An added complication is that increased grazer abundance found on substrates that are more complex could indirectly reduce or change the effect of geomorphic complexity on diatoms [10].

Among our three organism groups, diatoms showed the clearest differences in community composition among restoration status, despite the low replication of each restoration status. Partly, this reflected responses of fast colonizing species. *A. minutissimum* was the most abundant diatom and most important in contributing to differences among restoration status. *A. minutissimum* is often the first species to pioneer a recently scoured site, often dominates later due to its fast growth [82] and appears to be resistant to physical disturbances [83]. By contrast, *T. flocculosa* was the most abundant in the enhanced-restored sites and least abundant in the 25-year-old best practice sites. *T. flocculosa* has been shown previously to prefer physically disturbed sites in a lake [84], thus, there is good support that the change in *T. flocculosa* abundance indicates more disturbance from enhanced restoration measures compared with best practice techniques and/or the recovery of the restored sites with time. It could also be that differences in LAI among restoration statuses—with more light available

in channelized and enhanced-restored sites than in reference and 25-year-old sites—caused these differences in *T. flocculosa*. Differences in *E. incisa* var. *incisa* abundance are probably best explained by disturbance dissimilarities, as *E. incisa* is a late colonizer and, accordingly, was most abundant in the reference sites that had never been disturbed. Grazer pressure might also have contributed to the variation in *Fragilaria* spp. abundances. Since *Fragilaria* spp. live in long chains in the streambed sediment, they are vulnerable to grazers. The sum of the three species of *Fragilaria* that contributed to a combined 7.0% of the difference among restoration statuses was lowest in the 25-year-old streams where there were abundant macroinvertebrate grazers.

4.3. Macrophytes

As we hypothesized, variation in macrophyte species richness was best explained by reach-scale geomorphic complexity metrics; both variation in depths along the longitudinal profile and cross-section were significant and positively related to nearly all macrophyte response variables. Previous research on how stream depth affects light availability and water flows supports the positive relationship between macrophyte taxonomic richness and diversity and variation in stream depths [85,86]. In a restoration context, [49] found that restored reaches had higher macrophyte cover, richness, diversity, and number of growth forms compared to unrestored reaches. Furthermore, macrophyte diversity and richness both increased with depth, flow velocity, and substrate [87].

In our case, species richness of macrophytes decreased when variation in sediment sizes increased, unlike [49] and opposite to the pattern of macroinvertebrate and diatom species richness in our study. Although structurally simplified, the stream beds of channelized sites are likely to be more fixed and stable than those of not only the steeper reference sites, but also the newly added substrates of the recently restored enhanced-restoration reaches. Indeed, it is likely that the recent enhanced restoration actions, undertaken two years prior to sampling, entailed substantial physical disturbance of macrophyte beds, which might have contributed to the negative relationship between macrophyte diversity and sediment size variation. Additionally, it is possible restoration of natural fluvial processes of sediment transport have reduced the ability for certain species of macrophytes to establish. Macrophytes can require up to 8 years of recovery time after restoration in northern boreal systems that are often dominated by bryophytes [88,89]. Our sites are similar to these previous assessments, with 83% of our macrophyte cover made up of bryophytes. Additionally, macrophyte community composition did not significantly relate to any of our geomorphic complexity variables, which could be due to the need for more time for recovery. On the other hand, [30] found that macrophyte abundance and diversity was greatest in the youngest river restoration projects and declined over time. Overall, our results demonstrate that while two years post-restoration may be sufficient for assessing recovery of fast growing organisms such as diatoms and macroinvertebrates, at least on a preliminary basis (see [26]), it might be necessary to wait longer to assess macrophyte responses.

As hypothesized, we observed a positive relationship between macrophyte diversity and geomorphic planform metrics indicating a greater availability and complexity (small bends, irregularities) of edge habitat. However, these changes were not in line with restoration effort, with the planform not consistently improved from best practice to enhanced restoration. Kail et al. [30] compared the results of other restoration studies, and found that terrestrial and semi-aquatic organism groups, including floodplain vegetation and ground beetles, as well as macrophytes, benefit most from planform measures, and aquatic groups such as fish and invertebrates, from instream metrics. In our study, macrophytes were the only organism group to respond to a planform metric. Kail et al. [30] suggested that planform measures, such as widening and remeandering, often create terrestrial and semi-aquatic pioneer habitats like bare ground and open gravel bars that can promote macrophytes.

Four of the seven species that contributed to 50% of the dissimilarity among restoration status were species that form long streamers. The other three species, contributing to 50% of the dissimilarity, were liverworts and mosses that grow in short turfs. The long streamers persist over winter [90] and, thus, take years to grow to full length and easily break when driven over by excavators during restoration.

In Finland, the long streamer-forming moss species, *Fontinalis* spp., are sensitive to disturbances such as restoration [88,89], and we found this in our study as well. *F. dalecarlica* occurred at 100% of reference sites, 0% of enhanced-restored sites, 20% of 10-year-old sites, and 33% of 25-year-old sites, indicating that recovery time after disturbance influenced the presence of this species. *Schistidium* spp. was the most important taxon contributing to the variation among restoration statuses; and it seemed to prefer disturbed locations, occupying 80% of enhanced-restored sites and 40% of 10-year-old sites, but not occurring at any of the 25-year-old restored sites. None of our environmental or geomorphic variables could account for this difference based on what is known about the physiology of this genus [91].

4.4. A Gradient in Complexity/Restoration Effort

We found that the older best-practice methods of restoration rarely restored the large-scale features needed to bring the sites towards their full potential of geomorphic complexity. Much of the smaller sediment was washed away after channelization increased flow velocities [22,48]. Additionally, log-floating companies blasted bedrock outcrops and large boulders that were too big to move during the channelization process. Accordingly, both the largest and smallest sediment sizes were missing from the older best-practice restorations [48]. The addition of large boulders and instream wood not only restores large habitat elements, but also can facilitate natural recruitment of smaller sediment sizes. Along with the direct addition of coarse gravel, this contributes to restoration of geomorphic complexity in the enhanced reaches to levels beyond those of older best-practice techniques [53]. Significantly, even though the enhanced restoration sites were the youngest in our study, the restoration techniques applied in these reaches, including addition of big boulders, coarse gravel, and instream wood, increased complexity to a level that elicited responses in the diversity and community composition of our organism groups.

Previous research indicates that more extensive restoration efforts that bring restored reaches closest to reference conditions are more likely to have positive effects on ecosystem functioning [12,73] and food web diversity [92]. Restoration programs can be refined by including measures addressing geomorphic complexity metrics that affect the appropriate scale for the targeted organism group. For example, widening and remeandering alone may not be sufficient for benefiting a broad range of biotic groups, since these activities are unlikely to result in sufficient restoration of microhabitats relevant for organisms operating at smaller scales, e.g., macroinvertebrates and diatoms. [17,87]. On the other hand, widening and remeandering may lead to passive restoration in the long-term by restoring natural floodplain processes. Thus, restoration of complexity needs to find a scale that will prompt a biological response within large-scale landscape constraints (see [22]).

4.5. Implications for Restoration Practice

Based on our findings, we can make concrete recommendations for which attributes to address to improve outcomes of future restorations. For all organism groups, three variables—variation in smaller and larger (extreme) sediment sizes, longitudinal depth variation, and instream wood metrics—were consistently important for explaining the variation in biodiversity and abundance, and correlated most strongly with the community composition of macroinvertebrates and diatoms. Accordingly, we suggest the following when implementing measures for the restoration of geomorphic complexity in degraded streams: (1) variation at both extremes of the sediment size spectrum should be restored, i.e., both fine sand/gravel as well as large boulders are considered. One caveat is that close attention should be made to the historic size distribution of sediments, in order to make appropriate goals for restoration [22]. For example, in our stream systems, knowledge of the surrounding glacial legacy sediment is necessary to better understand the natural limits for restoring large sediment sizes [22]. In contrast, in parts of lowland Europe, where glaciation was less important, restoring boulders of the same size as in Sweden, for example, would not be appropriate given the potential complexity of this system.

Additionally, (2) the longitudinal profile should be configured to achieve more natural variations in channel depth, resulting in variable microhabitats with different depths and water velocities, such

as steps, riffles, and pools. Similar to the above recommendation, the exact morphology of the longitudinal profile should be consistent with the geomorphic constraints. Step-pools are increasingly being used during restoration to reduce the magnitude and frequency of peak discharges, duration and volume of flow, and deal with reduced sediment supplies [40], all of which have implications for instream microhabitats relevant to our three organism groups. However, step-pools form naturally in alluvial streams at steep slopes (4–7%), whereas pool-riffles or plane beds are common at lower slopes; forced steps or pool-riffles can be formed with the use of instream wood, large boulders, or bedrock outcrops [93]. In our stream systems with abundant coarse glacial legacy sediment, non-channel spanning steps form downstream of each boulder and form variation in the longitudinal profile without creating channel-spanning steps of coarse sediment separating discrete pools. Regardless of the morphological configuration of longitudinal variation in the channel, in the form of step-pools, large boulders, or pool-riffles, these features provide variation in water depth in the stream channel that has implications for light attenuation and, therefore, light availability for benthic organisms.

Finally, (3) instream wood should be restored and maintained. In a forested catchment with little human impact, wood recruitment into streams would happen naturally as trees age and die, or as a result of wind, fire, erosion, or beaver activities. However, in the managed forest landscape of Sweden where few trees reach a very advanced age and riparian buffers are small or non-existent, the periodic manual addition of new wood to streams is likely to be required to replace that lost to natural decomposition processes and in-channel movement. There is increasing interest in more broadleaf management near streams and wider riparian buffers [94] but, as of now, there are only non-legally binding guidelines in place in Sweden regarding width of buffers [95]. It is also important that buffers retain conifers, because their wood decomposes very slowly and, thus, creates longer-term structure in streams [96].

These recommendations are most suitable for restoration programs focused on improving diversity of particular organism groups. However, our results also point towards potential tradeoffs in outcomes of particular restoration measures for different aspects of community structure. This is seen most clearly in the contrasting relationships observed between sediment heterogeneity and diatom richness (positive) and biovolume (negative), and the opposite relationships observed between sediment heterogeneity and macroinvertebrate richness (negative) and abundance (positive). These contrasting responses highlight the importance of the clear definition of goals prior to embarking on a restoration program, including whether the focus is on improving diversity rather than abundance, and which taxonomic groups are prioritized. In practice, restoration focused on improving abundance and/or productivity of focal taxa might often involve a tradeoff with diversity, if those taxa come to dominate communities [97]. Such potential tradeoffs highlight ongoing challenges in designing restoration programs to meet multiple restoration goals, and the identification of a set of restoration measures that optimizes improvement in multiple ecological values (biodiversity, productivity, functioning, and keystone species) should be a priority for future investigation.

Appendix A. Correlation Matrix for Geomorphic Complexity Metrics

Table A1. Correlation matrix of the 14 (out of 29) measured geomorphic complexity metrics retained in [22] for all 20 study reaches. We reduced them further to 12 by excluding variables with a Pearson's correlation coefficient >0.7 from further analysis; Th_P and W_cv were removed. Pearson's correlation coefficients >0.7 are in bold.

Complexity Metric	Sediment Distribution				Longitudinal Profile			Cross-Section		Planform		Instream Wood		
	Het2	**Sort**	**Kurt**	**Skew**	**LP_R2**	**Rough**	**Thal_P**	**XS_CT**	**XS_CV_d**	**W_cv**	**Bratio**	**WV_tot**	**WV_beav**	**WV_saw**
Het2	1.00	−0.36	0.13	0.05	0.36	−0.63	**−0.77**	−0.25	0.04	**−0.71**	−0.11	−0.57	−0.29	−0.02
Sort		1.00	−0.03	0.05	0.08	0.69	0.36	0.47	−0.16	0.35	−0.04	0.50	−0.08	0.11
Kurt			1.00	0.38	−0.01	−0.21	0.08	0.10	0.17	−0.02	−0.09	−0.08	−0.25	0.12
Skew				1.00	0.16	−0.01	0.10	0.28	−0.06	−0.08	0.01	0.10	0.22	−0.25
LP_R2					1.00	−0.35	−0.24	0.05	−0.32	−0.50	0.24	−0.29	−0.44	−0.37
Rough						1.00	0.44	0.25	0.03	0.49	0.06	0.51	0.10	0.11
Thal_P							1.00	0.35	−0.20	0.69	0.00	0.51	0.40	0.06
XS_CT								1.00	−0.03	0.18	0.17	0.08	0.30	−0.26
XS_CV_d									1.00	0.04	−0.03	0.13	0.19	−0.28
W_cv										1.00	0.06	0.46	0.45	0.33
Bratio											1.00	−0.01	−0.16	−0.01
WV_tot												1.00	0.30	0.16
WV_beav													1.00	0.02
WV_saw														1.00

Appendix B. Differences for Site Characteristics among the Restoration Statuses

Table A2. Differences for site characteristics among the restoration statuses based on results of linear mixed-effect models (LMM). Differences among the restoration statuses were determined using pairwise comparisons among the least-square means, and equivalent test to Tukey's honest significant difference test, but for LMMs. Means and standard errors are reported; letters denote significant pairwise differences, values that share letters are not different from each other.

Site Characteristics	Reference		Control		Categories of Restored Sites						χ^2	p
	Unchannelized		Channelized		Enhanced 2-Year-Old		Best-Practice 10-Year-Old		Best-Practice 25-Year-Old			
Total N (µg/L)	261.33 ±	25.57	276.38 ±	27.89	259.50 ±	16.50	257.58 ±	16.92	242.50 ±	15.50	2.934	0.569
NH$_4$ (µg/L)	5.033 ±	1.467 [a,b]	4.250 ±	0.595 [b]	5.600 ±	0.332 [a,b]	5.500 ±	0.563 [a,b]	8.500 ±	0.500 [a]	12.22	**0.016**
NO$_3$ (µg/L)	9.500 ±	3.606	6.875 ±	2.511	5.800 ±	2.077	3.917 ±	0.970	3.500 ±	0.500	5.748	0.219
pH	7.197 ±	0.048	7.960 ±	0.557	7.412 ±	0.214	7.632 ±	0.270	7.920 ±	0.840	4.902	0.298
DOC (Absorbance-F4205)	0.143 ±	0.015 [a]	0.093 ±	0.015 [a,b]	0.094 ±	0.011 [b]	0.102 ±	0.011 [a,b]	0.133 ±	0.015 [a,b]	12.12	**0.016**
Drainage area (km^2)	27.12 ±	8.92	128.20 ±	60.24	75.18 ±	24.80	56.55 ±	26.25	37.23 ±	2.96	4.343	0.362
Latitude (DD)	64.85 ±	0.37	65.13 ±	0.13	65.06 ±	0.08	64.99 ±	0.10	64.56 ±	0.03	6.987	0.137
Longitude (DD)	18.76 ±	0.56	18.11 ±	0.09	18.32 ±	0.08	18.37 ±	0.12	18.82 ±	0.11	8.927	0.063
Stream depth (cm)	36.02 ±	5.97	38.38 ±	1.79	38.36 ±	3.94	33.65 ±	3.52	30.33 ±	3.18	3.436	0.488
Stream slope (m/m)	0.037 ±	0.004 [a]	0.008 ±	0.002 [b]	0.020 ±	0.004 [a,b]	0.013 ±	0.004 [b]	0.015 ±	0.007 [a,b]	16.59	**0.002**
Riparian buffer width (m)	70.00 ±	24.02	52.75 ±	22.65	23.88 ±	8.85	24.36 ±	4.71	15.19 ±	7.44	6.499	0.165
Leaf Area Index	1.353 ±	0.194 [a]	0.570 ±	0.131 [c]	0.578 ±	0.112 [c]	0.706 ±	0.110 [b,c]	1.256 ±	0.135 [a,b]	19.70	**0.001**
Distance to lake (km)	1.520 ±	0.427	0.988 ±	0.424	1.000 ±	0.415	0.825 ±	0.426	0.310 ±	0.080	5.262	0.262
N	3		4		5		5		3			

Appendix C. Differences among Restoration Statuses for Species Richness, Shannon Index, and Abundance of the Three Organism Groups

Table A3. Results of linear mixed-effect models (LMM) to determine differences among the different restoration statuses for species richness, Shannon index, and abundance. Differences in the site characteristics among the restoration statuses were determined using pairwise comparisons among the least-square means, and equivalent test to Tukey's honest significant difference test for LMMs. Means and standard errors are reported; letters denote significant pairwise differences, values that share letters are not different from each other.

Taxonomic Group	Metric	Reference Unchannelized			Control Channelized			Enhanced 2-Year-Old			Best-Practice 10-Year-Old			Best-Practice 25-Year-Old			χ^2	p
Macroinvertebrate	Species richness [†]	31.33	±	2.33	30.75	±	2.56	31.60	±	1.69	35.20	±	3.83	30.67	±	2.19	1.369	0.850
	Shannon index	2.59	±	0.06	2.44	±	0.14	2.45	±	0.16	2.41	±	0.13	2.59	±	0.08	1.869	0.760
	Abundance (#) [†]	1890.00	±	501.27	2490.21	±	1522.56	2186.00	±	1027.77	3129.60	±	941.89	1525.33	±	112.96	0.880	0.927
Diatom	Species richness [†]	37.33	±	3.71	31.25	±	2.75	30.80	±	4.81	32.80	±	5.47	26.67	±	0.33	2.769	0.597
	Shannon index	3.70	±	0.27	4.00	±	0.23	3.31	±	0.33	3.26	±	0.24	3.09	±	0.49	5.528	0.237
	Biovolume ($\mu m^3/cm^2$) [‡]	11.67	±	3.84	13.75	±	2.02	11.20	±	2.20	6.80	±	3.46	10.00	±	3.51	3.786	0.436
	IPS index	19.53	±	0.22	19.60	±	0.13	19.68	±	0.09	19.76	±	0.09	19.43	±	0.42	2.228	0.694
	ACID index	5.10	±	0.30	4.53	±	0.26	5.42	±	0.56	5.28	±	0.43	5.10	±	1.10	1.708	0.789
Macrophyte	Species richness	5.67	±	0.88	7.50	±	1.44	7.20	±	0.86	7.20	±	1.07	5.33	±	2.03	2.000	0.736
	Shannon index	0.538	±	0.187	0.581	±	0.140	0.682	±	0.174	0.774	±	0.125	0.467	±	0.257	2.369	0.668
	Percent cover [†]	26.15	±	12.60	16.09	±	7.01	4.31	±	1.50 [b]	7.97	±	2.03 [a]	34.25	±	15.95	13.02	**0.011**
	N		3			4			5			5			3			

Notes: * power-transformed variable, [†] $\log_{10}$-transformed variable, [‡] rank-transformed variable, average of bryophyte and vascular plant indices.

Appendix D. SIMPER Analysis of Benthic Macroinvertebrate Taxa

Table A4. SIMPER analysis of benthic macroinvertebrate taxa primarily responsible for the differences among streams that were unchannelized references (Unchan), channelized (Chan), restored using enhanced (E) techniques 2 years ago, restored using best-practice techniques about 10 years ago (10yo) or about 25 years ago (25yo). Taxa collectively explaining about 50% of the Bray–Curtis dissimilarity among sites are listed with their percentage contribution to total dissimilarity and mean abundance for each restoration status. Additionally, functional feeding group (FFG) and taxonomic affinity are listed (C, Coleoptera; D, Diptera; E, Ephemeroptera; O, Oligochaeta; P, Plecoptera; T, Trichoptera; V, Veneroida).

Taxon	FFG	Taxonomic Affinity	Average Dissimilarity	% Contribution	Cumulative %	Mean Abundance for Restoration Statuses				
						Unchan	Chan	E	10yo	25yo
Pisidium spp.	Collector-filterer	V	1.43	3.22	3.22	91.70	99.60	247.00	472.00	256.00
Hydropsyche siltalai	Collector-filterer	T	1.35	3.04	6.26	0.83	30.20	478.00	201.00	100.00
Ephemerella spp.	Collector-gatherer	E	1.26	2.84	9.09	38.30	148.00	71.00	31.40	1.33
Elmis aenea	Scraper	C	1.20	2.70	11.79	331.00	4.92	6.40	40.80	1.33
Heptagenia sulphurea	Scraper	E	1.10	2.48	14.28	10.00	14.50	86.40	44.60	68.00
Leptophlebia sp.	Gatherer	E	1.09	2.46	16.73	0.83	27.50	16.10	44.00	25.30
Neureclipsis bimaculata	Predator	T	1.07	2.41	19.14	0.00	243.00	3.50	124.00	1.33
Hydropsyche pellucidula	Collector-filterer	T	1.06	2.38	21.53	0.00	79.50	39.80	19.60	9.33
Protonemura meyeri	Shredder	P	1.03	2.33	23.86	103.00	3.33	10.00	5.20	47.30
Amphinemura borealis	Shredder	P	1.03	2.32	26.18	40.00	3.75	34.80	11.00	9.33
Polycentropus flavomaculatus	Predator	T	1.00	2.27	28.44	0.00	39.60	5.10	73.00	25.30
Nemoura flexuosa	Shredder	P	1.00	2.26	30.71	31.70	0.83	12.60	4.80	20.00
Leuctra digitata/hippopus	Shredder	P	0.99	2.23	32.93	55.80	32.90	36.00	39.60	3.33
Tanytarsini	Collector-gatherer	D	0.95	2.13	35.07	93.30	864.00	173.00	904.00	175.00
Taeniopteryx nebulosa	Shredder	P	0.94	2.12	37.19	18.30	24.30	10.00	8.00	0.00
Lepidostoma hirtum	Shredder	T	0.91	2.06	39.25	5.83	4.17	10.70	7.00	31.30
Oligochaeta	Collector-gatherer	O	0.88	1.98	41.23	12.50	111.00	21.10	12.00	10.70
Ceratopogonidae	Predator	D	0.87	1.97	43.20	20.00	1.46	14.90	20.40	10.70
Heptagenia dalecarlica	Scrapers	E	0.87	1.97	45.17	0.00	21.70	13.40	5.40	0.00
Isoperla sp.	Predator	P	0.86	1.93	47.10	11.70	12.80	29.40	19.20	14.00
Nigrobaetis niger	Scraper	E	0.84	1.90	48.99	77.50	51.10	30.10	31.40	107.00
Nigrobaetis digitatus	Scraper	E	0.84	1.89	50.88	5.00	6.88	10.20	77.00	0.00

Appendix E. SIMPER Analysis of Diatom Taxa

Table A5. SIMPER analysis of diatom taxa primarily responsible for the differences among streams that were unchannelized reference (Unchan), channelized (Chan), restored using enhanced (E) techniques 2 years ago, restored using best-practice techniques about 10 years ago (10yo) or about 25 years ago (25yo). Taxa collectively explaining about 50% of the Bray–Curtis dissimilarity among sites are listed with their percentage contribution to total dissimilarity and mean proportion (* 100 to get a percent) for each restoration status.

Taxon	Code	Ph *	Moisture †	Current ‡	Life Form	Average Dissimilarity	% Contribution	Cumulative %	Unchan	Chan	E	10yo	25yo
Achnanthidium minutissimum group 2	AMIN	3	3	1	2	3.13	5.82	5.82	22.90	12.20	32.10	32.60	33.20
Tabellaria flocculosa	TFLO	2	1	1	1	2.50	4.65	10.46	1.71	8.37	14.30	10.30	0.64
Brachysira brebissonii	BBRE	2	2	0	0	2.39	4.44	14.90	5.32	8.09	1.24	0.53	13.20
Eunotia incisa var. *incisa*	EINC	2	1	0	0	1.87	3.48	18.38	12.90	5.29	6.35	3.68	6.64
Fragilaria gracilis	FGRA	3	0	0	0	1.76	3.27	21.65	7.61	3.66	8.23	5.99	1.29
Frustulia crassinervia	FCRS	1	2	0	0	1.72	3.20	24.84	0.63	8.81	1.94	2.34	1.92
Rossithidium pusillum	RPUS	3	1	0	2	1.37	2.55	27.40	5.23	1.53	1.03	1.39	2.24
Encyonopsis subminuta	ESUM	3	0	0	0	1.34	2.48	29.88	0.08	4.46	0.80	2.19	0.00
Eunotia implicata	EIMP	2	2	0	0	1.34	2.48	32.36	4.30	4.02	2.72	3.50	4.47
Brachysira neoexilis	BNEO	2	1	0	0	1.32	2.44	34.81	7.69	6.36	7.70	10.80	2.56
Gomphonema exilissimum	GEXL	3	2	0	0	1.10	2.05	36.86	2.95	0.82	0.71	0.48	1.52
Peronia fibula	PFIB	2	1	0	2	1.10	2.05	38.90	0.00	2.33	1.71	0.34	0.32
Eunotia faba	EFAB	2	0	0	0	1.10	2.04	40.95	1.37	2.48	1.56	0.48	0.64
Eunotia minor	EMIN	2	2	1	2	1.10	2.04	42.98	1.16	1.54	0.33	1.06	4.32
Achnanthes linearioides	ALIO	3	0	0	0	1.07	2.00	44.98	0.32	2.25	2.00	0.72	0.08
Fragilaria nanoides	FNNO	3	0	0	0	1.02	1.90	46.88	0.62	1.35	1.13	1.50	0.00
Fragilaria capucina group 3	FCA3	3	1	1	1	0.99	1.83	48.71	4.40	0.00	0.41	0.56	0.00
Encyonema neogracile var. *neogracile*	ENNG	2	1	1	3	0.98	1.82	50.53	0.94	2.11	1.95	2.09	0.80

Notes: 0 = not classified for every category; * pH preferences from van Dam (1994): 1 = acidobiontic, 2 = acidophilous, 3 = circumneutral; † moisture preferences from van Dam (1994) and Denys (1991): 1 = only wet, 2 = on wet and moist, 3 = can withstand dry places; ‡ current preference from Denys (1991): 1 = indifferent; life form from Denys (1991): 1 = tychoplanktonic, epontic origin (free floating on channel bottom), 2 = epontic (attached to a surface), 3 = epontic and benthic (attached to a surface and/or living on the channel bottom).

Appendix F. SIMPER Analysis of Macrophyte Taxa

Table A6. SIMPER analysis of macrophyte taxa primarily responsible for the differences among streams that were unchannelized references (Unchan), channelized (C), restored using enhanced (E) techniques 2 years ago, restored using best-practice techniques about 10 years ago (10yo) or about 25 years ago (25yo). Taxa collectively explaining about 50% of the Bray–Curtis dissimilarity among sites are listed with their percentage contribution to total dissimilarity and mean abundance for each restoration status. Life form classifications are based on Mägdefrau (1982) and Glime (1968) for bryophytes and Bowden et al. (2006) for vascular plants.

Taxon	Taxonomic Affinity	Life Form	Average Dissimilarity	% Contribution	Cumulative %	Mean Percent of Sites Occupied				
						Unchan	Chan	E	10yo	25yo
Schistidium spp.	moss	short turf	4.29	8.55	8.55	66.7	75.0	80.0	40.0	0.0
Utricularia intermedia	forb	submerged plant	4.14	8.26	16.81	0.0	100.0	60.0	80.0	66.7
Myriophyllum alterniflorum	forb	submerged plant	3.97	7.92	24.73	33.3	50.0	40.0	20.0	66.7
Fontinalis dalecarlica	moss	streamer	3.84	7.67	32.40	100.0	25.0	0.0	20.0	33.3
Sparganium natans	forb	submerged plant	3.81	7.60	40.00	66.7	50.0	40.0	40.0	33.3
Jungermanniaceae	liverwort	short turf	3.35	6.69	46.69	100.0	75.0	60.0	80.0	66.7
Fissidens spp.	moss	short turf	3.35	6.67	53.36	33.3	25.0	40.0	40.0	33.3

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