

Assessing Stream Ecosystem Rehabilitation: Limitations of Community Structure Data

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Abstract

Inappropriate land use practices, pollutants, exploitation, and overpopulation have simplified stream habitats and degraded water quality worldwide. Management agencies are now being tasked to ameliorate impacts and restore stream "health," yet there is a dearth of rigorous scientific methods and theory on which to base sound restoration design and monitoring. Despite this, many localized restoration projects are being constructed to stabilize erosion and enhance habitat heterogeneity in streams. Many restoration attempts adopt the paradigm that increasing habitat heterogeneity will lead to restoration of biotic diversity, yet there have been few studies that have manipulated *variation* of a physical parameter independent of the mean to isolate the effects of heterogeneity *per se*. We conducted a field experiment to mimic restoration of habitat heterogeneity in a shallow, stony stream. By using an experimental approach rather than a detailed assessment of existing restoration work, we were able to control the starting condi-

tions of replicate riffles so that organism responses could be unambiguously attributed to the heterogeneity treatments. We successfully manipulated the *variability* of streambed particle sizes and consequently near-bed flow characteristics of entire riffles. These factors define axes of habitat heterogeneity at scales relevant to the resident macroinvertebrate fauna. Despite this, we were unable to distinguish differences in community structure between high and low habitat heterogeneity treatments. Power analysis indicated that macroinvertebrate populations were more sensitive to individual site conditions at each riffle than to the heterogeneity treatments, suggesting that increasing habitat heterogeneity may be an ineffective technique if the restoration goals are to promote macroinvertebrate recovery in denuded streams. With extremely high variability between replicate riffles, monitoring programs for localized restoration projects or point source impacts are unlikely to detect gradual shifts in community structure until the differences between the reference and treatment sites are extreme. Innovative measurement of other parameters, such as ecosystem function variables (e.g., production, respiration, decomposition), may be more appropriate indicators of change at local scales.

Key words: ecosystem rehabilitation, assessing restoration, environmental variability, heterogeneity, monitoring, ecosystem function, community structure.

Introduction

Human activities that directly or indirectly influence running-water ecosystems have been identified as one of the greatest threats to freshwater resources (Allan & Flecker 1993; Naiman et al. 1995). Stream ecosystems are increasingly being subjected to perturbations that result in severe habitat degradation, impairment of water quality, and loss of biodiversity (Gleick 1998; Sala et al. 2000; Vorosmarty et al. 2000). Human impacts on running-water systems are the result of activities on both large and small scales. Certainly, when a dam is built or a river diverted, the entire watershed may be impacted (Boon 1988). However, a substantial fraction of human impacts on fluvial systems also results from numerous small-scale or localized perturbations.

The environmental impacts of localized perturbations to running-water systems may be more subtle than for large-scale disturbances; however, there is increasing recognition that the cumulative effect of these "subtle" impacts may be considerable (Lake et al. 2000; Sala et al. 2000). For example, localized construction projects and road crossings may decrease water quality or otherwise directly modify short lengths of streams,

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which can have cascading effects downstream. Sediment deposition from eroding banks is a very common localized disturbance that leads to homogenization of particle sizes on the streambed, usually toward finer and more compact sediments (Waters 1995). Such streambed simplification and compaction can have negative impacts on benthic biota and fish at fairly broad scales (Williams 1980; Ryan 1991; Davies & Nelson 1994; USACE 2000).

Because streams and rivers are so important economically and ecologically, restoration of fluvial ecosystems is receiving a lot of attention (Angermeier et al. 1991; Cairns 1995; Gore & Shields 1995; Karr & Chu 1999). Many restoration efforts are focused on responding to the increasingly common small-scale perturbations. For example, agencies are attempting to repair localized problems such as fish blockages, eroding banks, and failed stormwater outfalls (e.g., FISRWG 1998; USACE 2000). Management agencies and concerned citizen groups readily identify such problems, and solutions seem tractable (Kondolf 1995). Thus, stream restoration efforts often concentrate on a discrete river reach or segment to repair localized problems even when larger-scale issues may be pertinent (Ziemer 1997).

Currently, an implicit assumption of many stream restoration projects is that maximizing physical habitat diversity leads to system restoration (Osborne et al. 1993; Gore et al. 1995; Gore & Shields 1995; Muhar et al. 1995; Stanford et al. 1996). At larger scales, habitat restorations often involve realignment of channel cross-sections and/or construction of in-stream structures to increase habitat heterogeneity for biota (Nickelson et al. 1992; Rabeni & Jacobson 1993; Gore et al. 1995; Rosgen 1996; USACE 2000). Local projects often involve manipulation of physical structures such as bed materials or woody debris (Hilderbrand et al. 1997; FISRWG 1998; Riley 1998; Boward et al. 1999). To evaluate the success of such habitat "improvements" the focus is most often on assessing the response of one or a few species of fish (Nickelson et al. 1992; Rabeni & Jacobson 1993; Kondolf & Micheli 1995). The effects of small-scale restoration efforts on biota other than fish (e.g., invertebrates) have received very little attention despite the fact that benthic invertebrates are extremely numerous, may respond more rapidly to environmental degradation than fish (i.e., are early-warning indicators), serve as prey to support the fish populations, and may influence rates of important key ecological processes (Rosenberg & Resh 1993; Loeb & Spacie 1994; Palmer et al. 1997a). Certainly, there is substantial literature on invertebrate biomonitoring that is directly relevant to efforts to use invertebrates in restoration assessments (e.g., Rosenberg & Resh 1993; Loeb & Spacie 1994; Norris 1995; Karr & Chu 1999), and there is increasing interest in broadening our approaches to assessing restoration of

aquatic ecosystems (e.g., Moy & Levin 1991; Mitsch & Wilson 1996).

Our goal was to investigate whether stream restoration efforts designed to enhance physical habitat heterogeneity at localized scales led to enhanced recovery of stream invertebrates. Controlled experiments were designed to mimic small-scale restoration of streambed heterogeneity in a shallow, stony stream in the Chesapeake Bay watershed (U.S.A.). We imposed identical streambed disturbances on multiple riffles in our study stream and then restored the heterogeneity of streambed substrates in each riffle to a level either below the natural (undisturbed) system or to a level of heterogeneity above the natural system. We tested the hypothesis that increasing the physical streambed heterogeneity at small scales (e.g., in single replicate riffles) led to faster recovery and/or higher species richness of invertebrates. We also examined whether flow was an important mediator of invertebrate recovery. We chose an experimental approach so that we could control the starting conditions of replicate sites. This allowed us to attribute organism responses unambiguously to the heterogeneity treatments, something that is not possible at existing restoration projects where state agencies typically have employed many different technologies and strategies simultaneously.

Methods

Study Site

Milltown Creek is low-gradient (1:125) Piedmont stream in northern Virginia (lat 39°14' N, long 77°36' W) that drains into the Catoctin River, a tributary of the Potomac River, which drains into the Chesapeake Bay. The experimental site is a third-order river segment approximately 1-km long exhibiting a distinct pattern of alternating riffles (depth 5–10 cm) and pools (depth <80 cm). The channel in the experimental section ranged from 2–5 m wide and was dominated by coarse gravels (median particle size ≈ 55 mm, with some boulders ≥250 mm in diameter). The riparian zone is predominantly intact and is dominated by *Platanus occidentalis* (sycamore), *Acer negundo* (box elder), *Celtis occidentalis* (hackberry), *Betula nigra* (river birch), *Liriodendron tulipifera* (tulip poplar), and the introduced *Rosa multiflora* (multiflora rose). Our experiment was performed in the late summer of 1998 (July–August) during a period of three months without significant rainfall that provided relatively constant but declining baseflow (Fig. 1).

Experimental Design

We manipulated habitat heterogeneity by altering the variability of streambed particle sizes (hereafter termed

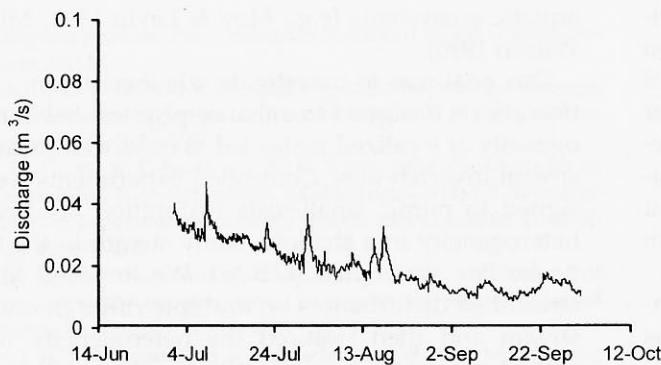


Figure 1. Discharge at the study site in Milltown Creek. The experiment began on 6 July and was terminated mid-September. A change in discharge from 0.02 to $0.04 \text{ m}^3/\text{s}^{-1}$ $\approx 5 \text{ cm}$ change in depth.

heterogeneity) in entire riffles. Replicate riffles were manipulated into "high" or "low" heterogeneity treatments, and the invertebrate assemblages were sampled over time. The design is a single-factor repeated-measures analysis of variance (ANOVA) with two levels of heterogeneity and repeatedly measured dependent variables (Neter et al. 1990).

Habitat heterogeneity was defined by the particle size ratio d_{84}/d_{50} (Wiberg & Smith 1991), where d_i represents the particle size larger than i percent of particles in the riffle and therefore d_{50} is the median particle size (Hey & Thorne 1983). This heterogeneity metric (one of many possible metrics) provides a simple measure of architectural habitat variability (i.e., structure) at scales relevant to aquatic organisms (Minshall 1984; Downes et al. 1998). In addition, the large d_{84} particles set up complex hydraulic environments in the riffles that also influence the distribution and abundance of aquatic fauna. (Davis 1986; Statzner et al. 1988; Hart & Finelli 1999). We selected eight treatment riffles that were separated by approximately 50 m and one or more pools greater than 50 cm deep. Four treatment riffles were randomly assigned to high heterogeneity (HH) treatments ($d_{84}/d_{50} = 2.5$), and the remaining four were assigned low heterogeneity (LH) treatments ($d_{84}/d_{50} = 1.5$). This range represented the maximum contrast that we could attain using existing bed materials. One of the low-heterogeneity riffles (riffle 17) was later excluded from the experiment because our manipulation of streambed heterogeneity did not remain intact throughout the study. This riffle had a higher proportion of fine sediments that skewed the median particle size so low that our final heterogeneity (d_{84}/d_{50}) had increased to an unacceptable 1.9 (target = 1.5) by day 32.

Prior to the manipulation of streambed heterogeneity (on 16 July 1998), we simulated a disturbance of equal magnitude on each of the treatment riffles. This distur-

bance was meant to mimic the impacts of local construction projects by killing fauna and disrupting the streambed. Applying an equivalent disturbance to all riffles minimized potential differences among treatments so results could be attributed to treatment effects rather than differences in initial conditions. Starting from the upstream end of the site, in each treatment riffle every particle larger than 5 cm diameter was removed from the streambed, scrubbed clean, and piled on the bank. The streambed was then disturbed to a depth of approximately 10 cm by teams of 10–12 students/riffle who repeatedly kicked, scrubbed, and raked the stream bottom with feet, brooms, and metal rakes for approximately 30 minutes.

Immediately after the disturbance, the streambed was reconstructed by hand to the assigned heterogeneity level for each riffle. Heterogeneity, as defined by d_{84}/d_{50} , was measured in the field by recording the second axis diameter of 100 or more randomly selected particles from each riffle (Wolman 1954). Particle heterogeneity for each treatment riffle was measured and re-manipulated until the desired parameter values were reached. High heterogeneity riffles were littered with boulders and cobble clusters (>250 mm diameter) interspersed with finer gravels. These large particles constituted only 12% of the particle count (Fig. 2) but exerted a disproportionate impact on flow due to their large size penetrating higher into the water column. Low heterogeneity riffles were dominated by particle diameters between 40 and 80 mm giving them a distinctly flat,

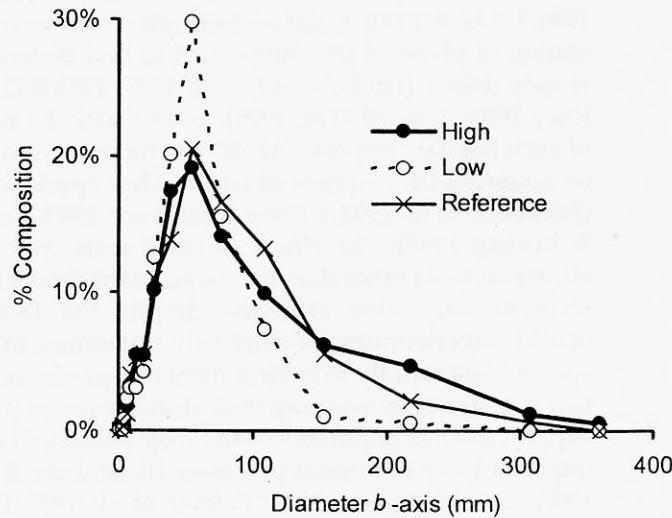


Figure 2. Frequency distribution of streambed particles in high-heterogeneity riffles (solid line), low-heterogeneity riffles (dotted line) and reference riffles (broken line) as a percentage of all particles measured ($n > 300$, 100+ stones per riffle). Trend lines are presented to clarify interpretation; percent composition is only valid for marked points.

"paved" appearance typical of heavily impacted streams in the region. Median particle size (d_{50}) was compared between treatments using a two-tailed *t*-test, whereas the d_{84}/d_{50} ratio was compared between treatments using one-tailed *t*-tests (due to the *a priori* expectation that HH > LH).

Three "reference" riffles were located upstream of the eight treatment riffles to protect them from suspended material generated by the disturbance of the treatment riffles. Reference riffles were not intended to serve as controls *per se* for the treatment manipulations, but rather as reference sites for assessing whether ambient abiotic conditions and rates of ecological processes in our treatments were within the realm of what occurs naturally in this stream system (Power et al. 1998).

Streambed Hydraulics

A depth transducer was installed to monitor fluctuations in discharge throughout the experiment. There were no major rainfall events for the duration of the experiment, and discharge remained relatively constant with a gradual decline throughout the summer (Fig. 1). The last bed-mobilizing flood prior to our experiment occurred in the previous January.

The flow field in each treatment and reference riffle was quantified 16–19 days after the manipulation (1–3 August) using an acoustic Doppler velocimeter (ADV) (10-MHz ADV, Sontek/YSI, Inc. San Diego, CA) at 20 randomly selected coordinates in each riffle. The ADV was mounted on a camera tripod and positioned to locate the 8-mm high \times 9-mm diameter sampling cell within 1–2 mm of the streambed. The dimensions of the sampling cell size were determined using the methods of Finelli et al. (1999). When acoustic reflection from the streambed prevented data collection at the prescribed location (30% of readings), the ADV was moved haphazardly within a 30-cm radius until a reliable reading could be collected. We could not identify a consistent streambed geometry that distinguished acoustically poor coordinates from good ones, and that indicated our sampling protocol was biased against certain habitat types. At each coordinate, three-dimensional velocity was recorded at 25 Hz for two minutes (yielding a temporal sequence of 3,000 data points at each coordinate). Prior work indicated that two minutes was required to characterize turbulence within 5% of the true mean calculated from a longer time series (20 minutes). For each of the 20 sampling points in each riffle we computed the mean velocity (independent of direction) by

$$\bar{q} = \frac{\sum_{i=1}^n \sqrt{u_i^2 + v_i^2 + w_i^2}}{n}$$

(where u , v , and w are the three orthogonal velocity vectors measured by the ADV for $n = 3000$ readings per time series). Turbulent kinetic energy was calculated using the equation

$$TKE = \frac{1}{2}\rho(u'^2 + v'^2 + w'^2)$$

where u' , v' , w' are RMS deviations from the respective means and ρ = density of water (Bradshaw 1971). For each replicate riffle we used the 20 subsamples to calculate the riffle mean and standard deviation (spatial variability) for velocity and turbulence. Differences in these flow parameters among treatments were identified using one-way ANOVA.

Macroinvertebrate Sampling

Macroinvertebrates were sampled in all riffles prior to the streambed manipulation and again on days 1, 19, 39, and 62. Previous studies have demonstrated that invertebrates have the capacity to recover from localized physical disturbance and floods within 30 days (review by Mackay 1992). We sampled for 62 days to capture a possible slowdown of recovery in our reduced heterogeneity treatments. The experiment terminated after 62 days. Subsequent rain resulted in sediment transport that broke down the treatments. Four replicate samples were collected from random locations in each riffle using a 50 \times 50-cm Surber sampler fitted with a 250- μ m mesh net (this large Surber sampler was necessary so that all particles in the high heterogeneity treatments could be sampled with equal probability). The four Surber samples were combined in a container and diluted to 10 L in the field. Four, 0.5-L-subsamples were collected while the container was vigorously mixed; they were then pooled to yield a 20% subsample that was preserved in 5% formaldehyde. Invertebrates were later extracted and identified to genus where possible. Chironomidae, Oligochaeta, and Nematoda were identified only to family or major taxa. Invertebrates were assigned to functional feeding groups and functional life-history mode using Merritt and Cummins (1978). Shannon Diversity and Evenness, Species Richness, EPT taxa (the number of Ephemeroptera, Plecoptera, and Trichoptera taxa) and the number of EPT individuals were calculated. These indices are commonly used in stream biomonitoring to summarize overall community structure and to discriminate between impacted and reference sites (Plafkin et al. 1989; Wright et al. 1989; Reynoldson et al. 1995; Parsons & Norris 1996; Karr & Chu 1999).

Statistical Analysis

Riffles were our unit of replication and thus particle heterogeneity (d_{84}/d_{50}), riffle mean flow (velocity, tur-

bulence), and spatial variability in flow were compared between LH riffles and HH riffles using one-way analyses of variance (ANOVA).

Common taxa were defined as those exceeding 1% of the total count per sample in at least two replicate riffles on at least two sampling dates. A two-factor ANOVA (time \times treatment) was used to test whether the initial riffle disturbance and manipulation successfully reduced invertebrate abundances to similar densities in both treatments. Repeated-measures ANOVA were used to detect differences in the total number of invertebrates, taxonomic richness, diversity (Shannon), EPT, functional groupings, and abundances of each of the common taxa between treatments (SAS Institute Inc. 1996). Abundance data were $\log_{10}(x + 1)$ when required to reduce heterogeneity of variances.

Spatial and temporal patterns in community structure were examined using multidimensional scaling ordination (MDS) to identify changes in invertebrate assemblage structure as indicated by a Bray-Curtis similarity index (Minchin 1987; Clarke & Warwick 1994). We performed global nonmetric multidimensional scaling (NMDS) using 20 random starting configurations using DECODA, version 2.04 (Minchin 1991). Procrustean analysis was applied to statistically compare all minimum stress configurations to ensure that the solution used was a "common" solution and not a rare artifact of a particular random starting configuration (Minchin 1991). Abundance data were rescaled to range between 0 and 1 across all samples to emphasize changes in species composition without going to the extreme of weighting all species equally (e.g., presence-absence data, correspondence analysis). Ninety-five percent confidence ellipses were used to clarify the distribution of sample points belonging to each group on the ordination diagram.

Results

Our initial disturbance and riffle construction significantly reduced invertebrate abundances by 67% in both HH and LH riffles ($F_{1,10} = 15.3, p = 0.003$), but invertebrate abundances and species richness did not differ between treatments ($F_{1,10} = 2.2, p = 0.165$ and $F_{1,10} = 1.122, p = 0.314$, respectively) setting the stage for us to monitor the influence of streambed heterogeneity on recovery from the same starting point. We successfully created riffles with contrasting particle size and flow heterogeneity in seven of our eight treatment riffles in Milltown Creek (Table 1; Fig. 2). The flow environment also differed significantly between our heterogeneity treatments (Fig. 3). Near-bed velocities in high heterogeneity riffles were significantly higher ($p < 0.01$, Fig. 3a) and the velocity fields significantly more variably distributed in space ($p < 0.03$, Fig. 3b) than in low heterogeneity riffles. Spatial variability is defined here as the

Table 1. Grain size distributions on day 20 of the experiment. d_{84}/d_{50} is geomorphic heterogeneity; d_{84} is the diameter at which 84% of the particles are smaller, and it is used to represent the size of commonly occurring large particles; d_{16} is used to represent the size of commonly occurring small particles; d_{50} is the median particle size.

Treatment	d_{84}	d_{50}	d_{16}	d_{84}/d_{50}
Reference	106 \pm 5	53 \pm 3	21 \pm 4	2.0 \pm 0.1
Low	74.5 \pm 7	48 \pm 5	26 \pm 5.5	1.5 \pm 0.5
High	118 \pm 2	51 \pm 4	21 \pm 3	2.4 \pm 0.2

per-riffle standard deviation of the 20 subsamples from the individual riffle mean. Figure 3b and 3d depict the average (\pm SE) standard deviation for all replicate riffles. Turbulent energy and the spatial variability of turbulence were almost three times higher in high heterogeneity riffles.

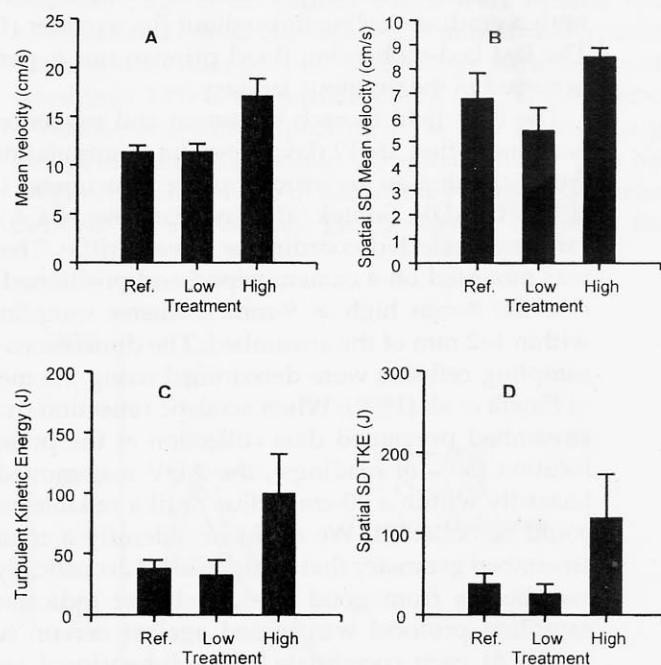


Figure 3. Mean (\pm SE) velocity (a), mean spatial variation in mean velocity (b), mean turbulent kinetic energy (c), and spatial variation in turbulence (d). ($n = 20$ flow-time series per riffle) among treatments ($n = 4$ HH treatment riffles, $n = 3$ LH treatment riffles). Flow was significantly faster in high-heterogeneity riffles than in low or reference riffles (log transformed, MS = 0.036, $F_{2,7} = 10.26, p < 0.008$). Spatial variability of flow was significantly higher in high-heterogeneity riffles than in low, but did not differ from reference riffles, which were intermediate (log transformed, MS = 0.035, $F_{2,7} = 6.405, p < 0.026$). Spatial variability of turbulence was significantly higher in HH treatment riffles than in LH or reference riffles (log transformed, MS = 0.417, $F_{2,7} = 6.177, p = 0.028$).

geneity riffles than in low heterogeneity or reference riffles ($p < 0.03$, Fig. 3c & 3d).

Despite large differences in both particle size heterogeneity and flow heterogeneity among treatments, not a single taxon of common aquatic invertebrate exhibited a difference in recovery (change in abundance through time) between heterogeneity treatments (Table 2). Similarly, classification of the invertebrate assemblage into functional feeding groups or life-history mode groups failed to identify a single functional grouping that exhibited significant differences in recovery among our treatments (Table 2). Total numbers of invertebrates in HH and LH riffles were similar (within 8%) on each sampling date (Fig. 4). This pattern is driven by three taxa (Chironomidae [midge], *Baetis* [mayfly nymph], and *Stenelmis* [beetle larvae]) that con-

stituted 74% of all invertebrates collected. Colonization rates in both HH and LH riffles were similar, with abundances comparable to those of reference sites being attained in only 19 days (Fig. 4). Taxonomic richness was also similar between treatments, differing by less than 25% at all times (Fig. 4). Analysis of other commonly used community structure measures (Diversity, Evenness, EPT) also failed to reveal any effect of our treatments on temporal recovery patterns (Table 2).

Community composition in HH and LH riffles was indistinguishable using a Bray-Curtis similarity index and MDS ordination (Fig. 5) with the confidence ellipses for the treatments being mostly contained within each other on days 16 and 62. On day 39 there was a distinct separation of the treatment communities in ordination space, but this pattern was not maintained

Table 2. Results from repeated-measures ANOVA on mean riffle community metrics, and abundances of common taxa, feeding groups, and life history groups. Heterogeneity had no significant effect on abundances or on recovery patterns (heterogeneity \times day interaction) for any taxon or functional group.

	Heterogeneity		Day		Heterogeneity*	Day
	F _{1,5}	p	F _{3,15}	p	F _{3,15}	p
Total individuals	0.77	0.422	5.33	0.011	0.45	0.721
Taxa richness	2.11	0.206	3.57	0.040	0.24	0.869
Diversity (Shannon)	0.81	0.410	4.09	0.026	0.55	0.653
Evenness	0.04	0.858	46.05	<0.001	3.19	0.055
EPT (individual)	3.78	0.110	3.27	0.051	0.16	0.919
EPT (taxa)	4.54	0.086	4.04	0.027	0.53	0.668
Common taxa:						
EPHEMEROPTERA						
<i>Stenonema</i>	1.64	0.257	3.61	0.038	0.60	0.628
<i>Stenacron</i>	0.09	0.781	7.00	0.004	1.21	0.339
<i>Baetis</i>	0.09	0.781	4.98	0.014	0.05	0.983
<i>Caenis</i>	2.60	0.168	1.14	0.364	0.17	0.914
PLECOPTERA						
<i>Neoperla</i>	0.25	0.636	5.21	0.012	0.78	0.525
TRICOPTERA						
<i>Cheumatopsyche</i>	1.63	0.258	0.88	0.476	0.11	0.953
<i>Chimarra</i>	1.95	0.222	1.44	0.270	0.32	0.811
COLEOPTERA						
<i>Stenelmis</i>	0.19	0.678	1.70	0.211	0.02	0.996
<i>Psephenus</i>	0.06	0.823	5.92	0.007	0.95	0.443
DIPTERA						
<i>Chironimidae</i>	0.18	0.689	6.56	0.005	0.71	0.561
Feeding groups						
Collector-gatherers	0.16	0.703	6.27	0.006	0.53	0.667
Collector-filterers	2.87	0.151	0.45	0.720	0.21	0.887
Predators	0.74	0.429	4.92	0.014	0.89	0.469
Scrapers	0.28	0.616	1.73	0.204	0.33	0.803
Life history						
Clingers	1.28	0.309	1.12	0.372	0.16	0.919
Climbers	0.34	0.585	4.75	0.016	0.53	0.669
Swimmers	1.24	0.315	3.00	0.064	0.41	0.750
Sprawlers	0.16	0.703	5.95	0.007	0.63	0.605
Burrowers	0.53	0.500	2.28	0.121	1.25	0.325

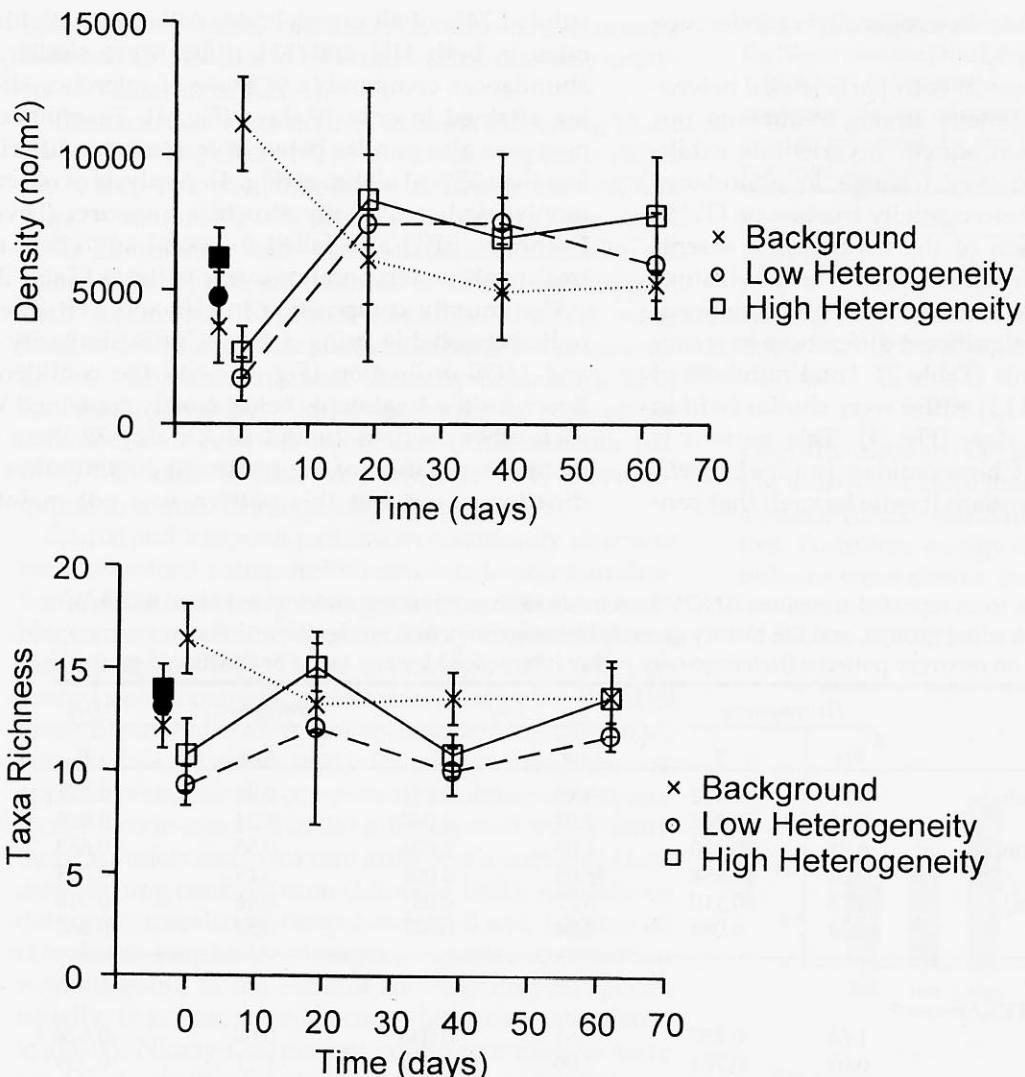


Figure 4. Recovery of taxa richness following the experimental manipulation to construct HH (solid line) and LH (broken line) riffles (Mean \pm SE). Richness at unmanipulated reference sites shown with dotted line. Pre-disturbance densities shown with solid symbols at time 0.

(Fig. 5). This temporary shift in the proportional composition corresponds with a decline in taxa richness on day 39 (Fig. 4). There is some separation of the unmanipulated reference sites from the manipulated riffles (Fig. 5, Day 19) in the ordination at the start of the experiment that decreased as the treatments recovered from the initial disturbance.

Discussion

Loss of habitat heterogeneity is generally considered to be one of the most serious problems threatening the persistence of natural communities (Bell et al. 1991; Pickett et al. 1996; Dobson et al. 1997). This problem is being exacerbated by many human activities that are reducing physical habitat heterogeneity, simplifying natural disturbance regimes, and homogenizing species pools worldwide (Stanford et al. 1996; Daily 1997; Rahel 2000). Streams and rivers arguably have experienced

some of the most dramatic forms of habitat simplification of any type of ecosystem (Brooks & Gregory 1988; Allan & Flecker 1993; Stanford et al. 1996; Sala et al. 2000). Within watersheds, the damming and straightening of stream channels have reduced spatial and temporal variability in flow (Ligon et al. 1995; Poff 1997; Graf 1999). Within stream reaches, the removal of physical structures such as woody debris or beaver dams has eliminated important types of stream habitat (Naiman et al. 1986; Frissell & Nawa 1992; Shields & Smith 1992).

More dominant impacts of stream simplification, however, have occurred at small spatial scales where benthic habitats crucial to stream organisms have been homogenized by increased rates of erosion and sedimentation (Phillips 1993; Palmer et al. 2000). Because small-scale, localized habitat heterogeneity is considered vital for the persistence of stream biota, restoration practices have historically focused on increasing local heterogeneity via morphological improvements of the

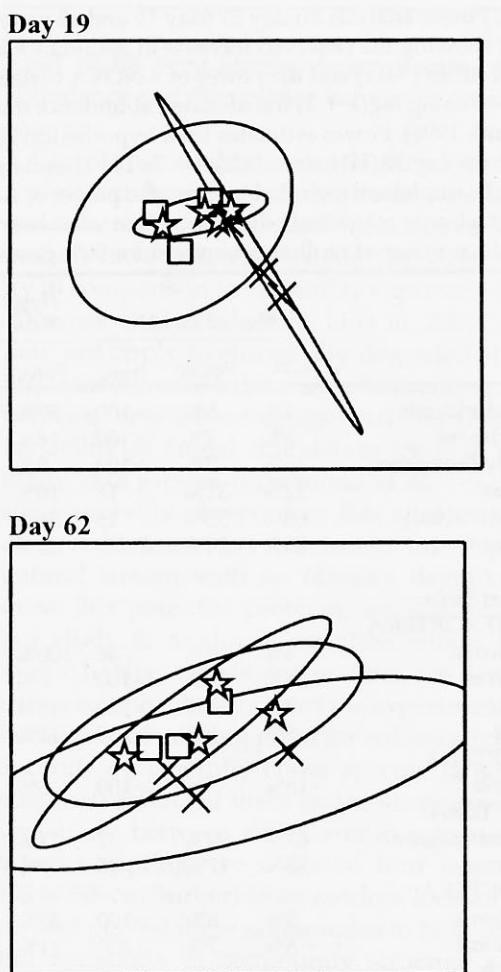


Figure 5. Multidimensional Scaling (MDS) ordinations of invertebrate community composition on days 19, 39, and 62 following experimental manipulation of treatment riffles; HH = \star , LH = \square , Reference = X. Confidence ellipses delineate 2 standard deviations around the mean coordinate for each treatment. Data were sample-standardized to emphasize changes in the relative abundances of common taxa. Stress = 0.12.

streambed and/or the addition of in-stream structures targeting fish (Gore & Shields 1995; Jungwirth et al. 1995; Muhar et al. 1995; Muhar 1996; Stanford et al. 1996; Palmer et al. 1997b). Yet the success of such efforts in restoring biological community structure has rarely been assessed (Karr & Chu 1999; Lake et al. 2000; Lake 2000).

We simulated local degradation and restoration of a stony stream by (1) degrading whole riffle habitats with a substantial physical disturbance (that resulted in 67% invertebrate mortality), (2) creating riffle habitats that had contrasting levels of streambed heterogeneity, and (3) tracking the recovery of macroinvertebrate communities in the riffles. We successfully manipulated streambed heterogeneity by changing variation in substrate particle sizes without altering the most common particles size (i.e., the median particle size was held constant). Thus our study had the potential to unambiguously relate variation in the abiotic environment to changes in biological community structure at a spatial scale relevant to many forms of stream simplification.

Surprisingly, however, we found no differences in the recovery of abundance, taxa richness, or composi-

tion of macroinvertebrate communities in riffle habitats of differing heterogeneity. There were also no differences in final community structure after abundances had reached levels that were comparable to background levels in the stream. For example, total abundance of macroinvertebrates after 19 days differed between the LH and HH riffles by only 17%, and species richness in the treatments differed by less than 15%. Given the magnitudes by which abundances fluctuated throughout this period (Figs. 4 & 5), these differences are too small to represent any biologically meaningful effects of the treatments on these aspects of community structure. These results do not support our prediction that the recovery of stream invertebrate community structure is influenced by physical habitat heterogeneity. The lack of response of community structure to changes in habitat heterogeneity were surprising given that our treatments not only differed in streambed heterogeneity, but also in the magnitude of flow, the spatial variability of flow, and in the temporal variability of flow (i.e., turbulence). Together, these factors are primary axes of local environmental variation thought to regulate the community structure of flora and fauna in-

habiting stream riffle habitats (reviews by Newbury 1984; Davis 1986; Minshall 1988; Statzner et al. 1988; Poff 1997; Hart & Finelli 1999).

Abundances of some individual taxa appeared to differ greatly between LH and HH riffles but exhibited such high variability between replicates that differences were not statistically significant. For example, several individual taxa had substantially higher mean abundance in HH treatments (e.g., *Stenacron* [mayfly nymph] by 135% or *Cheumatopsyche* [caddisfly] by 67%, Table 3), yet these were not statistically significant. The extremely high variability in invertebrate abundances suggests low statistical power. We therefore conducted power analyses to determine whether our inferences were constrained by high sample variance or by the small magnitude of mean differences.

Statistical power was estimated on each sampling date using the PiFace add-in for Microsoft Excel (Lenth 1996). Satterthwaite's approximation (Satterthwaite 1946) was used to obtain the degrees of freedom and account for residual heterogeneity of variances following data transformation. The resulting power estimates approximate the type II error rates from our repeated-measures analysis and are not exact measures; yet they are sufficient to reinforce biological inference (Toft & Shea 1983). We also compared power of our dataset to that of an "artificially" constructed dataset that estimated the power required to resolve 200% increases in each variable in HH riffles relative to LH riffles. A 200% increase was chosen somewhat arbitrarily but is based on the fact that (1) it is within the range that occurred for several aspects of community structure during this study, and (2) most ecologists would agree that a 200% change in community structure between treatments is biologically meaningful.

Table 3 indicates that detection of *any* differences among treatments was unlikely from our dataset and that high variance in community structure between replicate riffles constrained inferences. Even when there were very large differences between treatments (e.g., the abundance of *Stenacron*, which averaged 135% higher in HH riffles), our statistical power was extremely low (10%). An analysis of the artificially constructed dataset revealed that our analyses were also insensitive to most aspects of community structure when treatment abundances differed by 200%. Very often, the number of replicates required to achieve 90% statistical power to detect a 200% change were impractical. For example, we would have needed more than 100 replicate riffles of each treatment to detect a 200% change in diversity between the treatments. For brevity we report only the power calculations for day 39. Days 16 and 19 were strikingly similar, indicating that the high site-specific variability in macroinvertebrate abundances was established quickly (within 16 days) and was then

Table 3. Power analysis on day 39 (day 19 and 62 were similar) showing the observed increase in abundance in HH over LH riffles ($\% \Delta \bar{x}$) and the power of ANOVA to detect that difference using $\log(x + 1)$ transformed abundance data ($n = 3,4$) (Lenth 1996). Power estimates for a hypothetical 200% increase on day 39 (HH abundances = 2x LH abundances for every subsample) are included to show the power of ANOVA to detect a larger magnitude difference than was observed. $n_{90\%}$ is the number of replicates required for 90% power.

	Observed Day 39			Hypothetical $\% \Delta \bar{x} = 200\%$	
	$\% \Delta \bar{x}$	Power	$n_{90\%}$	Power	$n_{90\%}$
Total individuals	-1%	5%	>100	57%	9
Taxa richness	8%	8%	>100	14%	56
Diversity (Shannon)	15%	7%	>100	5%	>100
Evenness	22%	31%	18	10%	>100
EPT (individual)	68%	35%	15	58%	8
EPT (taxa)	29%	24%	29.7	43%	13
Common Taxa:					
EPHEMEROPTERA					
<i>Stenonema</i>	4%	16%	46	100%	2
<i>Stenacron</i>	135%	10%	>100	6%	>100
<i>Baetis</i>	2%	5%	>100	18%	40
<i>Caenis</i>	-9%	6%	>100	11%	83
PLECOPTERA					
<i>Neoperla</i>	-16%	5%	>100	6%	>100
TRICOPTERA					
<i>Cheumatopsyche</i>	67%	99%	2	21%	33
<i>Chimarra</i>	58%	17%	49	7%	>100
COLEOPTERA					
<i>Stenelemis</i>	5%	6%	>100	37%	16
<i>Psephenus</i>	-6%	7%	>100	21%	33
DIPTERA					
<i>Chironimidae</i>	-7%	12%	71	50%	11
Feeding groups					
Collector-gatherers	-6%	12%	69	68%	7
Collector-filterers	52%	24%	32	8%	>100
Predators	4%	6%	>100	38%	16
Scrapers	-1%	5%	>100	44%	13
Life history					
Clingers	7%	9%	>100	21%	34
Climbers	-13%	6%	>100	82%	5
Swimmers	14%	11%	76	18%	40
Sprawlers	-7%	13%	62	64%	8
Burrowers	-46%	23%	26	6%	>100

maintained for the duration of the experiment. Long-term exposure to the treatments could alter the magnitude of difference between treatments. For example, high heterogeneity riffles may retain leaves more efficiently, offering higher food levels for detritivorous taxa. Lack of power to detect a 200% change in abundance in our modeled dataset (an order of magnitude more than was observed for most taxa in the stream) suggests that such influences on abundance would

need to be very strong determinants of invertebrate abundance and distribution before our conclusions would change.

Clearly, variability in community structure between replicate riffles in our study stream was high enough to make meaningful statistical inference untenable. Other authors have also reported high between-riffle variability in comparison to variability expressed at other scales (Downes et al. 1993, 1998; Li et al. 2001). Our findings may not apply to chronically degraded streams suffering from extreme habitat simplification or chemical toxicity (e.g., acid mine drainage) that may reduce site-to-site variability in faunal abundances through extirpation of many taxa groups (Rosemond et al. 1992). High inter-site variability observed in this study may have been observed because we conducted this experiment in a natural stream with no obvious degradation. To address this potential problem, we specifically designed our study to minimize variation within treatments to mimic habitat simplification. First, we disturbed all the riffles equally at the start of the experiment to provide a homogenous starting point for colonization in all riffles. Second, we carefully chose specific ranges of particle sizes and arranged them on the streambed to minimize variability between riffles within a treatment. Finally, when sampling, we collected four large subsamples ($50 \times 50\text{-cm}$ Surber) from random locations in each riffle and pooled these subsamples to help overcome spatial variability in community structure within riffles. Despite these efforts to homogenize the physical environment, variability in abundances was high, and the minimum level of replication required to detect changes in community structure would prohibit any practical attempts to use stream invertebrates to assess recovery of the restored sites. This leads us to conclude that community structure was an insensitive indicator of ecological change in this stream, and to question the utility of using aspects of community structure to assess the success of restoration at similar sites.

Our results support a growing sentiment among some ecologists that changes in community structure may be poor indicators of environmental change in highly variable environments inhabited by mobile, fugitive taxa (Palmer et al. 1997b; Bunn & Davies 2000). Biomonitoring efforts may be better served by tracking community functions—that is, biotic processes involving the flux of energy or matter that are less variable. The results of a study concurrent with this one supports this. Cardinale et al. (2002) tracked the recovery of benthic respiration and primary production in the LH and HH riffles over the same period this study was performed. They found that two community-level functions (respiration and productivity) recovered to significantly higher levels in HH riffles compared to LH. The differences were not attributable to increased biomass

in the HH riffles; rather, the increase in habitat heterogeneity resulted in elevated biomass-specific rates of these two ecosystem functions that were maintained for the duration of the experiment (Cardinale et al. 2002).

Because Cardinale et al. (2002) used the same repeated-measures ANOVA models to analyze their ecosystem function data, we can directly compare variability in ecosystem function to variability in community structure by examining the relative goodness of fit of the two datasets to the ANOVA models (Table 4). For the same experimental riffles, the unexplained variability in ecosystem function was extremely low (average $r^2 = 0.9$; Table 4), compared to the unexplained variation in community structure metrics (average $r^2 = 0.3$; Table 4). Combining individual taxa into functional groupings did not improve our predictive power (Table 4). Thus, measurements of ecosystem function in the riffle habitats were less variable and more responsive to changes in habitat heterogeneity than were measures of invertebrate community structure. This suggests that measures of ecosystem functioning may be more useful indicators of ecosystem change and recovery that result from human-induced degradation of stream habitats. For bioassessment work, measures of ecosystem function often require higher levels of training and a larger investment in technology in the field. However, such drawbacks may be offset by the fact that functional data (1) measure the ecosystem processes directly rather than inferring process rates from community data, and (2) may be less variable in space and time and thus more easily interpreted. In addition, functional data can often be collected in a shorter period of time with no laboratory processing and thus may be considerably cheaper than obtaining community structure data.

The development of restoration ecology as a science is dependent upon tests of relevant ecological theory being conducted at scales appropriate for restoration. In

Table 4. Comparison of the amount of variation explained by ANOVA models for ecosystem function (Cardinale et al. 2002) and community structure metrics (this paper) for high heterogeneity riffles (r^2_{HH}) and low heterogeneity riffles (r^2_{LH}). The invertebrate community structure metrics are the average of the individual r^2 obtained for each member of the group (see Table 3 for details).

Dependent Variable	Variability	
	r^2_{HH}	r^2_{LH}
Ecosystem function		
Gross primary productivity	0.91	0.87
Respiration	0.87	0.89
Invertebrate community structure		
Common taxa	0.31	0.38
Feeding groups	0.29	0.22
Life history groups	0.41	0.32

doing so, we found we were unable to reject or accept our initial hypothesis that increasing habitat heterogeneity would lead to faster recovery of invertebrate populations. We did not have a sufficiently powerful test of that hypothesis using invertebrate community data, and we identified between-riffle variability in faunal abundance as being a critical constraint to monitoring that uses community structure data. If the science of restoration ecology is to be advanced through the careful study of real-world restoration, it is clear that the choice of appropriate indicators of change is of paramount importance. Monitoring and assessment work is likely to benefit from investigating new variables such as rates of ecological processes that are sensitive to ecosystem change following restoration without being disrupted by inherent site variability. Adaptive monitoring that is better able to capture and explain patterns of local variability are sorely needed to refocus efforts where they can best document recovery dynamics that are unambiguously attributable to restoration practices. Our study provides evidence that current methodologies relying purely on invertebrate community structure data may be insensitive to change in some streams and as such may be inappropriate for investigating recovery following restoration. In contrast, we suggest that direct measures of ecosystem function have a great potential to advance the science of restoration ecology.

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