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Habitat heterogeneity and disturbance influence patterns of community temporal variability in a small temperate stream

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Abstract Both habitat heterogeneity and disturbance can profoundly influence ecological systems at many levels of biological and ecological organization. However, the joint influences of heterogeneity and disturbance on temporal variability in communities have received little attention despite the intense homogenizing influence of human activity. I performed a field manipulation of substrate heterogeneity in a small New England stream, and measured changes in benthic macroinvertebrate communities for 100 days—a period that included both a severe drought and a flood. Generally, community variability decreased with increasing substrate heterogeneity. However, within sampling intervals, this relationship tended to fluctuate through time, apparently tracking changes in hydrology. At the beginning of the experiment, community temporal variability clearly decreased along a gradient of increasing substrate heterogeneity-a result consistent with an

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Present Address: B. L. Brown (⊠) Department of Forestry and Natural Resources, Clemson University, Clemson, SC 29634-0317, USA e-mail: bbrown3@clemson.edu observational study performed the previous year. During the subsequent weeks, droughts and flooding created exceptionally high variability in both hydrology and benthic macroinvertebrate community structure resulting in the disappearance of this relationship. However, during the last weeks of the experiment when hydrologic conditions were relatively more stable, the negatively sloped relationship between community temporal variability and habitat heterogeneity reemerged and mimicked relationships observed both early in the experiment and in the previous year's study. High habitat heterogeneity may promote temporal stability through several mechanisms including stabilization of resources and increased refugia from minor disturbances or predation. However, the results of this experiment suggest that severe disturbance events can create large-scale environmental variability that effectively swamps the influence of habitat heterogeneity, illustrating that a thorough understanding of community temporal variability in natural systems will necessarily consider sources of environmental variability at multiple spatial and temporal scales.

Keywords Community temporal variability · Habitat heterogeneity · Disturbance · Benthic macroinvertebrates · Drought · Flood · Temperate streams

Introduction

Habitat heterogeneity affects ecological processes at all levels of organization, including behavior (Holomuzki & Biggs, 1999; Kie et al., 2002), population dynamics (Silver et al., 2000), species interactions (Crowder & Cooper, 1982; Scognamillo et al., 2003), community structure (Hansen, 2000, Tews et al., 2004), and ecosystem functioning (Cardinale et al., 2002). Likewise, theoretical studies invoke habitat heterogeneity to explain a plethora of phenomena, including diversity (Pianka, 1966; Horner-Devine et al., 2004, but see Cramer & Willig, 2005 for an empirical counter-perspective), coexistence (Hutchinson, 1961; Holt, 1984), and variability in species interactions (Holt & Hassell, 1993). In addition, many conservation and restoration programs focus on generating and maintaining habitat heterogeneity in order to promote biodiversity and system stability (Palmer et al., 1997; Benton et al., 2003; Carey, 2003).

Habitat heterogeneity also interacts strongly with disturbance regimes on multiple scales. On a regional scale, habitat heterogeneity buffers disturbance impacts, which are rarely uniform across complex habitat matrices (Caswell & Cohen, 1991). As a result, organisms in less-affected areas contribute recruits which recolonize heavily affected areas (Pickett & White, 1985). This patch dynamics approach to disturbance and the role of extinction and colonization dynamics in defining regional communities is a persistent theme in ecology (Pickett & White, 1985) and is currently reflected by a contemporary surge of interest in metacommunity concepts (Holyoak et al., 2005).

On a local scale, habitat heterogeneity often provides microhabitat refugia in the form of physical structure that allows organisms to weather disturbances or escape predation. The phenomenon occurs in a diverse range of systems among diverse taxonomic groups (Crowder & Cooper, 1982; Caley & StJohn, 1996; Herrnkind et al., 1997; Lester et al., 1998; Bergey, 1999; Halaj et al., 2000; Finke & Denno, 2002; Lewis & Eby, 2002), but is particularly well-documented in temperate stream systems (Lancaster, 1999; Holomuzki & Biggs, 2003).

While the effects of habitat heterogeneity and disturbance on aggregate metrics like diversity and abundance receive considerable attention, ecologists have virtually ignored the joint influence of heterogeneity and disturbance on dynamics in communities even though community variability has implications for both ecological theory and management practices (Micheli et al., 1999). Most notably, temporal variability is a useful measure of community stability (Grimm et al., 1992) since variation in community processes can decrease reliability of ecosystem processes (Naeem & Li, 1997), indicate ecosystem stress (Odum et al., 1979), and even increase the risk of extinctions (Pimm, 1991). In addition, both compositional variability-changes in abundances of component species within a community-and aggregate variability are important sources of information about community dynamics (Micheli et al., 1999).

To examine the combined influence of habitat heterogeneity and disturbance on community variability, I created an experimental gradient of stream habitat heterogeneity and measured its influence on temporal variability in benthic macroinvertebrate communities. I performed this experiment during the summer and autumn of 2002 over an interval that included both drought and flood disturbances. Previous studies suggest that the temporal variability of stream macroinvertebrate communities decreases with increasing habitat heterogeneity (Brown, 2003). However, this prediction has not been tested during significant disturbance events. Given the docusignificance of habitat refugia for mented benthic macroinvertebrates during high discharge events (Lancaster & Belyea, 1997; Holomuzki & Biggs, 2000), I predicted that the relationship between community temporal variability and habitat heterogeneity would be strongest during floods. Though I did not consider a priori predictions about the influence of large drought events on this relationship, drought unexpectedly became an important element of this study.

Methods

I manipulated one aspect of benthic macroinvertebrate habitat heterogeneity, i.e., substrate heterogeneity, in a ~400 m reach of Alder Brook (AB) in Second College Grant, New Hampshire, USA. AB is a permanent stream with an estimated average discharge of $0.076 \pm 0.12 \text{ m}^3/\text{s}$ (mean \pm standard deviation), depth of $0.11 \pm$ 0.048 m and width of 2.86 ± 0.76 m during summer and autumn months in the study reach. Substrate composition includes a wide range of gravel and cobble sizes, boulders, exposed bedrock, fine sediments, aquatic bryophytes, and coarse woody debris in multiple size classes including large debris dams that span the stream.

I created 36 experimental units by manipulating substrate heterogeneity in 0.75×0.5 m plots in AB. First, I removed the top layer of substrate using trowels and crowbars and inserted 12 cm deep, open-topped wire-mesh baskets into the substrate such that the tops of the baskets were flush with the existing stream bottom. In order to maintain biological realism, the baskets were designed to constrain substrates within the manipulated area, but not to hinder either the movement of water or stream organisms. I collected ~3 metric tons of rock in three discrete cobble sizes from a local quarry and used those cobbles to create substrate heterogeneity treatments by varying the number and relative proportions of substrate types within a basket. Diameters of the three substrate types were: Large cobble = 12.1 ± 1.6 cm (mean \pm standard deviation based on a sample of 50 particles), small cobble = $8.6 \pm$ 1.1 cm, gravel = 3.7 ± 0.92 cm diameter. Each size class was naturally well-represented in Alder Brook, ensuring that effects observed in the experiment were not due to the introduction of novel substrates. I used these 3 classes of cobble to create a 7-level substrate heterogeneity treatment consisting of 6 levels of non-homogenous plots containing mixtures of substrate types to produce 6 levels of substrate heterogeneity, and homogeneous plots that contained only a single type of substrate (Table 1). There were 4 replicates for each of the 6 non-homogeneous treatment levels equaling 24 non-homogeneous plots (Table 1). Experimental units within the 6 nonhomogeneous treatment levels replicated substrate heterogeneity, but not necessarily substrate composition. In addition, there were 12 total homogeneous plots—4 replicates for each of the 3 size classes of cobble (Table 1). I also used the 12 homogeneous plots to test for the direct influence of substrate size class on measured response variables. However, except when testing for the direct influence of substrate size, I pooled the 12

 Table 1
 Treatment construction for the substrate heterogeneity experiment

Ratio of substrate types	Number of substrate types						
	One		Two	Three			
1	Simpson: 1 Contagion: 1 Evenness: 0	٩	12 EU: (3 substrate types × 4 replicates)				
9:1 (2 substrates) or 18:1:1 (3 substrates)		ſ	Simpson: 1.22 Contagion: 0.531 Evenness: 28.6	Simpson: 1.23 Contagion: 0.641 Evenness: 18.6			
4:1 or 16:1:1	24 EU: (4 replicates per treatment)	{	Simpson: 1.47 Contagion: 0.278 Evenness: 55.6	Simpson: 1.52 Contagion: 0.418 Evenness: 37.8			
3:2 or 3:1:1	,	l	Simpson: 1.92 Contagion: 0.029 Evenness: 94.3	Simpson: 2.27 Contagion: 0.135 Evenness: 74.7			

Changes in the relative proportions of three substrate types produced 7 substrate heterogeneity treatments. Simpson, contagion, and evenness are three of the four heterogeneity metrics used to characterize substrate heterogeneity. The fourth metric, particle size ratio, is calculated using physical measurements of substrate sizes and therefore differed for each experimental unit (i.e., plot). The table also shows how experimental units were allocated among treatments; EU = experimental unit

homogeneous plots into a single level of the habitat heterogeneity treatment. In other words, for the 7 total levels of the heterogeneity treatment, there were 12 replicates of the homogeneous level while the other 6 levels were represented by 4 replicate plots for a total of 36 plots (12 homogeneous + 24 heterogeneous). Assignment of a treatment to each plot was random.

I used four indices to characterize substrate heterogeneity: Simpson's index, contagion, Romme's relative evenness (Li & Reynolds, 1994), and particle size ratio d_{84}/d_{50} (PSR; Wolman, 1954). The first three indices are similar in that they are based on categorical maps or exact knowledge of plot composition and treat individual substrate types as 'categories' without regard for the physical characteristics of the substrates. Each index emphasizes a different aspect of heterogeneity: evenness is entirely based on the ratio of categories to one another, Simpson's relies on both the number of categories as well as their ratio, and contagion is based on the probability that two categories of the same type will be found in the same plot. The final heterogeneity metric, PSR, is based on the physical size distribution of grains (i.e., substrates) within a plot, and therefore differed for all experimental units since plots replicated heterogeneity in the sense of the first three metrics rather than physical substrate composition as measured by PSR.

Plots were placed in locations of similar depth and current velocity within a stream to reduce differences between plots created by hydrologic variation. At the beginning of the experiment, there were no significant differences between either depth or current velocity among the substrate heterogeneity treatments (MANOVA: $F_{6,29} = 0.60$, P = 0.73; mean depth = 0.40 ± 0.0058 m; mean current velocity = $0.32 \pm$ 0.0055 m/s).

After allowing 2 weeks for colonization of manipulated areas, I sampled stream macroinvertebrates on 8 dates from July 29, 2002 until October 30, 2002 by disturbing substrates, scrubbing cobbles, and capturing dislodged macroinvertebrates in a D-net (363 μ m mesh). To reduce the effects of repeated sampling, manipulated plots were designed to be 4× the area of a

standard benthic sample and on each date I sampled only a randomly chosen quadrant representing ~25% of the entire plot by using a 900 cm² metal frame to delineate the sampling area. My intent was to sample at weekly intervals, but drought prevented sampling for 5 weeks. Benthic samples were preserved in 75% ethanol and enumerated in the laboratory at a later date. Most taxa were identified to genus with some exceptions, most notably the Chironomidae which were identified to tribe.

I compared community temporal variability across the constructed substrate heterogeneity gradient by quantifying the variability between two or more samples of the same community through time using Euclidean distances (EDs) measured in an ordination space created from a correspondence analysis of macroinvertebrate abundances (Brown, 2003). I refer to this method of quantifying community change with the acronym EDCA, i.e., ED in correspondence analysis (CA) space (Brown, 2003). Similar methods have been utilized for examining directional change in natural and experimental communities through time (Collins et al., 2000). Prior to performing CA, I used a square-root transformation to reduce the influence of highly abundant taxa. Using EDCA, I calculated change in the macroinvertebrate community for each of the 7 sampling intervals (8 sampling dates = 7 sampling intervals) and regressed EDCA scores against the four heterogeneity metrics to investigate relationships between community temporal variability and substrate heterogeneity. I also summed EDCA scores across all sampling intervals to produce total community variability during the experiment and, again, compared this total across the heterogeneity gradient. Prior to regression, EDCA scores for each interval were corrected for interval length and log-transformed to meet the equal variance assumption of linear regression. The EDCA technique was robust to most possible options, including ordination technique (PCA produced qualitatively similar results), type of initial data transformation, total number of ordination axes included in the analysis, and exclusion of rare taxa. When PSR was the metric of habitat heterogeneity, I employed weighted

least squares (WLS) regression with weights scaled by standard deviation to correct for heteroscedasticity created by the distribution of plot heterogeneity values along the PSR axis that tended to be clumped at low values (Neter et al., 1996).

I also examined the effects of substrate heterogeneity on several other measures of benthic macroinvertebrate community change. I used repeated measures analysis of variance (RM-ANOVA) to examine changes in the abundances of individual macroinvertebrate taxa during the experiment, as well as changes in total macroinvertebrate abundance and taxon richness. In addition to simple taxon richness, I calculated rarefied estimates for number of taxa (sample-based rarefaction with 5,000 permutations; Gotelli & Colwell, 2001) that allowed me to compare diversity between samples that varied considerably in terms of overall macroinvertebrate abundance. Additionally, I compared the temporal variability of individual taxa (measured using the coefficient of variation (CV; Cottingham et al., 2001) across the gradient of substrate heterogeneity. Finally, I examined whether common taxa showed affinities for individual substrate types by examining differences in abundance in the twelve homogeneous plots. I performed these univariate analyses on only the 35 most common taxa since less common taxa were generally too rare to show any consistent or meaningful patterns in abundance.

In addition to collecting benthic samples, I also collected particulate organic matter (POM) from each plot on 4 sampling dates between July 22 and September 26, 2002 in order to assess possible effects of substrate heterogeneity on one of the primary resources for benthic macroinvertebrates in AB. I prevented additional disturbances to benthic macroinvertebrate communities during POM sampling by collecting from sections of manipulated areas that were not used for benthic macroinvertebrate sampling. Using a stovepipe sampler, I collected POM samples that were later ashed, weighed, and volume corrected in the lab (Wallace & Grubaugh, 1996). I analyzed POM data using RM-ANOVA to detect trends through time as well as possible differences in POM accumulation among the 7-substrate heterogeneity treatments.

Results

Two disturbances occurred during the 100-day experiment. First, a large drought severely reduced discharge in AB for several weeks during August and September. Logs of discharge (USGS water monitoring station # NH01052500) and precipitation (National Oceanic and Atmospheric Administration's National Climatic Data Center at Errol, NH, USA; 12.5 km from field site) indicated that the drought was the largest to occur in the 65-year record for the area. While the effects of the drought were severe, AB did maintain some surface flow throughout the experiment. However, surface flow was too low to permit collection of benthic samples on four planned sampling dates between July 29th and September 17th and I ultimately collected benthic samples on 8 dates (Fig. 2, top panel).

The second disturbance was a flood that reached an estimated discharge of $1.48 \text{ m}^3/\text{s}$ in AB on September 28, 2002. I singled out this event as a flood disturbance since peak discharge was >2 standard deviations above summer average discharge (Resh et al., 1988) based on 64-year historical discharge records. Flood duration was short and discharge returned to near pre-flood levels in 2 days.

I was forced to remove data for one experimental unit prior to analysis. The plot was originally situated near a small debris dam that was destroyed during flood conditions. The dam's removal dramatically altered the plot's hydrologic condition and violated the experiment's assumption that changes in depth or current velocity occurred primarily as stream-wide phenomena rather than selectively affecting individual experimental units.

EDCA analysis of macroinvertebrate temporal variability included 63 macroinvertebrate taxa and used 25 axes from CA describing 82% of the variability in benthic samples. In summarizing the temporal variability results, I primarily focus on the PSR and 'contagion' metrics of habitat heterogeneity since they had the greatest overall explanatory power In general, the three categorical metrics (Simpson's, contagion, evenness) produced very similar results. However, relationships generated with the PSR metric differed considerably from the categorical metrics because PSR classified several plots as low heterogeneity, which the categorical metrics defined as being relatively heterogeneous.

Substrate heterogeneity significantly influenced the temporal variability of benthic communities during the experiment. When I examined total temporal variability, i.e., temporal variability as EDCA scores summed across all sampling intervals, I found that temporal variability decreased significantly with increasing substrate heterogeneity as measured by PSR ($F_{1,34} = 7.21, P = 0.011$, $r^2 = 0.18$; Fig. 1). There was a qualitatively similar relationship when I defined habitat heterogeneity using the three categorical metrics, but the relationship was only marginally significant for the contagion ($F_{1,34} = 3.88, P = 0.057, r^2 = 0.11$) and Simpson's metrics $(F_{1,34} = 3.77, P = 0.061,$ $r^2 = 0.10$) and non-significant for the evenness metric ($F_{1,34} = 2.34, P = 0.14, r^2 = 0.07$). Qualitative similarity of results across heterogeneity metrics is not surprising since the 4 metrics are positively correlated with one another even though the metrics differ in their method of defining heterogeneity.

Perhaps even more interesting was that an examination of temporal variability within each sampling interval revealed that the relationship between temporal variability and substrate heterogeneity showed directional change that



Fig. 1 Total benthic macroinvertebrate community temporal variability (i.e., across all sampling dates) across the experimental habitat heterogeneity gradient. Habitat heterogeneity was measured using a particle size ratio d_{84}/d_{50} (PSR). Higher PSR values indicate higher habitat heterogeneity. $F_{1,33} = 7.22$, P = 0.011, $r^2 = 0.18$

tracked hydrologic conditions (Fig. 2). During sampling interval 1, community variability decreased ~40% along a gradient of increasing substrate heterogeneity (Fig. 2b) with a slope similar to that observed in the previous year's observational study (Fig. 2a) in which variability decreased ~45% across a comparable heterogeneity gradient (Brown, 2003). However, subsequent weeks brought drought conditions that persisted for over a month, followed by several rainy weeks that induced flooding (Fig. 2, top panel). During this period of high hydrologic variability, there was little indication of an effect of habitat heterogeneity on community temporal variability (Fig. 2c). However, post-drought, the relationship between benthic community variability and heterogeneity progressively reverted to a slope similar to both the first sampling interval and to observational data from the previous year, and during this final interval community variability decreased ~55% along the experimental heterogeneity gradient (Fig. 2d).

The effect of the substrate heterogeneity treatment on abundances of individual taxa was extremely variable. Of the 35 most common taxa, the abundances of 25 taxa demonstrated a significant or marginally significant effect of time. The majority of these taxa generally increased in abundance during the experiment, though a few taxa, most notably the stonefly Amphinemura and the caddisfly Glossosoma, decreased. In contrast, few taxa demonstrated either a significant or marginally significant overall direct effect of substrate heterogeneity (3 taxa), or a substrate heterogeneity \times time interaction (4 taxa). Similarly, the temporal variability of individual taxa showed little response to the substrate heterogeneity treatment with only one taxon showing a marginally significant difference in variability across the substrate heterogeneity gradient: the mayfly *Epeorus* (P = 0.068).

There was little or no indication that individual benthic macroinvertebrate taxa had affinities for individual substrates as assessed by testing abundances across the 3 classes of homogeneous plots (Table 2). There were no significant consistent associations of individual taxa, or of total benthic macroinvertebrates, when examined across all 8 sampling dates with two notable exceptions: the 100





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Fig. 2 (Top panel) Hydrograph of the 4th-order Diamond River (USGS water monitoring station # NH01052500), of which Alder Brook is a 2nd order tributary, showing general hydrologic condition of the Diamond watershed. Black arrows indicate sampling dates for the substrate manipulation experiment. (Lower 4 panels): Relationship between community temporal variability and habitat heterogeneity measured using the metric that explained the most variability in each year (evenness in 2001 and contagion in 2002). (a) Results of a 45-day observational study performed the previous year; $F_{1,8} = 13.1$, P = 0.007, $r^2 = 0.62$ (Brown, 2003). The temporal variability measure was summed across 4 sampling intervals since the relationship was similarly shaped in all intervals. The scale and statistics in panel A differ from their original

representation in Brown 2003 due to a log-transformation of EDCA scores so that data from the two years would be directly comparable. (B-D) Benthic community temporal variability (EDCA) across the experimental gradient of stream substrate heterogeneity during particular sampling intervals: (b) 1st sampling interval, $F_{1,33} = 5.8$, P = 0.022, $r^2 = 0.15$. (c) Temporal variability averaged across the middle 5 sampling intervals; there were no detectable relationships between community variability and habitat heterogeneity during any of the 5 individual intervals; $F_{1,34} = 0.78$, P = 0.38, $r^2 = 0.023$. (d) Final (7th) sampling interval, $F_{1,33} = 14.6$, P = 0.0006, $r^2 = 0.31$. In all figures, habitat heterogeneity increases on the x-axis from left to right

Table 2 Plot-level means (± 1 SE) of total benthic macroinvertebrate abundance, macroinvertebrate richness, andmacroinvertebrate diversity (Shannon index) of the 3 types

of homogeneous plots on each sampling date to examine possible direct effects of substrate type/size. G = gravel, SC = Small cobble, LC = Large cobble

		Sampling date							
		1	2	3	4	5	6	7	8
Total Abund.	G	22.5 ± 7	25.3 ± 4	24.8 ± 12	32.0 ± 14	60.5 ± 30	70.8 ± 28	162.5 ± 54	157.2 ± 49
	SC	28.0 ± 5	43.5 ± 25	16.3 ± 7	19.5 ± 8	54.0 ± 17	47.0 ± 10	110.8 ± 70	193.8 ± 89
]	LC	34.3 ± 6	23.3 ± 5	26.2 ± 9	23.0 ± 2	57.8 ± 15	45.0 ± 7	174.0 ± 55	302.7 ± 167
Taxon richness	G	7.5 ± 1.3	9.5 ± 0.6	7.5 ± 1.8	10 ± 2.3	10.5 ± 2.7	12.3 ± 1.2	12.3 ± 1.8	12.8 ± 1.0
	SC	9.5 ± 1.2	8.3 ± 1.9	7.5 ± 1.3	7.3 ± 1.5	10.8 ± 2.1	9.3 ± 0.8	10.5 ± 2.3	13.0 ± 1.5
	LC	9.8 ± 1.7	8.8 ± 1.5	9.8 ± 1.5	9.0 ± 0.8	11.8 ± 1.0	9.8 ± 0.9	12.0 ± 0.7	14.5 ± 1.4
Shannon diversity	G	1.6 ± 0.1	1.9 ± 0.1	1.7 ± 0.2	2.0 ± 0.2	1.9 ± 0.3	2.0 ± 0.09	1.8 ± 0.08	1.9 ± 0.1
	SC	1.8 ± 0.2	1.5 ± 0.2	1.8 ± 0.2	1.7 ± 0.2	1.9 ± 0.2	1.8 ± 0.07	1.8 ± 0.1	1.9 ± 0.06
	LC	1.9 ± 0.1	1.9 ± 0.1	1.9 ± 0.09	1.9 ± 0.1	2.0 ± 0.08	1.8 ± 0.1	1.8 ± 0.09	1.9 ± 0.1

caddis *Glossosoma* only occurred in mediumsized cobble and the caddis *Apatania* occurred only in large cobble during the experiment. On individual dates, there were some statistically significant differences in the abundances of individual taxa among the classes of homogeneous plots, but the number of significant habitat associations was actually less than would be expected by random chance (i.e., 1/20). In addition, there were no differences in richness or Shannon diversity among the classes of homogeneous plots, and average diversity was almost identical to average diversity of non-homogeneous plots (Table 2).

Both total invertebrate abundance and taxon richness changed significantly through time during the experiment (RM-ANOVA effect of time, taxon richness: $F_{7, 203} = 6.27$, P < 0.0001; abundance: $F_{7,189} = 19.13$, P < 0.0001; Fig. 3a). However, there was no significant effect of substrate heterogeneity on either total abundance ($F_{6,29}$ = 0.74, P = 0.62) or taxon richness ($F_{6,29} = 1.67$, P = 0.17), nor were there significant substrate heterogeneity × time interactions (total abundance $F_{42,203} = 0.81$, P = 0.68; taxon richness: $F_{42.196} = 0.30, P = 0.28$). Furthermore, when I examined rarefied estimates of number of taxa, there was no effect of time (Fig. 3b), indicating that the observed temporal changes were due to the effect of increased macroinvertebrate abundances on detection probability. Stream-wide increases in both richness and abundance late in the experiment were due in large part to summer reproduction for many taxa that resulted in

dramatic late-summer increases in early-instar larvae.

There was no effect of substrate heterogeneity on POM accumulation, either as a direct effect $(F_{2,4} = 1.75, P = 0.28)$ or as an interaction $(F_{6,12} = 1.72, P = 0.25)$. However, POM accumulation did change significantly through time $(F_{3,12} = 6.15, P = 0.034)$, decreasing between the first two sampling dates and gradually increasing



Fig. 3 (a) Total benthic macroinvertebrate taxon richness (black) and abundance (grey). Points represent means across all plots (± 1 SE) since there was no effect of habitat heterogeneity treatment on either richness or abundance. (b) Same data as in (a). But showing rarefied estimates of number of taxa (± 1 SE) using sample-based rarefaction with 5,000 permutations (Gotelli & Colwell, 2001). In several instances error bars are

	Ν	Min	Max	Mean	S	Median
2001-Taxon richness	40	9	23	16.6	3.50	17
2001-Rarefied richness	40	21	38	34.1	3.66	35.1
2002-Taxon richness 2002-Rarefied Richness	280 280	2 15	19 48	10.6 42.3	3.46 5.94	11 44.3

Table 3 Comparison of taxon richness and estimated rarefied taxon richness in Alder Brook in 2001 and 2002 across all 900 cm^2 samples

N = the number of included samples, s = standard deviation

over the remainder of the experiment (means \pm SE across all samples, units = mg/ml/900 cm² of substrate; July 22 = 1.12 \pm 0.19, July 28 = 0.083 \pm 0.020, Aug. 12 = 0.065 \pm 0.014, Sept. 26 = 0.20 \pm 0.045).

Discussion

The results of this experiment demonstrate how habitat heterogeneity and disturbance interact to influence short-term temporal variability in stream macroinvertebrate communities. The relationship observed between community variability and substrate heterogeneity was negatively sloped with community variability decreasing along a gradient of increasing habitat heterogeneity. This relationship was apparent for total benthic community temporal variability (i.e., across all sampling dates) only with the PSR metric, a result that may hint at some of the mechanisms involved in producing habitat heterogeneity-variability relationships in this study. Of the 4 heterogeneity metrics, PSR is a physical metric that relies on actual size measurements of the substrates within a plot as opposed to simply the distribution of substrates among categories as with the other 3 metrics. PSR may very well have exposed an important physical aspect of substrate heterogeneity and its influence on the benthos that the other metrics did not detect, for example the influence of physical substrate stability (Matthaei et al., 1999; Holomuzki & Biggs, 2003). However, some caveats are warranted. As mentioned previously, there was no direct influence of substrate identity (from comparing the multiple types of homogeneous plots) as would be expected if simple substrate stability driven by size were of strong influence, though some more complex

properties of substrate may still be influential (Holomuzki & Biggs, 2003). As a second caveat, the regression results for this particular relationship are almost completely driven by 6 plots with a high PSR since the majority of plots had low PSR (Fig. 1) and the relationship is not particularly strong ($r^2 = 0.18$).

Within individual sampling intervals, negatively sloped relationships between community variability and habitat heterogeneity occurred at both the beginning and end of the experiment and, in both cases, closely resembled the results of an observational study conducted in AB during the previous year (Brown, 2003; Fig. 2a). However, in the current study, there were also sampling intervals during which there was no detectable relationship between community temporal variability and habitat heterogeneity (Fig. 2c). This result is in sharp contrast to the 2001 study when negative slopes persisted over all sampling intervals of the 45-day study (Brown, 2003). These results suggest two questions about this system: (1) What processes create negative relationships between community temporal variability and substrate heterogeneity?, and (2) in 2002, why are there sampling intervals in which there is no observed relationship between variability and heterogeneity, and why does the 2002 result differ in this respect than the previous year's study?

A decrease in community temporal variability along an increasing gradient of habitat heterogeneity may arise due to several processes in streams. High substrate heterogeneity provides refuge from predation (Hildrew & Townsend, 1977; Warfe & Barmuta, 2004) and very likely from hydrologic disturbance. While there has been no direct test of the influence of substrate heterogeneity on the efficacy of stream substrates as refugia during hydrologic disturbances, substrate characteristics, including sorting and grain size, strongly influence refuge quality (Holomuzki & Biggs, 2003) and suggest that substrate heterogeneity generally enhances in-stream refuge quality. Either mechanism-refuge from predation or disturbance-could produce enhanced temporal stability of benthic communities in high heterogeneity areas. That there was a relationship between total community variability (i.e., across the entire 93-day experiment) and the PSR metric suggests that some aspect of the physical size structure of substrates in plots affected benthic communities, perhaps by enhancement of refugia. However, it is worth noting that contrary to my original prediction, there was no detectable relationship between community variability and habitat heterogeneity over the sampling interval that included significant flooding, suggesting that refugia from predation may be a more significant mechanism in this particular case.

In addition, species richness and abundance of benthic macroinvertebrates often increase with substrate heterogeneity (Minshall, 1984; Poff & Ward, 1990; Beisel et al., 1998; Stewart et al., 2003) and thus may promote stability (Brown, 2003). However, in the current experiment, there was no consistent influence of substrate heterogeneity on either abundance or taxon richness (rarefied or raw) of benthic macroinvertebrates that would imply stabilization through a 'greater number of niches' effect (Beisel et al., 1998). Previously I did observe a positive relationship between diversity and substrate heterogeneity in AB (Brown 2003). In the current study, there was no relationship, possibly due to an influence of drought (Table 3), but it is worth noting that rarefied estimates of taxon richness in 2002 were actually slightly larger than those in 2001. However, this effect is due in large part to decreased overall abundances in 2002 changing the shape of the rarefaction curve used for estimation.

Areas of high habitat heterogeneity may also provide more stable sources of both algal and detrital resources (Suren, 1992; Biggs & Smith, 2002; Stewart et al., 2003; Horvath, 2004), but again, there was little evidence for heterogeneity effects on detrital resources in this experiment, as described in Results, in contrast to some previous studies (Stewart et al., 2003).

Of course, the experiment produced not only inverse relationships between community variability and habitat heterogeneity, but also intervals during which there were no detectable relationships between community temporal variability and habitat heterogeneity-a phenomenon not observed in the previous year's study (Brown 2003). A comparison between the hydrograph and the regressions in Fig. 2 suggests that hydrology plays a key role in determining the importance of substrate heterogeneity to benthic organisms. The highest observed average temporal variability during the experiment was during intervals 2 (mean \pm SE of all plots; 0.39 \pm 0.03) and 4 (0.21 \pm 0.02), the intervals containing the drought and flood respectively. High community variability spanning a drought period is not surprising since habitat use of benthic macroinvertebrates changes dramatically when the only local (i.e., in-stream) refugia for most benthic macroinvertebrates are deep pools or interstitial space in the hyporheos (Lake, 2003). In a drought as severe as in 2002, many organisms perish, either from desiccation, or by being forced into unfavorable habitat where they die from starvation or intensified predation (Lake, 2003). Postdrought, all organisms present either (1) survived the drought in local refugia, or (2) are new colonists from the regional species pool. In both cases, these organisms are rapidly dispersing within the stream to find habitat that confers survival in non-drought conditions (e.g., refuge from predation, nutrition). The flood in interval 4 also appears to have resulted in high temporal variability. Thus, the data suggest that hydrologic variability may overwhelm the stabilizing influence of habitat heterogeneity when hydrologic variability is high.

A second indicator of the influence of hydrology on the current experiment is that community temporal variability was generally high during flood and drought conditions and during those intervals (2 & 4) there were no detectable relationships between community variability and substrate heterogeneity. Overall variability was also high during interval 1, yet there was a significant linear relationship between variability and heterogeneity (Fig. 2b), suggesting that hydrologic condition, rather than simply high variability, determines whether substrate heterogeneity will influence community temporal variability. Biologically, this conclusion is logical since major droughts and floods push organisms to extremes that are difficult to tolerate with usual behavioral mechanisms (Lancaster & Belyea, 1997; Lake, 2003).

Finally, high variability in hydrologic condition may also explain the differences between the 2002 experiment and the 2001 observational study. In 2001, the coefficient of variation (CV) in mean daily discharge (m³/s, based on the USGS Diamond River gauging station) over the study period was 0.88 and during that period I observed consistent negatively sloped relationships between community temporal variability and substrate heterogeneity. In contrast, the CV during the 2002 experiment was 1.27, despite the fact that average discharges were quite similar between the two years (1.77 m³/s in 2001 and 1.83 m^3 /s in 2002). During the 2001 study, there were simply no extreme hydrologic events-either floods or droughts-that rivaled either the flood or drought captured by the 2002 experiment.

Several lines of evidence suggest that the periods of no observed relationship in 2002 were created by extreme hydrologic variability in the form of flooding and drought. Unfortunately, in this particular study, hydrology was not under experimental control, nor was the experiment designed with hydrology as a treatment. Therefore any conclusions about hydrologic variability must be inferred based on incidental evidence. Unfortunately, such is often the case in studies where major hydrologic events become unplanned treatments (Lake, 2003).

It is also worth noting that the experiment spanned 3.5 months and that seasonal changes in the benthic macroinvertebrate community undoubtedly influenced measures of community change. The total abundance of benthic macroinvertebrates as well as actual taxon richness (though not rarefied estimates of taxa number) increased dramatically in the last several weeks of the experiment as is frequently the case in many temperate streams when adults reproduce in the early summer months creating a visible recruitment pulse in the late summer. As with disturbance, it is difficult to estimate the influence of seasonality on this experiment since only one stream was involved. In actuality, I performed the substrate manipulation in two streams: AB and Loomis Valley Brook, a very similar stream in the same watershed. The paired comparison between streams would have allowed an examination of landscape-level influences like recruitment. Unfortunately, Loomis Valley Brook was tremendously impacted by the drought and had no surface flow for nearly 2 months of the experiment rendering most comparisons impossible. However, such landscape-level influences would not be expected to effect the observed differences in community temporal variability among heterogeneity treatments in AB which were the focus of the experiment.

The relationships between macroinvertebrate community temporal variability and habitat heterogeneity are community patterns that are recognizable only by considering all or most of the taxa in the community simultaneously. Univariate analyses alone do not lead to the same conclusions as the multivariate analysis because, while many individual taxa did respond significantly to the substrate manipulation, the responses of taxa were idiosyncratic with respect to treatment, both across sampling dates and between taxa. These differences are not surprising since they reflect the biology of 63 individual taxa as well as complex interspecific and environmental interactions. In addition, because macroinvertebrate taxa demonstrated many different responses to the heterogeneity treatment, relationships between community variability and habitat heterogeneity cannot be explained by either a single dominant taxon responding to the substrate manipulation or a large-scale synchronous effect of many taxa.

Conclusions

Even though much of the collective attention of community ecology has recently shifted to the importance of colonization-extinction dynamics in a metacommunity framework (Holyoak et al., 2005), understanding local (i.e., within-patch) dynamics is still essential to understanding populations and communities at any spatial scale (Friedenberg, 2003; Barnes & Roderick, 2004; Jakalaniemi et al., 2005). This study demonstrates that local habitat heterogeneity may exert a stabilizing force on local community dynamics under many conditions. However, it also demonstrates that large disturbances can generate overwhelming environmental variance that swamps the more subtle influence of habitat heterogeneity, thus illustrating the importance of considering sources of environmental variance on multiple spatial and temporal scales. Given the increased homogenization of natural habitat (Dobson et al., 1997), understanding the role habitat heterogeneity plays in regulating populations, dictating community structure, and influencing ecosystem functions, becomes increasingly important for managing and preserving natural systems (Cardinale et al., 2002). Only by continuing to rigorously investigate the consequences of habitat heterogeneity across multiple scales and levels of biological organization can we expect to successfully understand the role of habitat heterogeneity in stream benthic systems, it's interaction with disturbance regimes, and it's potential as a tool for management.

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