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Effects of disturbance frequency, intensity, and area on assemblages of stream macroinvertebrates

Abstract Disturbance frequency, intensity, and areal extent may influence the effects of disturbance on biological communities. Furthermore, these three factors may have interacting effects on biological diversity. We manipulated the frequency, intensity, and area of disturbance in a full-factorial design on artificial substrates and measured responses of benthic macroinvertebrates in a northern Vermont stream. Macroinvertebrate abundance was lower in all disturbance treatments than in the undisturbed control. As in most other studies in streams, species density (number of species/sample) was lower in disturbed treatments than in undisturbed controls. However, species density is very sensitive to total abundance of a sample, which is usually reduced by disturbance. We used a rarefaction method to compare species richness based on an equivalent number of individuals. In rarefied samples, species richness was higher in all eight disturbed treatments than in the undisturbed control, with significant increases in species richness for larger areas and greater intensities of disturbance. Increases in species richness in response to disturbance were consistent within patches, among patches with similar disturbance histories, and among patches with differing disturbance histories. These results provide some support for Huston's dynamic-equilibrium model but do not support the intermediate-disturbance hypothesis. Our analyses demonstrate that species richness and species density can generate opposite patterns of community response to disturbance. The interplay of abundance, species richness, and species density has been neglected in previous tests of disturbance models.

Key words Intermediate disturbance hypothesis · Dynamic equilibrium model · Stream invertebrate community · Rarefaction · Diversity

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Introduction

The intensity, frequency, and area of disturbance may determine the abundance and species richness of an assemblage (Abugov 1982; Sousa 1985; Resh et al. 1988; Huston 1994; Townsend et al. 1997). Increasing disturbance intensity may remove more individuals, more species, and more of the food resources necessary for recolonization. If disturbance frequency is greater than the rate of competitive exclusion, diversity may be maintained at a high level (Huston 1979). Increasing the areal extent of disturbance removes more individuals, thus reducing the local pool of potential colonists. Although all three aspects of disturbance can affect species richness (Sousa 1985), little is known about their interactions (Death and Winterbourn 1995).

The intermediate-disturbance hypothesis (IDH; Connell 1978) continues to be an important hypothesis explaining the effects of ecological disturbance (Collins et al. 1995; Hiura 1995; Hacker and Gains 1997; Dial and Roughgarden 1998; Wilkinson 1999). The qualitative prediction that diversity should peak at an intermediate disturbance level has been tested in marine, freshwater, and terrestrial communities (Collins and Glenn 1997). Supporting evidence for the IDH has been found in communities with high rates of competitive displacement (Huston 1994).

However, the IDH has been criticized as being too simplistic to account for the structure of communities (McGuinness 1987) and for being difficult to falsify (Juhász-Nagy 1993). The IDH is also dependent on a tradeoff between colonization and competitive ability (Collins and Glenn 1997), which may not be realistic for assemblages of highly mobile species, such as stream invertebrates. Finally, the IDH assumes disturbances affect only competing species at a single trophic level. Predictions of the IDH may not be supported if species from different trophic levels are analyzed (Wootton 1998). Huston's (1979, 1994) dynamic-equilibrium model offers a broader range of predictions than the classic IDH. Depending on the rates of competitive exclusion and the

rates of population growth, species diversity can peak at low, high, or intermediate levels of disturbance (Figs. 5, 6 in Huston 1994).

In contrast to the predictions of the IDH, disturbance in streams usually reduces invertebrate species richness (Lake 1990; Englund 1991; Matthaei et al. 1996, 1997; reviewed by Vinson and Hawkins 1998), although rapid recolonization may quickly restore diversity (Townsend and Hildrew 1976; Boulton et al. 1988; Lake and Schreiber 1991). Resh et al. (1988) and Reice et al. (1990) reviewed the role of disturbance in streams and concluded that the dynamic-equilibrium model (Huston 1979, 1994) is generally applicable to stream communities. In contrast, Lake (1990) suggested that Huston's model appears too simple to explain the structure of stream communities.

Whereas the IDH predicts that diversity will peak at some intermediate intensity or frequency of disturbance (Connell 1978; Collins and Glenn 1997), Huston's dynamic-equilibrium model predicts that the location of the diversity peak depends on the rates of population growth and competitive displacement in the community (Figs. 5, 6 in Huston 1994). Huston's (1994) model assumes that competitive exclusion occurs more rapidly when populations have high growth rates. At low rates of population growth and competitive displacement, maximum diversity is predicted at minimum disturbance frequency or intensity; at intermediate growth rates, diversity peaks at intermediate disturbance levels (as predicted by the IDH); at high growth rates, diversity peaks at maximum disturbance intensity or frequency (Huston 1994). Huston's model assumes that disturbance reduces population sizes and that competitive exclusion is more likely when populations are large. If the interval between disturbances is less than the time to competitive exclusion, then equilibrium conditions are never reached, competitive exclusion does not occur, and diversity is maintained at a high level (Huston 1979; Resh et al. 1988). The essential difference between Huston's (1994) model and the IDH is that the former predicts that the position of the diversity peak with respect to disturbance frequency depends on population growth rates.

Despite widespread interest in disturbance of stream assemblages, intensity, frequency, and area of disturbance have not been simultaneously manipulated in a controlled field experiment. In studies to date, frequency (Reice 1985; Robinson and Minshall 1986; Lake et al. 1989; Death 1996), intensity (Boulton et al. 1988; Rosser and Pearson 1995), and area of disturbance (Dudgeon 1991; Rosser and Pearson 1995) have all been manipulated separately. Accordingly, we know nothing of the potential interactions between these factors (Death and Winterbourn 1995).

In addition, effects of disturbance may depend on precisely how diversity is quantified. Most ecologists have not disentangled the effects of abundance, species density (number of species/area; Simpson 1949), and species richness (number of species/number of individuals sampled; James and Wamer 1982; Downes et al. 1998). All diversity and richness measures are influenced by sample size, and statistical procedures such as rarefaction (Simberloff 1978) are necessary for valid comparisons of samples (Gotelli and Graves 1996; Vinson and Hawkins 1996). This topic, and the related issue of using fixed counts versus standardized areas for evaluating benthic communities, has been the focus of recent debate in the freshwater ecology literature (Larsen and Herlihy 1998 and references therein). These issues are especially important in evaluating effects of disturbance, because disturbance reduces abundance.

The purpose of our study was to examine the impacts of physical disturbance on macroinvertebrates of a northern Vermont stream. We manipulated intensity, frequency, and area of physical disturbance on artificial substrates in a full-factorial design. Our disturbances mimicked natural substrate scouring events. We used a rarefaction technique (Gotelli and Entsminger 1999) to quantify effects of disturbance on macroinvertebrate abundance, species density, and species richness. Our experimental design enabled us to test for main effects and interactions between intensity, area, and frequency. We were also able to assess the effects of disturbance within and among patches, a recent source of controversy in the disturbance literature (Wilson 1994; Collins and Glenn 1997).

Materials and methods

Study site

We conducted this study in a third-order perennial reach of the La Platte River in Chittenden County, Vermont. Mean annual discharge for the 5 years prior to this study was 1.1 $m^3 s^{-1}$ (Hammond et al. 1997). The channel gradient was low at the study site, and the maximum stream depth was 1 m under baseflow conditions. The stream bank was lightly wooded, with little canopy cover over the channel. Stream bed substrates included boulders, cobbles, gravel, and sand. This stream is highly prone to spring spates caused by snow melt and rain storms. Periodic spates following rain storms continue through fall (Fig. 1; data from Coakley et al.
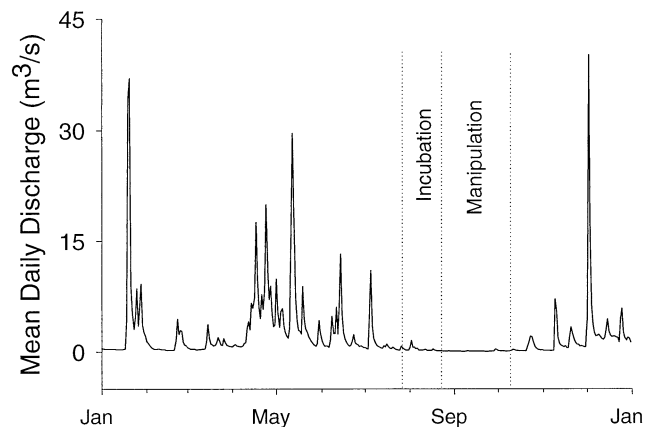

Fig. 1 Mean daily discharge of the LaPlatte River at the Shelburne Falls USGS gauging station (Coakley et al. 1997, 1998). The gauging station is approximately 5 km downstream from the study site. Incubation and manipulative periods are indicated

1997, 1998). The year we conducted this study was unusual, in that there were no large spates during the months of field work. During winter, the stream surface freezes, and ice buildup can be significant, although the stream continues to flow throughout the year.

Disturbance manipulations

We manipulated the frequency, intensity, and area of disturbance on artificial substrates and monitored the response of benthic invertebrate assemblages. We created two levels of each disturbance factor. The three disturbance factors (frequency, intensity, area) were applied in a full-factorial design, yielding eight treatments and an unmanipulated control. We replicated each treatment seven times and arrayed the replicates in the stream in a randomized-block design. Each block, consisting of nine treatments, was positioned across the width of the stream, and treatment position within blocks was assigned randomly. Treatments were not replicated within blocks. Patio stones within a block were separated by 15 cm, and blocks were separated by 50 cm.

We used the upper surfaces of rectangular cement patio stones (19.2×39.2×4 cm) as experimental substrates. Cement stones were chosen because they provided comparable texture to stream substrates. Treatments were applied only to the upper surfaces and, at the end of the treatment period, samples were taken from only the upper surfaces. Because the disturbances were applied during daylight hours, invertebrates that spend daylight hours on rock tops would be more strongly affected. We made no attempt to prevent colonization of the upper surfaces by invertebrates from the under surfaces or surrounding benthos. To allow for colonization by periphyton and invertebrates, we placed all of the patio stones in the stream on 29 July 1996, 27 days before initiating disturbances. We checked and repositioned the stones during the colonization period to ensure constant submersion.

Disturbances were initiated on 28 August 1996 and maintained until 10 October 1996. Spates are less frequent during this time than during spring and summer, but they do occur year-round. We applied the experimental disturbances with a frequency of either once or twice weekly. We chose these frequencies because other stream assemblages typically recover fully from disturbances within 8–30 days (Boulton et al. 1988; Lake and Schreiber 1991). Weekly disturbances are common in this stream, and even higher frequencies of spates are not unusual (Fig. 1). When we collected the macroinvertebrates from the substrates, the high-frequency treatments had been disturbed 4 days previously whereas the low-frequency treatments had been disturbed 7 days earlier. Thus, the high-frequency treatments could also be thought of as 'young' or recently disturbed patches and the low-frequency treatments as relatively 'old.'

We used a wire scrubbing brush to simulate intense disturbance and a paintbrush to simulate mild disturbance. The intense disturbance removed sediment, insects such as *Hydropsyche* sp. and *Antocha* sp., filamentous algae, and many of the diatoms. The mild disturbance removed sediment and some insects, but left much of the filamentous algae intact.

Disturbances were applied to 50% or 100% of the surface area. The 50% disturbances were applied to four randomly selected circular patches, with each patch representing 12.5% of the total area. For each disturbance, we randomly assigned the location of the four patches on a substrate. This created patches of mixed age, or time since disturbance. The 50% area disturbances were designed to simulate creation of a disturbed area adjacent to an undisturbed area. Small-scale patchiness of this sort can result when stones are rolled and partially abraded. We applied disturbances beginning at the upstream end of the experimental array and proceeded downstream. We completed each block before disturbing a second block. There were no major spates during the manipulation period, although two minor spates occurred before and during data collection (Fig. 1).

Sample processing

After 43 days of maintaining the disturbance regimes, we collected macroinvertebrates from the tops of the patio stones. All samples were taken during daylight hours. We began collecting at the downstream end, one block at a time, to ensure that dislodged insects did not colonize other experimental substrates. We carefully lifted the stones from the stream to avoid dislodging insects from the upper surfaces. We did not use a downstream net because it would have sampled organisms from the undisturbed, lower surfaces of the substrates and from underlying substrates (McAuliffe 1984). We removed invertebrates from the stones with a paint scraper and scrubbing brush. The scrubbing required to collect the invertebrates was more intense and of far longer duration than the experimental scrubbing. We applied the same scrubbing intensity to all treatments to ensure consistent sampling among treatments and replicates. We rinsed the scrubbed material in a 145-μm sieve to remove sediment and preserved each sample in 95% EtOH. All samples were taken between the 1000 and 1800 hours. On average, 15 min were required to collect each sample.

In the laboratory, we split the samples using a Folsom plankton splitter (Wildco, model number 1831-f10 0298). The number of splits varied with treatment and depended on the abundance of insects in the samples. To adequately represent the community on each substrate, we identified a minimum of 300 randomly selected invertebrates per sample (Vinson and Hawkins 1996). With the exception of chironomids, invertebrates were identified to the lowest possible taxonomic level. We have therefore measured 'taxon richness' but will refer to it as 'species richness' throughout the paper.

We identified 42 taxa from the samples. The most common taxa were chironomids (76%), early-instar hydroptilids (6.7%), and *Hemerodromia* sp. (3.3%). Eight taxa accounted for 96% of the total abundance in the samples. The four most common taxa (Chironomidae, early-instar Hydroptilidae, *Hemerodromina* sp., and *Antocha* sp.) were more abundant on controls than on any of the disturbed treatments. There were more than twice as many chironomids on controls than any of the disturbed treatments. Free-living, early-instar hydroptilid (Trichoptera) larvae were more than five times more abundant on controls than on disturbed treatments. *Aturus carolinensis*, *Sperchon pseudoplumifer* (Acari; Hydracarina), and *Hydropsyche* sp. (Trichoptera; Hydropsychidae) reached highest abundance on the low-frequency, low-intensity, 50% area disturbance treatment. *Oecetis avara* (Trichoptera; Leptoceridae) was most abundant on the high-intensity, high-frequency, 100% area treatment.

Because chironomids could not be identified to species, taxonomic lumping could have biased our results. Therefore, we reanalyzed the dataset without the chironomids and obtained very similar results. Compared to other diversity indices, the rarefaction method we used is relatively insensitive to taxonomic bias and distortion (Antia 1977; Gotelli and Graves 1996). Analyses of the full dataset, with chironomids constituting a single taxon, are presented in this paper.

Data transformations

We rescaled the abundance data to account for the sample splits and used a log_{10} transformation to normalize the distribution of the abundance data. Because abundance varied within and between treatments, species richness counts could not be compared directly. Most studies of 'species richness' are actually describing 'species density,' that is the number of species per unit area or per sample (Simpson 1949). We use the term 'species richness' to mean the expected number of species for a given number of randomly sampled individuals. Species richness enables us to compare species counts among treatments that differ in abundance. This statistical adjustment is important because of the major effect of disturbance on abundance.

We used a Monte Carlo method similar to rarefaction (Hurlbert 1971; Simberloff 1972) to estimate the expected species richness

for a given number of individuals drawn randomly from a sample. The least abundant replicate in our samples had 281 individuals. Therefore, we randomly sampled 281 individuals from each replicate and recorded the observed number of species, using Ecosim simulation software (Gotelli and Entsminger 1999). We repeated the randomization 100 times for each replicate and used the average number of species as the expected species richness. Expected species richness for each replicate was then used as a response variable in analyses of variance.

We determined species density as the number of species recorded from one-sixteenth of each sample. One-sixteenth was the smallest portion of any sample counted and identified (average 472 individuals in 1/16 of sample). To measure species density from samples for which a greater proportion had been identified, we randomly sampled a number of individuals equal to one-sixteenth of rescaled abundance (as described above) for that sample. Using Ecosim (Gotelli and Entsminger 1999) we repeated this procedure 100 times for each sample and recorded the mean number of species for the 100 replicates as species density. Species density is therefore the number of species expected in one-sixteenth of the area of the upper surface of an experimental substrate. As with expected species richness, we used species density as a response variable in the analyses of variance.

Within-patch analysis

The response variables in our analyses were $\log_{10}$(total abundance) and species richness. We first analyzed these data as a MANOVA, which was highly significant for both the one-way and the factorial three-way designs. This result justifies the use of separate ANOVAs for abundance and species richness. We have presented only the ANOVA results (Tables 1, 2).

For each response variable, we first used a randomized-block one-way ANOVA to compare all nine treatments (eight disturbance regimes plus the unmanipulated control). This model assumes there is no interaction between blocks and treatments (Underwood 1997). We used an a priori linear contrast to test the null hypothesis that the control mean did not differ from the average of the eight disturbance means. Next, we deleted the control data and used a randomized block three-way factorial ANOVA to evaluate the main effects and interactions of frequency, intensity, and area of disturbance.

Among-patch analysis

To compare within- and among-patch patterns, we used the upper surface of a patio stone to represent a single patch. Rock surfaces of this size are natural habitat patches that are disturbed when overturned by stream current. Rocks in this size range and larger overturn frequently in the LaPlatte River and similar streams. To address whether the effects of disturbance are comparable within and among patches (Wilson 1994; Collins and Glenn 1997), we pooled the seven replicates (i.e., patches) within each treatment and then used Ecosim to create a single rarefaction curve for each treatment. This approach enabled us to examine the effect of increased spatial scale on the richness responses of the assemblages.

In a separate analysis, we pooled all the data from the eight disturbance treatments and created an aggregate rarefaction curve, which represents diversity measured across patches of different disturbance histories. This aggregate curve was compared to the rarefaction curve of the pooled control replicates, which were never disturbed.

Finally, we used total abundance as a surrogate to measure the overall impact of disturbance. We reasoned that abundance would be highest in undisturbed assemblages, and lowest in assemblages that had been most heavily disturbed. Next we plotted expected species richness as a function of total abundance in each replicate. The IDH predicts a hump-shaped curve, whereas Huston's (1994) other disturbance models predict a monotonic increase or decrease in species richness, depending on individual growth rates and

competitive responses. Our plot is analogous to Huston's (1994) Figs. 5 and 6, but with the direction of the disturbance gradient running from high (=low abundance) to low (=high abundance).

Results

Abundance

There was a significant effect of disturbance on total abundance (Table 1). Abundance in all eight disturbed treatments was lower than in unmanipulated controls ($P<0.0001$; a priori linear contrast; Fig. 2). The factorial ANOVA revealed significant main effects of disturbance intensity and area on total abundance. Effects of disturbance frequency were not significant. Treatments receiv-

Table 1 ANOVA of effects of disturbance on $\log_{10}$(abundance). *All treatments* is a one-way ANOVA comparing means of all nine treatments. *Disturbed vs controls* is an a priori contrast comparing the undisturbed control with the mean of the eight disturbance regimes (*$P<0.05$, **$P<0.01$, ***$P<0.005$)

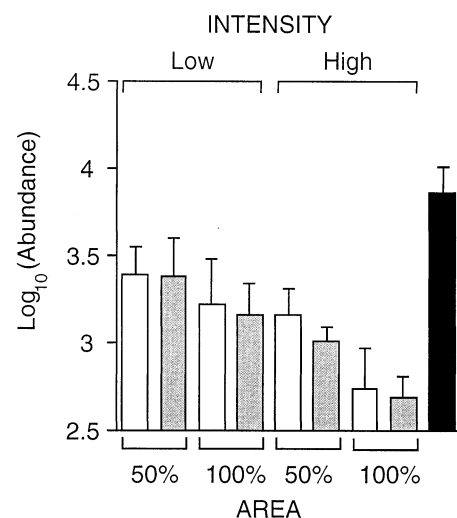| Effect	df	SS	MS	F-ratio
Block	6	0.520	0.087	3.330**
Intensity (I)	1	2.110	2.110	81.107***
Area (A)	1	1.102	1.102	42.336***
Frequency (F)	1	0.069	0.069	2.638
I×A	1	0.113	0.113	4.346*
I×F	1	0.018	0.018	0.702
F×A	1	0.002	0.002	0.066
I×A×F	1	0.022	0.022	0.852
Error	42	1.093	0.026	
All treatments	8	7.060	0.883	35.273***
Block	6	0.555	0.093	3.699***
Error	48	1.201	0.025	
Disturbed vs control	1	3.624	3.624	144.863***

Fig. 2 $\log_{10}$(abundance) (mean+1 SD) of macroinvertebrates in disturbance treatments and controls [*open bars* low frequency of disturbance (once per week), *gray bars* high frequency (twice per week), *black bar* undisturbed controls]

**Table 2** ANOVA of effects of disturbance on expected species richness. See legend to Table 1 for further details

Effect	df	SS	MS	F-ratio
Block	6	11.720	1.953	0.559
Intensity (I)	1	22.470	22.470	6.436*
Area (A)	1	14.100	14.100	4.037 (P=0.051)
Frequency (F)	1	0.011	0.016	0.030
I×A	1	2.563	2.563	0.734
I×F	1	7.402	7.402	2.119
F×A	1	0.004	0.004	0.001
I×A×F	1	8.378	8.378	2.399
Error	42	146.699	3.493	
All treatments	8	134.302	16.788	5.474***
Block	6	12.201	2.034	0.663
Error	48	147.220	3.067	
Disturbed vs control	1	79.270		25.845***

Fig. 3 Expected species richness (mean+1 SD) of macroinvertebrates in disturbance treatments and controls [*open bars* low frequency of disturbance (once per week), *gray bars* high frequency (twice per week), *black bar* undisturbed controls]

ing the high-intensity disturbance had lower abundance than treatments receiving the low-intensity disturbance (Fig. 2). Abundance in the 100% area disturbance was significantly less than in the 50% area disturbance (Fig. 2). Finally, there was a significant area×intensity interaction: the area effect was stronger at high intensity than at low intensity. The highest average abundance was recorded in the undisturbed control. The lowest average abundance was recorded in the high-frequency, high-intensity, 100% area treatment. Abundance in this treatment was less than 5% of that in the undisturbed controls, which had the highest abundance of any treatment. There were significant differences among blocks in average abundance, which was higher in upstream versus downstream blocks (Table 1; correlation of log abundance and block number: $r^2=0.696$, $P=0.012$).

Species richness

There was a significant effect of disturbance on species richness (Table 2). Species richness was significantly higher in disturbed treatments than in the undisturbed controls ($P<0.0001$; a priori linear contrast). Species richness was higher in high-intensity treatments than in low-intensity treatments (Fig. 3). Effects of the other factors and interactions were not significant (full-factorial ANOVA). The effect of area was marginally non-significant ($P=0.051$), with higher species richness in the 100% area treatment than in the 50% area treatment. The highest average species richness was recorded in the high-frequency, high-intensity, 100% area treatment. The lowest average species richness was in the undisturbed controls. There were no significant effects of disturbance frequency or block on species richness.

The rarefaction curves from the individual disturbance treatments clustered together, but fell outside the 95% confidence limit of the rarefaction curve of the controls (Fig. 4). The rarefaction curve based on pooling of all disturbance treatments also fell outside the 95% confidence limit of the rarefaction curve of the controls (Fig. 5).
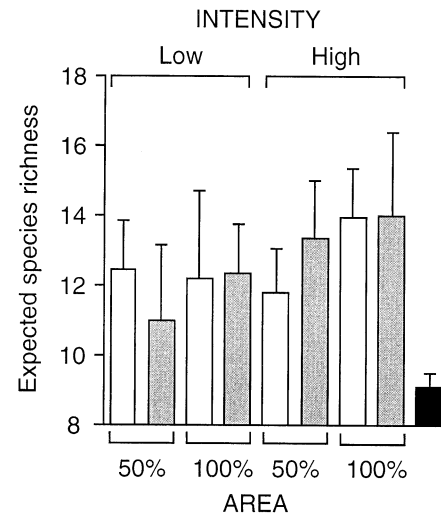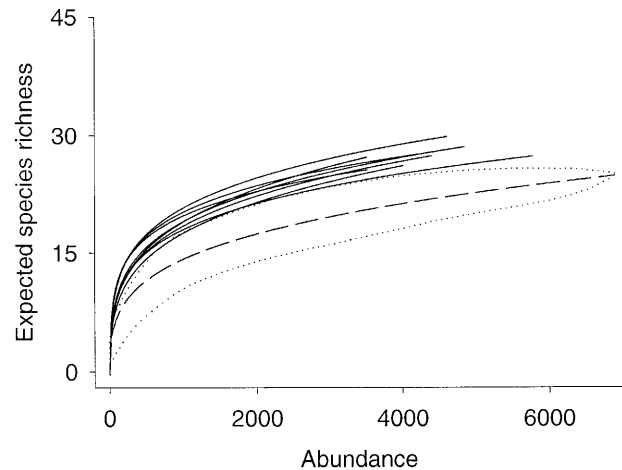
Fig. 4 Rarefaction curves of the pooled replicates of disturbed treatments and controls. *Solid lines* indicate the eight disturbance treatments. *Dashed line* indicates the undisturbed control. *Dotted lines* represent the 95% confidence limits of the control curve. The curves show the expected species richness for a given number of randomly sampled individuals

When the species richness of each replicate was plotted against total abundance, there was a significant negative relationship ($r=-0.64$, $P<0.0005$). Expected species richness was highest in intensely disturbed treatments with low abundance (Fig. 6). Species richness was lowest in undisturbed controls with high abundance (Fig. 6, open triangles).

Species density

Effects of disturbance treatments on species density were significant (Table 3). In direct contrast to the expected
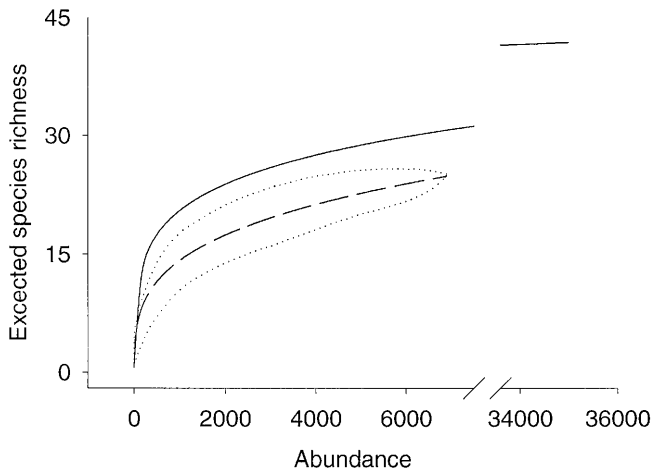
Fig. 5 Rarefaction curves of the pooled disturbed treatments and undisturbed substrates. The *solid line* was generated by pooling data from all eight disturbance treatments and randomly sampling. *Dashed line* indicates the undisturbed control. *Dotted lines* represent the 95% confidence limits of the control curve
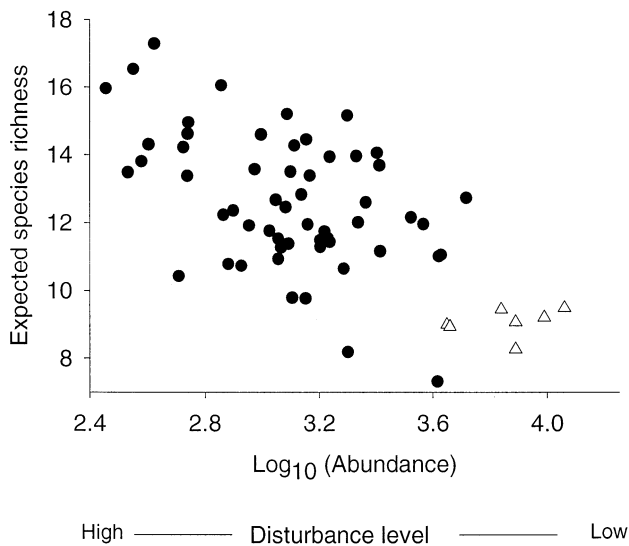
Table 3 ANOVA of effects of disturbance on species density. See legend to Table 1 for further details

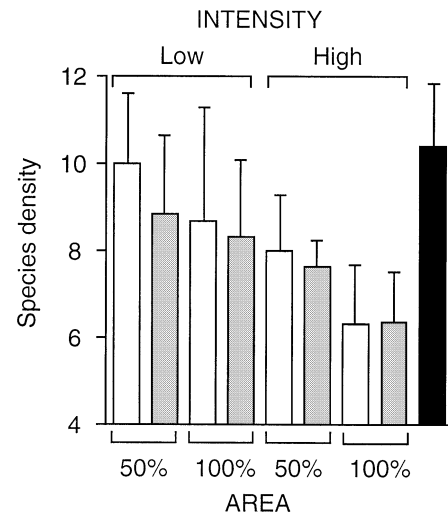| Effect	df	SS	MS	*F*-ratio
Block	6	51.851	8.642	4.972***
Intensity (I)	1	49.200	49.200	28.308***
Area (A)	1	20.389	20.389	11.731**
Frequency (F)	1	2.912	2.912	1.675
I×A	1	1.013	1.013	0.583
I×F	1	1.227	1.227	0.706
F×A	1	1.318	1.318	0.758
I×A×F	1	0.147	0.147	0.085
Error	42	72.998	1.738	
All treatments	8	110.771	13.846	8.277***
Block	6	57.122	9.520	5.691***
Error	48	80.298	1.673	
Disturbed vs control	1	34.566		20.663***

Fig. 7 Species density (mean+1 SD) of macroinvertebrates in disturbance treatments and controls. [*open bars* low frequency of disturbance (once per week), *gray bars* high frequency (twice per week), *black bar* undisturbed controls]

Fig. 6 Relationship between macroinvertebrate abundance and expected species richness. The *x*-axis is the total abundance of macroinvertebrates in a replicate. The *y*-axis is the expected species richness based on a random subsample of 281 individuals. Each *point* represents a different replicate. *Closed circles* represent disturbance treatments, *open triangles* represent undisturbed controls (r=–0.64, P<0.0005, n=63 replicates)

species richness response, species density was lower in disturbed treatments than in undisturbed controls (P<0.001, a priori linear contrast). Species density was lower in high-intensity disturbance treatments than in low-intensity treatments (Table 3, Fig. 7), again opposite to the expected species richness pattern (Fig. 3). Species density was higher when 50% of the substrate area was disturbed than when 100% of the area was disturbed (Table 3, Fig. 7). Disturbance intensity and interactions among disturbance factors did not have significant effects on species density (Table 3). Highest species densi-

ty was recorded on undisturbed controls and lowest species density was found on low-frequency, high-intensity, 100% area disturbance treatments. Species density responses to disturbance (Fig. 7, Table 3) were qualitatively similar to the abundance responses (Fig. 2, Table 1) including the significant block effect with higher species density in upstream versus downstream blocks (Table 3; correlation of species density and block number: r^2=0.123, P=0.003).

Discussion

Effects of disturbance on species richness and species density

As in other studies (Boulton et al. 1988; Lake et al. 1989), macroinvertebrates rapidly colonized our experimental substrates following disturbance. Species rich-

Table 4 Field experiments examining the effects of artificial physical disturbance on stream macroinvertebrates. Predator exclusion studies and individual-species-removal experiments have not been included. Only those studies reporting diversity and/or abundance measures have been included ($D<C$ disturbed treatments had significantly lower means than controls, $D=C$ disturbed treatments did not differ significantly from controls, $D>C$ disturbed treatments had significantly higher means than controls)

Study	Stream order	Disturbance type	Disturbance factor manipulated	Frequency or time since disturbance (days)	Diversity measure	Diversity response	Abundance response
Boulton et al. (1988)	5	Stones overturned, brushed, acid-scoured	Intensity, time since	15	Species density	$D<C$	$D<C$
Clifford (1982)	3	Riffles kicked and raked	Time since	14–62	H'	$D=C$	$D<C$
Death (1996)	1–3	Substrate baskets shaken	Frequency	21, 63	Species density	$D<C$	$D<C$
Doeg et al. (1989)	4	Riffles kicked and raked	Time since	10–70	Species density	$D<C$	$D<C$
Englund (1991)	3, 4	Stones overturned	Time since	60–421	Species density, H'	$D=C$, $D>C$[a]	$D<C$
Johnson and Vaughn (1995)	2	Bedrock scraped	Time since	30	None	–	$D=C$
Lake et al. (1989)	4	Riffles kicked and raked	Frequency, time since	10	Species density	$D<C$	$D<C$
Matthaei et al. (1996)	4, 6	Riffles kicked	Time since	1–30	Species density	$D<C$	$D<C$
Matthaei et al. (1997)	6	Riffles kicked	Time since	1–40	Species density	$D<C$	$D<C$
Reice (1985)	4	Substrate baskets tumbled	Frequency	21–42	Species density, H'	$D=C$	$D<C$
Robinson and Minshall (1986)	3	Bricks up-turned	Frequency	3–54	Species density, H'	$D<C$, $D>C$[b]	$D<C$
Rosser and Pearson (1995)	2, 3	Bricks tumbled and scrubbed	Intensity, area[c]	1	Species density	$D<C$	$D<C$

[a] Species density fell and H' increased after stone turning (decrease in diversity was reported in the abstract)
[b] Species density was reduced by disturbance, H' was increased by disturbance
[c] Intensity and area manipulated in separate experiments

ness was higher in all of our disturbance treatments than in undisturbed controls (Fig. 3). This pattern is predicted by Huston's (1979, 1994) dynamic-equilibrium model when the species populations are growing rapidly and have high rates of competitive exclusion (Figs. 5, 6c in Huston 1994). Although we did not assess competitive interactions in our experiment, other studies have documented competition among species in the genera *Hydropsyche*, *Simulium* (Hemphill and Cooper 1983), and *Leucotrichia* (McAuliffe 1984; Hart 1985), all of which were present at our site. Resh et al. (1988) and Reice et al. (1990) also concluded that the dynamic-equilibrium model (Huston 1979) is generally applicable to stream communities, although they did not clearly state which of Huston's (1994) specific hypotheses were supported.

The increased richness we observed following disturbance is in sharp contrast to the results of most stream experiments (Table 4). In most other studies, experimental disturbance decreased species density and was followed by a rapid recovery to control levels or predisturbance levels (but see Englund 1991). This pattern was consistent across disturbance types including stone turning (Englund 1991), and substrate kicking and raking (Doeg et al. 1989; Lake et al. 1989). However, the reduction in species density we observed after disturbance (Fig. 7) is consistent with the results of most disturbance experiments in streams (Table 4).

Our results emphasize the importance of appropriately quantifying richness in benthic community samples. In community samples, number of individuals sampled and the number of species in a sample are positively related (Gotelli and Graves 1996). Because disturbance lowers abundance, we expect fewer species per unit area in disturbed substrates. Whereas most studies have used only species density (number of species/area, or number of species/sample) to quantify diversity (Table 4), we also determined expected species richness (number of species/number of individuals sampled), based on a Monte Carlo simulation (Gotelli and Entsminger 1999) that is analogous to rarefaction (Simberloff 1978). Although species density is strongly influenced by total abundance, expected species richness is free from this bias. Because disturbance lowers total abundance, it is important that the measure of diversity used be free of influence from total abundance. Use of species density as a diversity measure in previous disturbance studies may have masked increased species richness in disturbed treatments. Species density responses in our experiment are directly opposite to the species richness responses and emphasize the importance of choosing the measure of diversity most appropriate to the questions being addressed in community studies.

Effects of disturbance on abundance

Our disturbance manipulations decreased macroinvertebrate abundance (Fig. 2), consistent with most disturbance experiments in streams (Table 4). Reduced abun-

dance of organisms is central to many definitions of ecological disturbance (Connell 1979; Sousa 1985; Townsend and Hildrew 1994). Although the abundance of some individual taxa can increase following disturbance (Levey 1988; Englund 1991; Wootton et al. 1996), total abundance of the community is typically reduced (Death 1996; Pringle and Hamazaki 1997).

Although definitions of intensity and frequency of disturbance are not consistent in the literature (White and Pickett 1985; Petraitis et al. 1989; Turkington et al. 1993), there appears to be broad agreement that disturbance removes individuals (Connell 1979; Sousa 1985; Townsend and Hildrew 1994). Therefore, we used total abundance of organisms in a patch as a surrogate for the total effect of disturbance. This approach seems valid for an experimental study in which only the disturbance regime varied systematically among replicates. We reasoned that abundance would be reduced more by disturbances of larger area, greater frequency, or greater intensity. Using abundance as a measure of the overall effect of disturbance enabled us to rank the different disturbance treatments and examine patterns of species richness.

Although total abundance varied among samples, our measure of species richness is adjusted by rarefaction to a common abundance, so that sampling effects are removed. The same cannot be said for species density. Across all treatments, expected species richness decreased with total abundance (Fig. 6), and the undisturbed controls represent the extreme endpoint of this density spectrum. In other words, even with standardized samples of an equivalent number of individuals, low-density assemblages had greater species richness than high-density assemblages. This pattern matches one of the scenarios in Huston's (Figs. 5, 6c in Huston 1994) dynamic equilibrium model. In this scenario, competitive exclusion is expected to lower diversity when disturbance frequency is lower than the rate of competitive exclusion. As disturbance frequency and/or intensity increase, diversity increases because density is reduced such that competitive exclusion no longer occurs. These data also suggest that recolonization after disturbance is affected by species interactions. If patches randomly accumulated colonists that did not interact (Coleman et al. 1982), species richness would have been similar in all of our experimental treatments after we had adjusted for abundance.

Interactions of disturbance frequency, intensity, and area

Although there were strong effects of disturbance intensity and area on abundance and species richness, we detected few interactions between these factors. The only significant interaction we detected was between the effects of intensity and area on total abundance (Table 1). There was a larger reduction of abundance between low- and high-intensity treatments when 100% of the area was treated than when 50% of the area was treated (Fig. 2). One explanation for this pattern is that undisturbed areas of the substrate served as sources of colonists for the disturbed areas. In the 50% area treatments, the undisturbed portions of the substrate may have served as spatial refugia from disturbance. Other studies have also demonstrated the potential importance of refugia as sources of recolonization in streams after disturbance (Palmer et al. 1992, 1995; Dole-Olivier et al. 1997).

Although disturbance frequency is thought to influence community structure (Huston 1994), the disturbance frequencies we used (once or twice weekly) may have been too frequent to allow for much colonization between events. If once per week was too frequent, then disturbing substrates a second time per week would make little difference to the response variables. This may explain the absence of significant effects of disturbance frequency in our experiment.

Within- versus among-patch patterns

Collins and Glenn (1997) advocated application of the IDH without restrictions on spatial or temporal scale. Our statistical analyses (Table 2) described within-patch patterns because they averaged diversity among a set of similar patches. However, our data can be analyzed to demonstrate that disturbance increases diversity both within and among patches.

Diversity patterns among patches might be greater than within patches because a set of patches accumulates diversity across a larger spatial scale. To analyze this pattern, we pooled replicates and constructed a separate rarefaction curve for each treatment. The result was that species richness in the eight disturbed treatments was substantially higher than in the controls (Fig. 4).

A related argument is that diversity is higher at the among-patch scale because it incorporates patches with different disturbance histories (Pickett 1980; Wilson 1994). To test this hypothesis, we pooled all of the replicates from the eight experimental treatments and compared this single rarefaction curve to the pooled controls. As before, the rarefaction curve for the pooled disturbance data was substantially higher than the controls (Fig. 5). Interestingly, the multitreatment rarefaction curve (Fig. 5) fell among the curves of the individual disturbance treatments (Fig. 4) suggesting that combining patch types contributed no additional diversity. Thus, the increase in diversity caused by disturbance emerges at three scales of analysis: within patches (Fig. 3), among patches with identical disturbance history (Fig. 4), and among patches with heterogeneous disturbance history (Fig. 5).

Despite the scale-independent nature of the response to disturbance, we do not necessarily advocate extrapolation of these results to larger scales. It is important to note that larger-scale disturbances, while removing individuals from patches, can also remove individuals from surrounding patches. Thus the number of potential colonists of disturbed patches would tend be reduced by larger-scale disturbances. Whereas macroinvertebrates in streams may use the hyporheic zone (Dole-Olivier et al. 1997) as a refugium and avoid being removed by distur-

bance events, the number of macroinvertebrates available to colonize disturbed patches would still be reduced. Our disturbance manipulations are better suited to model the effects of patch scale disturbances.

Species richness versus species density

Should assemblages be compared on the basis of species density (number of species per unit area or sampling effort) or species richness (number of species per a standardized number of individuals)? Most ecologists have measured species density, even though they often call it species richness. Species density is a natural choice because it follows from the sensible practice of using standardized samples of equivalent area or sampling effort. However, because more abundant samples will tend to have more species, differences in species density among samples of differing abundance must be viewed as potential sampling artifacts unless a rarefaction technique provides evidence to the contrary. Rarefaction of our data confirms that decreases in species density after disturbance can in large part be explained by changes in abundance.

Furthermore, measures of species richness may be preferable because most ecological models describe changes in abundance or species richness, not changes in density or species density. In particular, 'classical' ecological models that are based on ordinary differential equations (e.g., Wootton 1998) usually do not contain terms for area or density. Instead, these models are built on per capita interaction effects of one population or species on another. To test these models, we think it is more relevant to use species richness than species density, which is affected by both species richness and abundance.

A more practical reason for preferring expected species richness is that it allows us to subsample and efficiently compare very large collections of individuals. In our study, rock surfaces constitute 'natural' patches that are potentially affected by disturbances. Even at this relatively small spatial scale, a single patch may contain thousands of individuals, and it would be too time-consuming to sort the entire collection. If we had restricted patches to a constant area that contained a reasonable number of individuals, the area would have been so small that it was biologically unrealistic. For example, if we had reduced the substrate areas of all treatments so that control samples contained 300 individuals, a number recommended by Vinson and Hawkins (1996) for making inferences from samples of aquatic invertebrates, samples from the most disturbed treatments would have had fewer than 8 individuals. This example illustrates the advantages of rarefaction when comparisons are made between samples that vary in abundance by orders of magnitude.

Conclusions

In summary, our analyses show that increasing disturbance intensity and area, but not frequency, decreases abundance and increases expected species richness of stream benthic assemblages. These results contradict the classic IDH, but they match with some scenarios of Huston's (1994) dynamic-equilibrium model. These results are also consistent with multitrophic disturbance models (Wootton 1998), which do not predict maximum richness at intermediate disturbance levels.

Testing hypotheses in community ecology – even with experimental data – can be tricky because of subtle ambiguities in the definition of richness. Should assemblages be compared on the basis of the area sampled or the number of individuals sampled? Although the concepts of standardized sampling and the rarefaction methodology are well understood, ecologists have not often distinguished the patterns of abundance, species richness, and species density of assemblages (James and Wamer 1982). These metrics should be carefully disentangled in any test of the effects of disturbance because of the strong effects of disturbance on total abundance.

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