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Diversity-productivity relationships in streams vary as a function of the natural disturbance regime

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Understanding the key ecological factors that moderate the relationship between biodiversity and the productivity of ecosystems is a major challenge for ecological research. Here we show that the relationship between the species richness of primary producers and net rates of biomass production in streams depends on the history of discharge-related disturbances. Using common methods to study 83 streams in the mid-Atlantic United States, we demonstrate that a positive relationship between producer richness and the net production of biomass only occurs in streams characterized by highly variable, unpredictable discharge regimes that represent frequently disturbed environments to benthic organisms. This pattern is partly explained by predictable changes in the composition of species assemblages among disturbed streams. The pattern also results because, in disturbed systems, species have faster rates of biomass accumulation when they are a part of species-rich assemblages. We discuss several possible explanations for this result. Our study supports qualitative predictions from theoretical and small-scale experimental work that the strength of the diversity-productivity relationship will depend explicitly on the disturbance regime of an ecosystem. The results have important implications for the management and conservation of aquatic resources as they suggest that changes to the productivity and diversity of streams may have their greatest impacts on organisms and systems that are most sensitive to disturbance.

DIVERSITY–PRODUCTIVITY RELATIONSHIPS IN STREAMS VARY AS A FUNCTION OF THE NATURAL DISTURBANCE REGIME

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Abstract. Understanding the key ecological factors that moderate the relationship between biodiversity and the productivity of ecosystems is a major challenge for ecological research. Here we show that the relationship between the species richness of primary producers and net rates of biomass production in streams depends on the history of discharge-related disturbances. Using common methods to study 83 streams in the mid-Atlantic United States, we demonstrate that a positive relationship between producer richness and the net production of biomass only occurs in streams characterized by highly variable, unpredictable discharge regimes that represent frequently disturbed environments to benthic organisms. This pattern is partly explained by predictable changes in the composition of species assemblages among disturbed streams. The pattern also results because, in disturbed systems, species have faster rates of biomass accumulation when they are a part of species-rich assemblages. We discuss several possible explanations for this result. Our study supports qualitative predictions from theoretical and small-scale experimental work that the strength of the diversity–productivity relationship will depend explicitly on the disturbance regime of an ecosystem. The results have important implications for the management and conservation of aquatic resources as they suggest that changes to the productivity and diversity of streams may have their greatest impacts on organisms and systems that are most sensitive to disturbance.

Key words: ecosystem functioning; floods; periphyton; species richness; stream algae.

INTRODUCTION

There is a long history of scientific interest in the relationship between the biological diversity and productivity of ecosystems. However, the amount of research dedicated to understanding this relationship has increased over the past several decades as human activities have begun to alter diversity and productivity at unprecedented rates (Vitousek et al. 1997, Chapin et al. 2000, Sala et al. 2000). Despite increased effort, the links between diversity and biomass production remain tentative. In part, this is because empirically derived relationships have proven to be highly variable for different types of ecosystems and for different groups of organisms (Johnson et al. 1996, Waide et al. 1999, Mittelbach et al. 2001, Schmid et al. 2001). Furthermore, the relationships documented at the small spatial and short temporal scales of experimental work have often been qualitatively different from the patterns observed across larger scales in natural ecosystems (Gross et al. 2000, Fridley 2001, Bengtsson et al. 2002, Chase and Leibold 2002, Symstad et al. 2003, Cardi-

nale et al. 2004). As a consequence, identifying the key ecological factors that moderate the diversity–productivity relationship across systems and scales is a major challenge for ecological research.

Prior study of the diversity–productivity relationship has taken one of two routes. In the first, ecologists have asked how the availability of resources that limit biomass production simultaneously affects the number of coexisting species (see reviews by Rosenzweig and Abramsky 1993, Waide et al. 1999, and Mittelbach et al. 2001). In the second, researchers have asked how the number of species in a “regional” colonist pool can regulate the capture and conversion of resources into local community biomass (e.g., reviews by Tilman 1999, Loreau et al. 2001, and Naeem 2002). Amid current efforts to combine these perspectives into a more synthetic understanding of causality between diversity and productivity (e.g., Grime 1998, Fridley 2002, Schmid 2002), certain commonalities have emerged. For example, both lines of study suggest the effects of diversity and production on one another will depend explicitly on the disturbance regime of an ecosystem. Indeed, multivariate models of species coexistence argue that the frequency and severity of disturbances can alter the availability of resources that, in turn, limit both primary production and the strength of interac-

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tions that determine the diversity of competing species (Grime 1973, Huston 1979, Rosenzweig and Abramsky 1993, Kondoh 2001, Worm et al. 2002). A complementary set of studies predicts that the reverse effect of species richness on biomass production will depend on how disturbance (1) moderates the balance of positive and negative interactions that regulate per capita resource capture (Mulder et al. 2001, Cardinale and Palmer 2002, Cardinale et al. 2002) and (2) alters rates of dispersal that determine the number of species and rate of biomass accrual in a recovering site (Kondoh 2001, Mouquet et al. 2002, Loreau et al. 2003, Cardinale et al. 2004). Unfortunately, predictions from these theoretical studies and small-scale, controlled experiments are varied, and the proposed mechanisms underlying some of the predictions have been questioned on theoretical grounds (Chesson and Huntly 1997, Chesson 2000). As a result, there is little consensus as to whether disturbance influences the diversity–productivity relationship in natural communities of organisms, and if so, how.

A dominant form of disturbance in streams occurs as temporal variation in hydrologic regime (Resh et al. 1988, Allan 1995, Poff et al. 1997). Daily and monthly changes in discharge interact with the frequency and unpredictability of extreme flow events (e.g., floods) to influence the productivity and diversity of nearly all groups of streams organisms (Vannote 1980, Allan 1995). Here we present results of a study in which we used standardized methods to measure the species richness and productivity of assemblages of primary producers in streams across the mid-Atlantic region of the United States. The data were used to test the prediction that the diversity–production relationship would differ among streams that are most characterized by a history of discharge-related disturbances vs. those least characterized by disturbance. The geographic patterns we report shed light on how the diversity–productivity relationship is influenced by disturbance in natural communities, and they suggest that disparate conclusions reached in past studies may partly be explained by differences in disturbance history among sites.

METHODS

Stream disturbance regime

Streams characterized by highly variable, unpredictable changes in discharge represent frequently disturbed environments for stream organisms compared to streams having more stable, predictable discharge regimes (Resh et al. 1988, Allan 1995, Poff et al. 1997). We used records of discharge from the U.S. Geological Survey (NWISWeb, *online*)⁷ to identify streams in the mid-Atlantic United States that are most characterized by a history of variable/unpredictable discharge events, and streams most characterized by stable/predictable discharge relative to average conditions for the region. Rec-

ords of mean daily discharge were obtained for the 10-year period preceding our study (1 October 1989–30 September 1999) for all streams gauged in Maryland, North Carolina, Pennsylvania, Virginia, and West Virginia. Streams were eliminated from the data set if >365 d were missing from the record, and the smallest and largest streams (mean daily flow <0.85 or >113 m³/s) were eliminated because many were too ephemeral or too deep to sample.

For the 473 streams remaining, records were used to calculate six metrics that collectively describe the long-term variability and predictability of discharge in each stream. These included: (1) the coefficient of variation of mean daily discharge, (2) the coefficient of variation of mean monthly discharge, (3) the mean number of floods per year, and the temporal predictability of (4) daily discharge, (5) monthly discharge, and (6) flooding (calculated as Colwell's index; Colwell 1974). These metrics were chosen partly because they have been used before to characterize the multivariate effects of disturbance on stream organisms (Poff and Ward 1989), and because they describe hydrologic variation at time scales that are relevant to the assembly of periphyton communities. For purposes of this study, we defined a flood as any discharge exceeding the 1.67-yr recurrence interval. This magnitude of event is thought to represent a "bank-full" discharge where physical forces are great enough to mobilize streambed sediments (Leopold et al. 1964, Poff and Ward 1989). Given that sediment movement is a major source of mortality for stream organisms (e.g., Biggs et al. 1999, Bond and Downes 2000, Matthaei et al. 2003), this definition of a flood most certainly characterizes a major disturbance to periphyton. The frequency and temporal predictability of floods were calculated separately for each stream using a flood frequency analysis of the annual maximum event series (Black 1991).

Principal components analysis (PCA) was used to ordinate streams along orthogonal axes describing the 10-year variability and predictability in stream hydrology based on the six discharge metrics (Fig. 1A). From this ordination, we identified two study groups having streams of contrasting disturbance regimes: (1) streams that have historically had high variability and low predictability of daily/monthly discharge with frequent floods that occur at unpredictable times of the year (high-disturbance or HD streams), and (2) streams that have historically had low variability and high predictability of daily/monthly discharge with infrequent floods that occur at predictable times of the year (low-disturbance or LD streams).

Standardizing the two stream study groups

We used a stratified sampling design to standardize environmental conditions among the two study groups as much as possible. We began by plotting all HD and LD streams onto a GIS map of the U.S. Environmental Protection Agency's Type III ecoregions (Fig. 1B).

⁷ (<http://waterdata.usgs.gov/nwis>)

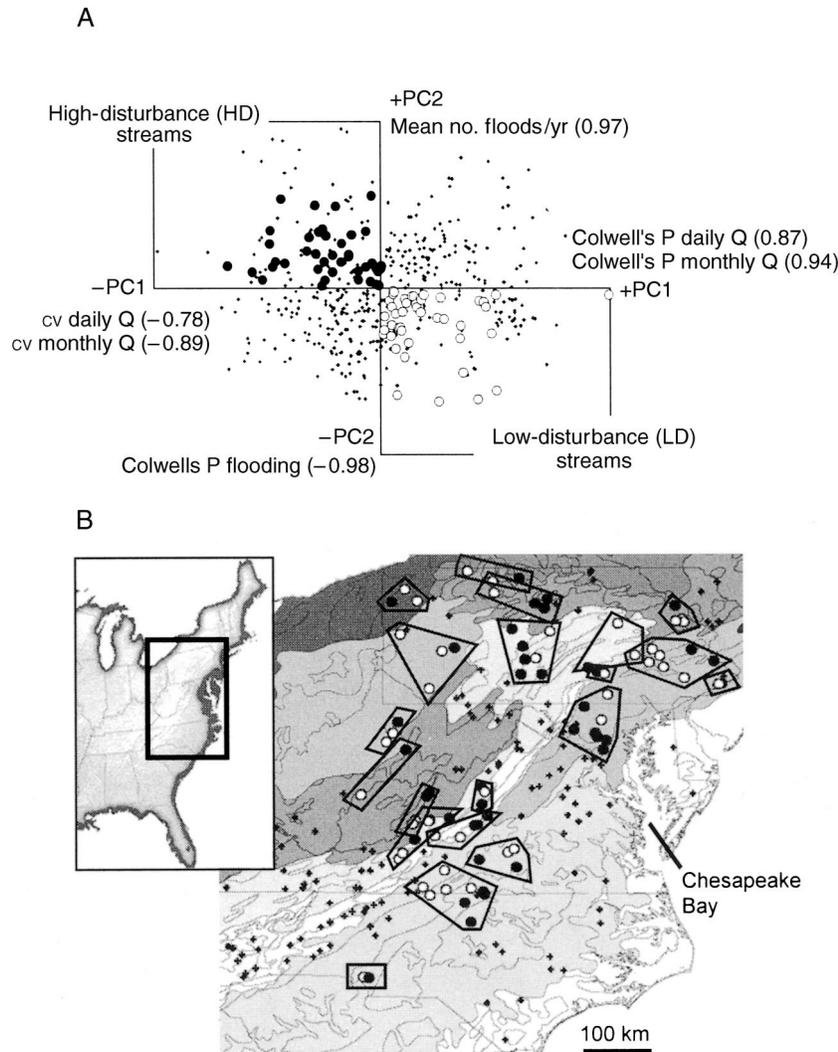


FIG. 1. (A) Principal components analysis (PCA) was used to ordinate 473 streams in the mid-Atlantic United States according to six metrics that collectively describe the 10-year history of variation and unpredictability in discharge in each stream (see *Methods* for a description of the metrics). Factor scores for the streams are plotted along orthogonal axes that explain 82% of the variation, with metric loadings given in parentheses. Streams in the upper left quadrant represent highly disturbed ecosystems (HD streams) relative to streams in the bottom right with relatively low disturbance regimes (LD streams). (B) To standardize conditions between study groups, HD and LD streams were plotted onto a GIS projection of the Environmental Protection Agency's Type III ecoregions (shaded areas), which are geographic regions characterized by similar geology, soil characteristics, climate, and vegetation types. We chose to study streams found in 20 naturally occurring "clusters" where one or more stream of each disturbance regime was located within a 48 km radius in the same ecoregion (enclosed by polygons). The 40 HD and 43 LD streams selected for sampling are shown as the large circles: open circles are low-disturbance streams, and solid circles are high-disturbance streams.

These ecoregions represent geographic areas of the country that have similar soil and vegetation types, similar climate, and comparable geologic histories (Omerik and Griffith 1991). We limited our sampling efforts to 40 HD and 43 LD streams found in 20 naturally occurring clusters where streams of each disturbance regime were located within a 48-km radius in the same ecoregion (polygons in Fig. 1B). This ensured that streams of both study groups were in close proximity within areas defined by similar environmental conditions. The design also allowed us to account for

correlations between diversity and productivity that might result from confounding of hydrology with geographic location of the streams (e.g., trends that might correlate to latitude or longitude).

Diversity and production

During the summer of 2001 (28 June–16 October), we used a common assay to measure net biomass production and species richness of primary producers in all 83 streams. Six sets of unglazed ceramic tiles (each set consisted of 15 5.29-cm² tiles connected in a 3 ×

5 rectangular array) were staked flush with the surface of the streambed at equidistant positions across two riffle habitats in a stream reach. Primary producers were allowed to colonize and grow on the tile substrates for a mean of 15 d (Table 1). This duration was chosen because it generally represents the period of exponential biofilm growth where accrual rate is a reliable indicator of net production (explained further after Eq. 1 below). After the incubation period, a randomly selected tile was collected from each of the six sets, and the periphyton was removed and pooled into a composite sample used to estimate diversity and biomass production for the stream. While the tiles were incubated and collected at different times of the summer for different streams, the stratified sampling design of the study ensured that LD and HD streams within a cluster (polygons in Fig. 1B) were sampled at the same time. As a result, streams of the two study groups were sampled over comparable time frames (Table 1).

The number and density of all diatoms (Bacillariophyceae) and "soft" taxa (Cyanobacteria, Chlorophyceae, Euglenophyceae, and Pyrrophyta) were determined from aliquots of diluted material allowed to settle in a Utermöhl chamber overnight. A minimum of 400 units (where units were individuals, colonies, or filaments) were counted and identified from randomly selected transects at 480 \times magnification. The entire chamber was then scanned at lower magnification (240 \times) for rare taxa. As diatoms cannot all be accurately identified to species at 480 \times , frustules were cleaned to remove the chloroplast (via boiling in 30% hydrogen peroxide), mounted in Hyrax (Custom Research and Development, Incorporated, Auburn, California, USA), and identified to species at 1500 \times .

Individual cells of each species were approximated to a geometric shape, and cell biovolume was calculated using dimensions measured on a minimum of 10 individuals per sample. The total biovolume of each species was converted to biomass assuming a specific gravity of 1.0, and the rate of biomass accumulation was calculated as the summed biomass of all taxa per tile area divided by the period of incubation. The rate of biomass accumulation is one of several metrics commonly used to estimate productivity in aquatic ecosystems (Hall and Moll 1975). We chose this method because it is the only one that allowed us to determine species-specific contributions to production: Information that is vital for interpreting diversity-productivity relationships. It should be noted, however, that this measure represents the sum of several processes:

$$P = I + G - D - E \quad (1)$$

where I , G , D , and E are the immigration, growth, death, and emigration rates of producer populations, respectively (McCormick and Stevenson 1991). It is likely that losses of biomass from cell death, D , and sloughing, E , were negligible in this study because the incubation times of tiles in the streams were kept short

to approximate the exponential phase of biofilm growth. This is important because it allows one to achieve reliable estimates of accrual rate (Stock and Ward 1989, Peterson and Stevenson 1992, Cardinale et al. 2001). However, because we cannot distinguish immigration, I , from local cell division and growth, G , we explicitly consider hypotheses that make different assumptions about the relative importance of these two factors.

Supplementary variables

To aid in interpretation of patterns, we collected data on a number of supplementary variables thought to influence, or be closely associated with, diversity and productivity in streams. Stream size was characterized using three complementary variables: wetted channel width (measured with a tape measure in small streams, or a handheld GPS in larger streams), drainage area (from USGS records), and water depth (measured at each tile location with a wading rod). Sunlight penetration to the stream channel was measured as the percent canopy cover above tile substrates using a spherical densiometer. Total N and P export from the stream watersheds were taken from predictions of the USGS SPARROW models of surface water quality (Alexander et al. 1998, 2004). As these models were last calibrated for watershed characteristics dated to 1989, their ability to accurately portray water quality for the period of our study is not entirely certain. Nevertheless, the SPARROW data set is the only one we know of that characterizes long-term, whole-stream nutrient dynamics across the broad geographic range of our study. Water velocity and turbulence intensity were measured 6-cm above the streambed at each tile location using a Flo-Mate electromagnetic flow meter (Marsh-McBirney, Incorporated, Frederick, Maryland, USA). Water temperature, pH, and conductivity were measured in each stream using electronic probes. Herbivore biomass was determined by taking three 900-cm² Surber samples (Ben Meadows Company, Janesville, Wisconsin, USA) from riffle habitats in each stream, identifying invertebrates to genus, and measuring the ash-free dry mass of the herbivore guild.

RESULTS AND DISCUSSION

A total of 189 species of primary producers were identified in our survey of streams throughout the mid-Atlantic United States. Of these, 103 taxa (54%) were found in both the LD and HD study groups, with streams in a geographic cluster (polygons in Fig. 1B) averaging 38% overlap in species composition (mean \pm 95% CI for Jaccard's index = 0.39 \pm 0.04 for HD streams, and 0.38 \pm 0.05 for LD). The richness of producer assemblages found on the sampling tiles in individual streams ranged from 12 to 40 species, and the net production of biomass spanned more than two orders of magnitude (Table 1). Across all 83 streams in the region, there was a significant positive correla-

TABLE 1. Comparison of variables measured in high-disturbance (HD) and low-disturbance (LD) streams.

Variable	HD streams				
	<i>N</i>	Minimum	Maximum	Mean (95% CI)	Partial <i>r</i>
Periphyton species richness, <i>S</i>	40	12	40	25 (2)	
Net biomass production, <i>P</i> ($\mu\text{g} \cdot \text{cm}^{-2} \cdot \text{d}^{-1}$)	40	0.13	45.65	8.71 (2.76)	
Tile incubation period (d)	40	14	17	15 (0.25)	0.48*
Day of water year samples collected†	40	270	380	308 (11)	0.50*
Stream discharge regime (from Fig. 1A)					
PC1 factor scores	40	-2.04	-0.02	-0.69 (0.16)	
cv daily Q	40	1.34	4.05	1.97 (0.18)	0.55*
cv monthly Q	40	0.71	1.40	0.97 (0.04)	0.48*
Colwell's P daily Q	40	0.41	0.53	0.46 (0.01)	0.48*
Colwell's P monthly Q	40	0.40	0.58	0.47 (0.01)	0.49*
PC2 factor scores	40	0.01	4.54	0.66 (0.24)	
Mean no. floods/yr	40	1.10	3.40	1.49 (0.11)	0.48*
Colwell's P flooding	40	0.39	0.67	0.60 (0.02)	0.48*
Supplemental variables					
Canopy cover (%)	40	0	93	32 (8)	0.47*
Channel width (m)	40	3	46	18 (3)	0.38*
Conductivity ($\mu\text{S}/\text{cm}$)	40	20	1370	274 (79)	0.52*
Drainage area (km^2)	40	37	1966	450 (141)	0.48*
Herbivore biomass (mg/m^2)	30	0	9574	603 (647)	0.48*
Latitude (degrees)	40	35.14	41.82	39.09 (0.54)	0.53*
Longitude (degrees)	40	-80.77	-75.12	-78.35 (0.41)	0.46*
pH	40	5.20	8.90	7.57 (0.23)	0.52*
Total N export from watershed (kg/d)	40	2257	21342	8881 (1374)	0.49*
Total P export from watershed (kg/d)	40	127	1978	701 (145)	0.48*
Turbulence intensity (m/s^2)	27	0.02	0.58	0.09 (0.04)	0.52*
Water depth (cm)	40	8	48	20 (2)	0.48*
Water temperature ($^{\circ}\text{C}$)	40	11	29	23 (1)	0.48*
Water velocity (m/s)	33	0.07	0.53	0.24 (0.04)	0.63*

Notes: Partial *r* is the Pearson partial correlation coefficient relating $\ln(P)$ to *S* after holding the listed variable constant (* $P < 0.05$; NS, not significant). See *Methods* for a full description of variables.

† "Water year" begins on 1 October, as defined by the USGS.

tion between the net production of biomass and the richness of periphyton assemblages found on the tiles ($r = 0.34$ for $\ln(P)$ vs. *S*, $P < 0.01$). This general relationship was, however, due to a strong correlation that existed between species richness and net production in streams most characterized by disturbance (Fig. 2A). In contrast, no correlation existed between richness and production in streams least characterized by disturbance (Fig. 2B).

Although we chose the HD and LD streams as categories representing different ends of a disturbance continuum, it is important to note there is considerable variation within each group (Table 1, Fig. 1A). Given this, it seems prudent to ask whether variation in disturbance regime itself can explain the patterns in Fig. 2. One way to address this question is to statistically hold the factor scores for PC1 and PC2 constant (which collectively describe stream disturbance regime; Fig. 1A), and then examine the residual correlations between producer richness and net production (i.e., the partial correlations). On doing this, the Pearson partial correlation coefficients relating $\ln(P)$ to *S* were $r = 0.49$ for HD streams ($P < 0.01$) and 0.23 ($P = 0.15$) for LD streams. Identical results are obtained if each of the six variables that comprise PC1 and PC2 are held constant individually (Table 1). These results in-

dicate that the patterns in Fig. 2 are robust to variation in disturbance regime within study groups.

Many of the measured supplemental variables were found to have been standardized between the two study groups (compare ranges and means in Table 1). An exception was stream size, with streams in the LD study group tending to be wider, deeper, and having a larger drainage area than those of the HD streams (Table 1). Perhaps related to this, LD streams appeared to have a greater range and mean export of total N (Table 1). Given the heterogeneity among the two stream study groups, we decided to ask whether any of the supplemental variables covaried with periphyton diversity and productivity in a manner that might explain trends in Fig. 2. After statistically holding all of the supplemental variables constant, the partial correlation coefficients relating *S* and $\ln(P)$ were $r = 0.75$ for HD streams ($P = 0.01$, $N = 24$) and 0.24 ($P = 0.36$, $N = 30$) for LD streams. Note that these analyses were performed on just a subset of the data because there were missing observations for some of the variables. Yet, similar results were obtained when each supplemental variable is held constant individually (Table 1).

The analyses above indicate that, after accounting for all other variables measured in this study, there remains an independent correlation between periphyton

TABLE 1. Extended.

LD streams				
<i>N</i>	Minimum	Maximum	Mean (95% CI)	Partial <i>r</i>
43	15	37	24 (2)	
43	0.17	45.60	8.62 (3.12)	
43	14	16	15 (0.16)	0.22 NS
43	271	357	301 (7)	0.25 NS
43	0.01	2.98	0.60 (0.18)	
43	0.65	2.38	1.36 (0.11)	0.26 NS
43	0.48	0.97	0.75 (0.03)	0.23 NS
43	0.44	0.73	0.53 (0.02)	0.20 NS
43	0.51	0.75	0.57 (0.01)	0.22 NS
43	-2.08	-0.08	-0.65 (0.17)	
43	0.5	1.4	1.01 (0.06)	0.20 NS
43	0.63	0.86	0.72 (0.02)	0.21 NS
41	0	84	24 (7)	0.18 NS
43	0	61	27 (4)	0.21 NS
42	70	1280	352 (76)	0.21 NS
43	72	8441	1331 (551)	0.21 NS
32	0	20254	1070 (1253)	0.09 NS
43	35.15	41.94	39.26 (0.56)	0.24 NS
43	-80.86	-75.03	-78.41 (0.53)	0.17 NS
42	6.5	8.70	7.79 (0.16)	0.18 NS
43	2267	47386	11772 (2413)	0.20 NS
43	145	5220	1280 (407)	0.20 NS
37	0.02	0.54	0.10 (0.04)	0.14 NS
41	12	56	28 (3)	0.18 NS
42	18	29	24 (1)	0.23 NS
39	0.09	0.58	0.31 (0.04)	0.11 NS

diversity and productivity in HD streams, but one that does not exist in LD streams. We see only two possible explanations for this. First, there may have been some other important factor we did not consider. Certainly, we did not account for all of the variables that can influence periphyton diversity and productivity in streams, which would be both impractical and impossible. Thus, we cannot rule out this possibility. An alternative, equally plausible explanation of the correlation structure in Fig. 2 is that stream disturbance regime altered a direct causal link between periphyton diversity and production. We consider this possibility in the remainder of our paper.

The observation that species-rich communities in HD streams attained higher production of periphyton biomass (Fig. 2A) can be explained by two non-mutually exclusive factors. First, streams with higher production may contain species that, on average, achieve higher biomass across all streams in the region. This would reflect differences in species composition among the streams; not only differences in the number of species, but also potentially the productivity of individual taxa in a given assemblage. Second, individual species may, on average, achieve higher biomass when they occur in streams with greater species richness. This would reflect a systematic change in the performance of species among streams, which could result for any number of reasons, several of which we will discuss. To examine how variation in species composition and

species performance contributed to the diversity–productivity relationships, we partitioned the observed productivity of a stream into the two components. For each of the $n = 189$ taxa, we calculated the median rate of biomass accrual over all sites at which a species was found (referred to as the “median regional productivity” of species i , \hat{P}_i). We used the median because the distribution of biomass production across sites was skewed for many taxa, making the median a better measure of central tendency than the mean. The production of periphyton biomass in a stream, P , was then partitioned as follows:

$$P = \sum_{i=1}^n \pi_i (\hat{P}_i + \delta P_i) = \sum_{i=1}^n \pi_i \hat{P}_i + \sum_{i=1}^n \pi_i \delta P_i \quad (2)$$

where π_i is the presence (0) or absence (1) of species i on the sampling tiles, and δP_i is the deviation in the productivity of species i from its median regional productivity, \hat{P}_i . The first term in Eq. (2), $\sum_{i=1}^n \pi_i \hat{P}_i$, represents the rate of biomass accrual in a stream that is expected from the species composition of the periphyton assemblage. Note this is simply the summed regional productivity of each taxon, which takes account of both the number of species in a stream ($\sum_{i=1}^n \pi_i$) and the “typical” (i.e., median) level of production for each taxon (\hat{P}_i). We did not attempt to separate these two facets of composition (which is not possible given the observational nature of our study); thus, our goal was

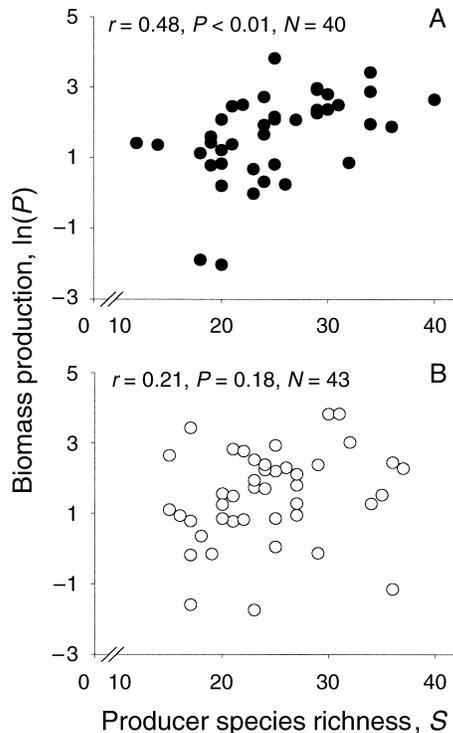


FIG. 2. The correlation between the net production of algal biomass, P ($\mu\text{g}\cdot\text{cm}^{-2}\cdot\text{d}^{-1}$), and species richness of an algal assemblage, S , in (A) streams most characterized by disturbance (HD streams) and (B) streams least characterized by disturbance (LD streams).

not to contrast the contribution of species richness to that of species “identity.” Rather, our goal was to separate the amount of production that can be predicted from knowledge of the species composition of a stream from the residual variation ($\sum_{i=1}^n \pi_i \delta P_i$) that results whenever species deviate from their median regional productivity. This second term measures the collective performance of species after one accounts for the particular combination of species in a stream. By partitioning productivity in this manner, we can (1) determine how much variation in production can be explained by changes in species composition among streams and (2) assess whether residual variation can be explained by systematic deviations in the performance of species in communities of differing richness.

Based on species composition alone, $\sum_{i=1}^n \pi_i \hat{P}_i$, we would expect the productivity of a stream to increase by $\sim 2\%$ per species (Fig. 3A–B), with no significant difference in this expectation between the HD and LD streams ($P = 0.53$ for comparison of the slopes). Expected values accounted for 27% of the variation in the observed productivity among HD streams (Fig. 3C), indicating that a significant portion of the diversity–productivity relationship in HD streams (Fig. 2A) can be explained by changes in species composition among the streams. In LD streams, high variation in observed productivity among streams contributed to there being

no significant relationship to the expected values (Fig. 3D; it’s worth noting, however, that the slope is in the anticipated direction). For HD streams, the slope of the relationship in Fig. 3C indicates that observed values of productivity increased by a factor of $e^{0.99} = 2.69$ relative to expected values. This trend resulted, at least in part, from systematic deviations in the collective performance of species, $\sum_{i=1}^n \pi_i \delta P_i$, among HD streams. Collective species performance increased by $\sim 6\%$ per additional species in HD streams (Fig. 3E), suggesting that species were more productive, on average, when they were a part of species-rich assemblages. In contrast, species performances in LD streams were not associated with species richness (Fig. 3F). Additional support for these conclusions comes from examining correlations between the productivity of individual species, $\log(P_i)$, and species richness, S . For the $N = 31$ species found at 10 or more sites in both study groups (an arbitrary cut-off chosen a priori), the distribution of coefficients was greater than zero for HD streams (r for the species = 0.33 ± 0.08 [mean \pm 95% CI]), but not different from zero for LD streams (0.09 ± 0.10).

The trends in Figs. 2 and 3 could be explained either by local processes involving growth of species on the sampling tiles, or by stream-wide processes involving stream colonization of tiles by propagules. Local processes might generate the patterns if (1) the strength or frequency of interactions among species on the tiles differed between the two disturbance regimes and (2) they varied systematically as a function of species richness. Specifically, the patterns could be explained if species interactions in HD (but not LD) streams increased the average performance of species on tiles as species richness increased. The only interaction we can think of that is consistent with this possibility is facilitation. Several studies suggest that the probability of positive species interactions increases with species richness (Vandermeer 1989, Mulder et al. 2001, Cardinale and Palmer 2002, Cardinale et al. 2002), and that positive interactions are often more frequent and intense in harsh and variable environments (Bertness and Leonard 1997, Callaway and Walker 1997, Bruno et al. 2003). Upon first consideration, it strikes us as unlikely that facilitation could explain the enhanced performance of so many different species in HD streams. However, there have been experimental demonstrations of positive interactions among producer species that occur when benthic organisms retard flow or induce turbulence near a substrate in ways that broadly enhance the capture of resources or facilitate colonization of numerous other species (Raven 1992, Stevenson and Glover 1993, Escartin and Aubrey 1995, Blanchette et al. 1999, Dodds and Biggs 2002). We do not know of studies that have asked whether such forms of facilitation are more likely to occur in streams characterized by disturbance, but this possibility merits some attention.

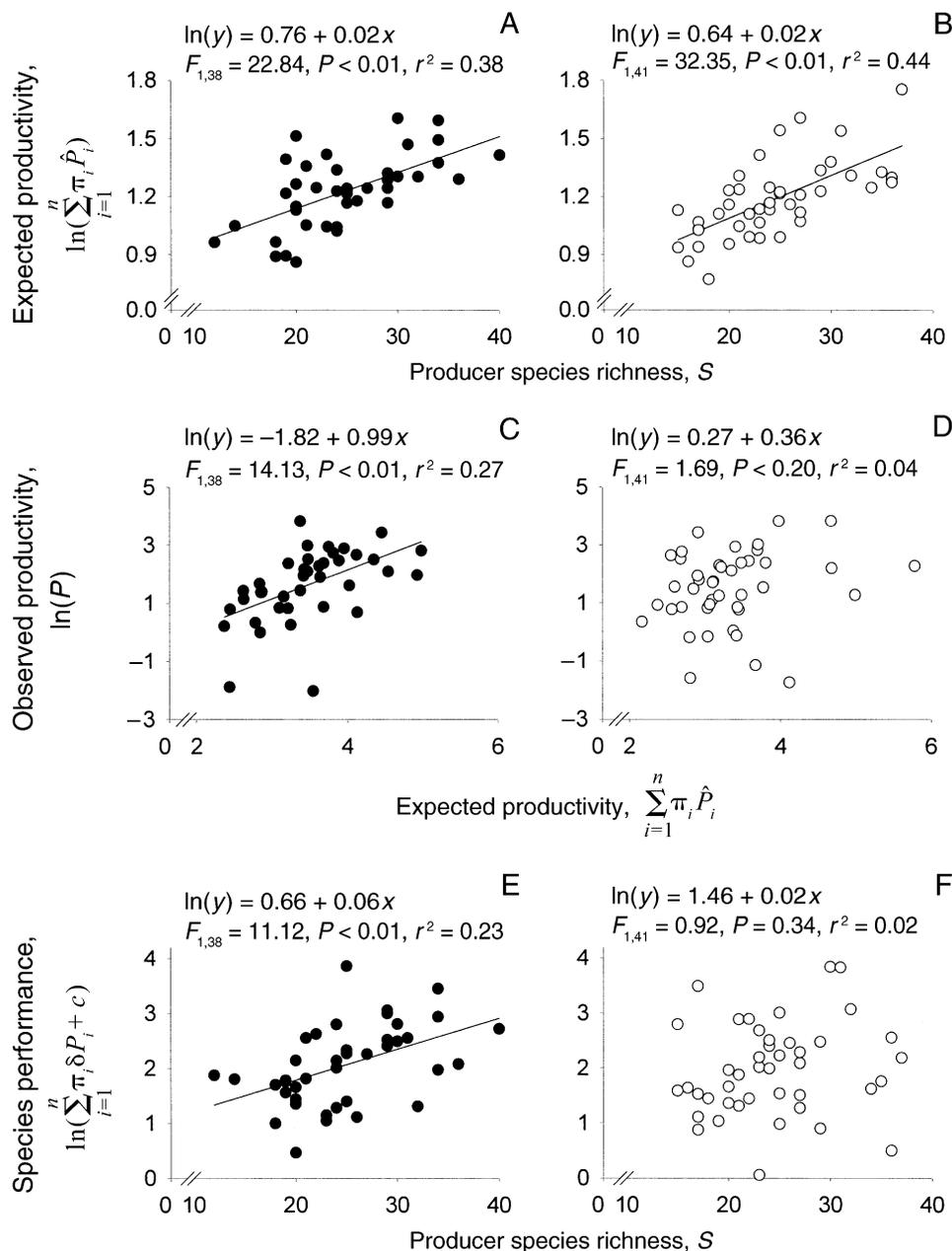


FIG. 3. (A–B) The amount of biomass production expected from the species composition of a periphyton assemblage as a function of species richness in (A) HD and (B) LD streams. (C–D) The net production of algal biomass, P ($\mu\text{g}\cdot\text{cm}^{-2}\cdot\text{d}^{-1}$) observed in a stream plotted as a function of the production expected from the species composition in (C) HD and (D) LD streams. (E–F) The collective performance of periphyton species plotted as a function of species richness of the assemblage for (E) HD and (F) LD streams (note: a constant, c , was added to allow transformation). See Eq. 2 and accompanying text (*Results and Discussion*) for explanation of how expected productivity and collective species performances were calculated.

Alternatively, the diversity–productivity relationships on the sampling tiles (Figs. 2 and 3) may simply reflect patterns that are occurring stream-wide. This possibility has been outlined in recent theoretical developments that suggest the processes of dispersal and colonization can generate local relationships between species diversity and productivity that reflect larger

scale patterns (Loreau et al. 2003, Mouquet and Loreau 2003, Cardinale et al. 2004). If, for example, the number of propagules available for colonization was positively related to the total number of species in HD streams (but, for whatever reason, was not related to total richness in LD streams), then (1) more species would immigrate to an open patch in systems having

a diverse colonist pool and (2) patches would be colonized earlier, thus increasing the period for local population growth. Together, (1) and (2) would produce a positive relationship between local species richness and biomass production that reflects a correlation between colonist pool richness and propagule production at larger spatial scales (Cardinale et al. 2004).

To the extent that patterns on the tiles reflect processes occurring stream-wide, then the explanation for our study is simply elevated to a larger spatial scale where one must ask whether stream-wide species richness does in fact influence the number of colonists arriving to an open patch and, if so, why this might be true only in frequently disturbed systems. As of now, we cannot answer these questions. Nevertheless, the important role of immigration in determining both species richness and the accrual of epilithic biomass after disturbances is well known both theoretically and empirically (Stevenson 1986, McCormick and Stevenson 1991, Peterson et al. 1994). We suspect, therefore, that dispersal and colonization processes could be important in explaining local diversity–productivity relationships in systems where recruitment limitation has a strong influence over community dynamics (Stevenson 1986, McCormick and Stevenson 1991, Palmer et al. 1996, Tilman 1997, Hubbell et al. 1999). Such a mechanism provides a valuable contrast to other explanations of diversity–productivity relationships, all of which focus on the role of local species interactions.

SUMMARY

We have described an ecological pattern spanning a large spatial scale that shows the relationship between primary producer diversity and productivity in stream ecosystems varies as a function of disturbance history. This pattern supports predictions of theoretical and small-scale empirical studies that the diversity–productivity relationship will vary as a function of the natural disturbance regime of an ecosystem. The mechanism underlying this dependence is currently uncertain; however, we have outlined two possibilities that merit attention. When the results of our study are coupled with those of past work, the evidence collectively suggests that human-induced changes to biodiversity and productivity are likely to have their greatest impacts on ecosystems most characterized by disturbance and for organisms whose populations are most sensitive to disturbance. Therefore, if we are to better understand how environmental change is altering the structure and function of communities, future studies will need to consider the diversity–productivity relationship within a broader ecological context that, among other things, explicitly considers the disturbance regime of an ecosystem.

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SUPPLEMENT

The data sets analyzed in this paper are available online in ESA's Electronic Data Archive: *Ecological Archives* E086-037-S1.