

DISTURBANCE MODERATES BIODIVERSITY–ECOSYSTEM FUNCTION RELATIONSHIPS: EXPERIMENTAL EVIDENCE FROM CADDISFLIES IN STREAM MESOCOSMS

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Abstract. We present empirical evidence that the direct and indirect effects of species richness on ecological processes depend on a system's disturbance regime. We manipulated the number of species of freshwater suspension feeders (net-spinning caddisflies) in laboratory stream mesocosms where communities were either subject to a periodic mortality or were left undisturbed. We hypothesized that disturbance would alter the direct effect of suspension-feeder species richness on the flux of their resource, particulate organic matter (POM), and alter the indirect effects of suspension-feeder species richness on algal productivity and biofilm respiration (via nutrient recycling). The direct effect of suspension-feeder species richness on POM flux did indeed change with disturbance regime. The flux of POM from the water column to stream bed was not influenced by species richness in the absence of disturbance, but increased as species richness was increased in disturbed streams. This apparently occurred because a high taxonomic evenness in disturbed streams minimized current "shading" (i.e., the blocking of flow from upstream to downstream neighbors) that, in turn, allowed diverse assemblages to capture a greater fraction of suspended resources. Disturbance also altered the indirect effect of suspension feeder species richness on algal productivity. In the absence of disturbance, increasing species richness led to dominance by a competitively superior suspension feeding taxon that had particularly low rates of nutrient excretion. Reduced nutrient availability, in turn, caused algal productivity to decline as a function of species richness. Periodic disturbances, however, prevented taxonomic dominance and eliminated this indirect effect of suspension feeder species richness on stream productivity. Our results suggest that disturbance can moderate relationships between biodiversity and ecosystem functioning by (1) increasing the chance that diversity generates unique system properties (i.e., "emergent" properties), or (2) suppressing the probability of ecological processes being controlled by a single taxon (i.e., the "selection-probability" effect).

Key words: *biodiversity; emergent properties; hydroptychid caddisflies; lotic filter feeders; niche complementarity; selection probability and sampling effects; species diversity.*

INTRODUCTION

Determining how species diversity affects the functioning of ecosystems has been a fundamental endeavor of ecology for much of the past decade. Growing interest in the ecosystem-level consequences of biodiversity has been driven, in part, by our need to understand how species loss and homogenization of the world's biota might alter ecological processes thought to sustain the Earth's ecosystems. Research to date has focused primarily on the importance of species richness—an aspect of biodiversity that has long been thought to influence ecosystem functioning (Tilman 1999). Recently, however, ecologists have begun to recognize that numerous aspects of community structure frequently covary with species richness and can exert greater control over ecological processes than the number of species per se. For example, the probability of taxonomic dominance is often correlated with species richness, and this can lead to ecological processes being

controlled by the biological traits of individual species (Naeem et al. 1996, Aarssen 1997, Huston 1997, Symstad et al. 1998, Wardle 1999). Such findings have fostered a growing sentiment among ecologists that we need to move away from simple considerations of the role of species richness in ecosystem functioning, towards a more comprehensive understanding of the diversity-function relationship as it is influenced by numerous aspects of community structure (Cardinale et al. 2000, Naeem et al. 2000, Wilsey and Potvin 2000).

Ecologists have recently begun to explore how forces that modify community structure might simultaneously modify the effects of species richness on ecological processes. Mulder et al. (1999), for example, provided evidence that the ecosystem-level consequences of species richness could be controlled by interspecific interactions that take place between different functional groups of organisms. They showed that the addition of herbivores to a system changed the relationship between plant species richness and productivity by differentially altering plant biomass and the relative abundance of plant taxa across levels of plant species rich-

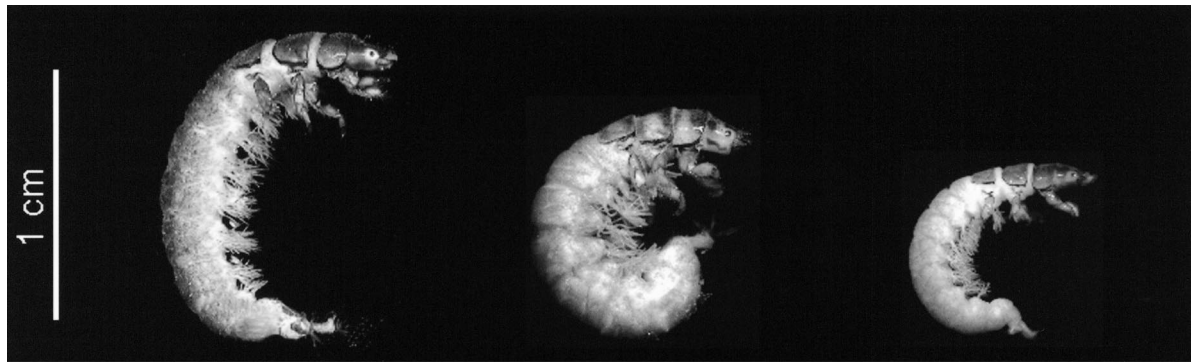
*Hydropsyche depravata**Ceratopsyche bronta**Cheumatopsyche* sp.

FIG. 1. Three species of net-spinning caddisflies (Trichoptera: Hydropsychidae) used for this experiment. Net-spinning caddisflies are a predominant group of lotic insects found in streams throughout the world. These particular taxa co-occur from the midwest to eastern United States where they often dominate suspension feeder abundance and biomass.

ness. Similarly, Klironomos et al. (2000) found that the relationship between plant species richness and primary productivity could change in both form and magnitude depending on whether plants formed symbiotic associations with mycorrhizal fungi.

Ecological factors regulating interspecific interactions also have the potential to mediate the relationship between species richness and ecosystem functioning. Cardinale et al. (2000) used a theoretical argument to show how periodic disturbances (e.g., mortality induced by fires, floods, herbivory, predation, parasitism, etc.) might modify the effects of species richness on ecosystem-level processes by controlling how the relative abundance of competitively superior and inferior species changes across levels of species richness. Given that disturbance is a feature of all ecosystems at some spatial or temporal scale (Pickett and White 1985, Petraitis et al. 1989), and that many types of disturbance promote species coexistence by precluding competitive dominance (Paine 1966, Armstrong 1976, Connell 1978, Huston 1979, Sousa 1979, Holt and Picherling 1985, Poff et al. 1997, and many others), the role of species richness in ecosystem functioning may depend on how disturbances regulate community structure.

Here we report the results of an experiment explicitly designed to test whether disturbance mediates the response of stream ecosystem processes to changes in species richness. We manipulated the number of species of a ubiquitous group of freshwater suspension feeders in stream mesocosms that were either subject to a periodic mortality, or were left undisturbed. We characterized the rates of several ecological processes that collectively influence stream "functioning" (algal productivity, biofilm respiration, and the flux of suspended particulates) and compared how these processes related to species richness in disturbed and undisturbed systems. We hypothesized that disturbance would alter the effects of suspension feeder species richness on stream

ecosystem processes by any of three potential mechanisms: (1) suppressing the "selection-probability" effect (i.e., the probability that processes are controlled by a single, dominant taxa; Huston 1997), (2) altering complementary resource use (i.e., the division of resources used by locally coexisting taxa; McNaughton 1993, Hooper 1998), or by (3) modifying the likelihood of emergent properties (i.e., unique physical or biological properties that can accompany changes in species diversity; Lawton 1994).

METHODS

Study system

We studied a group of suspension feeders that are common in streams throughout the world (Trichoptera: Hydropsychidae). Larval hydropsychid caddisflies construct silk catchnets in the pore spaces of streambeds and passively filter particulate organic matter (POM) from the water. Their feeding activities can exert a substantial influence on the flux of carbon from the water column to the benthos (Georgian and Thorpe 1992) and, via the recycling of biologically important nutrients, they may also indirectly affect metabolic processes of the benthic biofilm (Wallace and Merritt 1980).

We focused on a system of three caddisfly species that co-occur throughout the eastern United States (Fig. 1). These three taxa differ considerably in larval body size and, therefore, potentially differ in (1) their ability to acquire and defend space (larger individuals are usually better competitors; Jansson and Vuoristo 1979, Boon 1984, Englund and Olsson 1990, Matczak and Mackay 1990, Englund 1993), and (2) the amount and size of suspended particles they consume (larger individuals typically construct larger, more porous nets; Wallace 1974, Wallace and Merritt 1980, Loudon and Alstad 1990). Thus, we expected disturbance might alter the effects of caddisfly diversity on stream processes

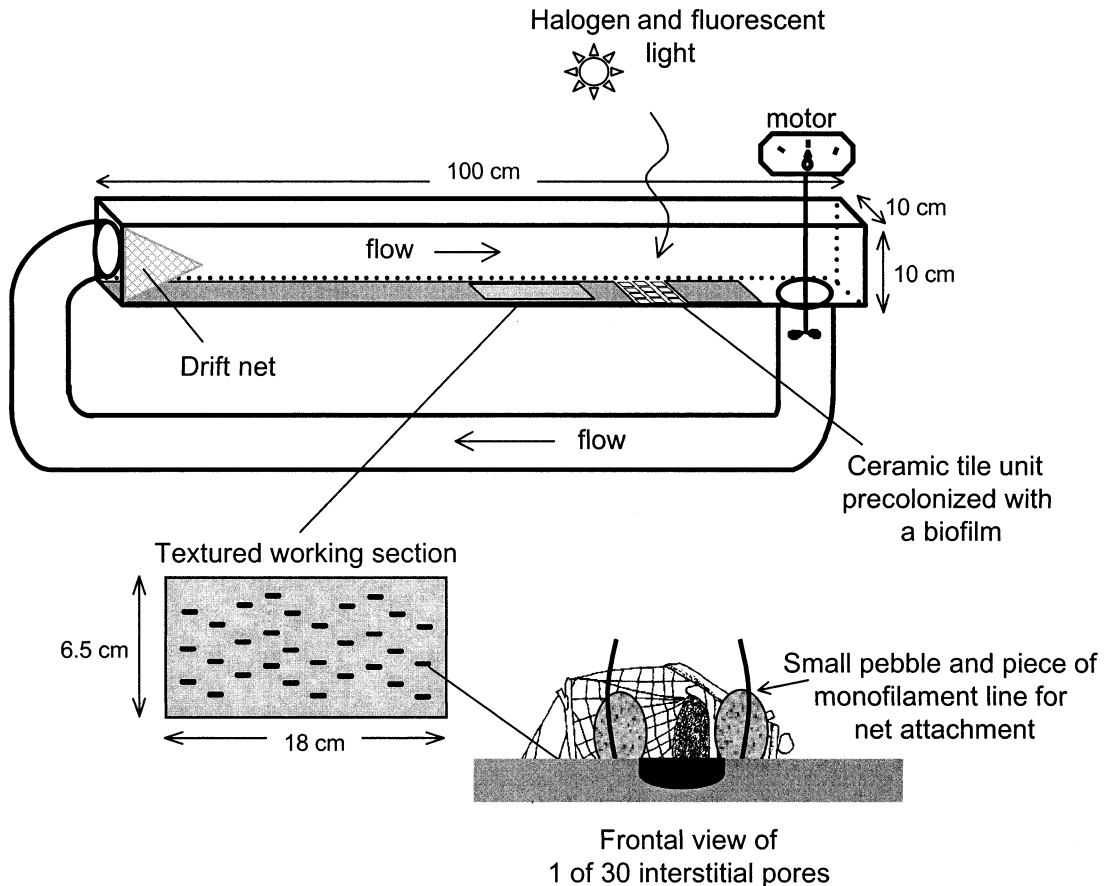


FIG. 2. A diagram of one of the recirculating streams used for this experiment. Larvae colonized the interstitial pores provided in the working section. Ceramic tiles, incubated downstream of the caddisflies, were used to measure the response of biofilm respiration and production to changes in suspension feeder species richness.

by moderating the absolute and relative abundances of large- and small-bodied taxa. One advantage of studying this system is that it was simple enough that mechanisms could be identified and generalized, yet it was still characteristic of the number of locally coexisting species common for natural assemblages of caddisflies (Rhame and Stewart 1976, Doledec and Tachet 1989, Downes and Jordan 1993, Voelz and Ward 1996, Benke and Wallace 1997) and for other functional groups of aquatic organisms (Palmer et al. 1997, Limburg et al. 2001).

Experimental units

The experimental units for the study were recirculating laboratory stream mesocosms (Fig. 2) having a constant water depth (8.5 cm) and velocity (midchannel flow = 24 ± 1 cm/s; mean ± 1 SD). Each stream had an 18×6.5 cm working section (70 cm downstream of the flow entrance) textured with sand (glued to the surface with silicon) such that larval caddisflies could crawl around and search for 30 equally spaced pores provided for colonization ($15 \times 5 \times 2.78$ mm grooves; Fig. 2). Every pore had a pebble and piece of mono-

filament line on either side that provided physical support for construction of larval filtration nets. All three species readily colonized interstitial pores and built fully functioning nets.

Twelve unglazed ceramic tiles (5.29-cm² tiles connected in a 3×4 array) were placed in the streams as standardized substrates to measure the response of the stream biofilm to manipulations of caddisfly diversity. Because the location of the tiles precluded direct contact with larval caddisflies (Fig. 2), effects of suspension-feeder species richness on biofilm processes were indirect. Prior to being used in the experiment, all tiles were incubated for 14 d in a common laboratory aquarium (that had been inoculated with biofilm from a natural stream) to initiate colonization. Halogen and fluorescent lamps were positioned over the streams to maintain photointensity at levels sufficient to saturate photosynthesis of attached algae ($\sim 200 \mu\text{mol}/\text{m}^2/\text{s}$; Hill 1996).

Experimental design

The experiment was designed as a randomized complete block having three levels of species richness (1,

2, or all 3 caddisfly species in the colonist pool), two levels of disturbance (no disturbance vs. + disturbance), and nine experimental blocks corresponding to different start dates. On each start date we randomly assigned two replicate streams to each treatment (i.e., 3 levels of species richness \times 2 levels of disturbance [=6 treatments] \times 2 replicates each = 12 streams per block). Taxa for the one and two-species treatments were randomly selected with the constraint that every taxonomic combination was equally replicated over the course of the experiment (i.e., $N = 6$ streams per species or species combination). This design resulted in 18 replicates of each level of species richness being run in each level of disturbance.

Experimental blocks spanned a 12-d study period. On the first day, 18 caddisfly larvae (equally divided among all taxa assigned to a stream) were released uniformly over the working section of the stream. Larvae were given 10 min to colonize pore spaces before flow in the streams was gradually increased to 24 cm/s (measured midchannel at half depth). Any larvae drifting out of the working section were captured in a drift net (Fig. 2), discarded, and replaced with new larvae to ensure all streams were initially colonized by an equal number of animals. On each of days 2–11, 46 mg of particulate organic matter (63–149 μm POM made from Formula II algalivorous fish food [Ocean Nutrition, San Diego, California, USA]) was added as a single pulse of food to each stream. We have previously found that all three species readily eat and grow on this food source.

Larval immigration was simulated in the experiment by adding six larvae per day (on days 2–11) to randomly selected pores. The number of immigrants was equally divided among all species assigned to a stream. Given the initial colonists and daily addition of immigrants, 78 caddisfly larvae were added to each stream over the course of the experiment. Because more larvae were added than could be accommodated in the 30 pore spaces in the working sections of the streams, population sizes were not limited by recruitment during this experiment.

A disturbance was imposed on streams assigned to the “+ disturbance” treatment on each of days 2–11 by using forceps to remove larvae and their nets from six randomly selected pore spaces in the working section of the streams. This simulated mortality was density dependent (the probability of a randomly selected pore having a larval colonist depended on the number of larvae having colonized the working sections), of a constant frequency (daily) and magnitude (proportion of pore spaces disturbed always equaled 20%), and assumed all three species were equally susceptible to disturbance (all taxa were 100% likely to experience mortality if inhabiting a pore space chosen for disturbance). This form of mortality was specifically chosen to simulate how moderate levels of a periodic disturbance (e.g., grazing, predation, parasitism, fires, floods,

etc.) might prevent competitive exclusion and increase the evenness of species (Paine 1966, Armstrong 1976, Connell 1978, Huston 1979, Sousa 1979, Holt and Pichering 1985, Poff et al. 1997, and others).

Measurement of ecological processes

At the end of each experimental block, we measured the rates of three ecological processes: (1) respiration of the benthic biofilm, (2), primary productivity of benthic algae, and (3) the flux of POM from the water column to the benthic habitat. Biofilm respiration and algal productivity were measured on day 11 by removing ceramic tiles from the streams and incubating them in individually sealed, 0.5-L airtight chambers (described in Cardinale et al. 2002b). Each chamber, filled with water from the corresponding stream and incubated in a water bath to maintain temperature, contained a pump that circulated water at a velocity comparable to that of the streams (~ 22 cm/s). Biofilm respiration (total $R = R$ of autotrophs + R of heterotrophs) was measured as O_2 consumed over 1 h in the dark (measured with an Orion model 830 oxygen probe [Thermo Orion, Beverly, Massachusetts, USA]), and net metabolism (=gross productivity – total R) was measured as the change in O_2 over a second 1-h incubation under lighting identical to that over the streams. Gross primary productivity of the algae (GPP) was calculated as the sum of net metabolism and respiration (Bott 1996). Following these measurements, tiles were placed in 90% ethanol to extract chlorophyll a (minimum of 48 h), which was later analyzed spectrophotometrically to estimate algal biomass (as in Steinman and Lamberti 1996, but using the absorption coefficient for samples extracted in ethanol derived by Nusch 1980).

On day 12 of each block, we added 278 mg POM as a pulse to every stream and measured the flux of particulates from the water column to the streambed. Water samples (250 mL) collected at 3, 10, 25, 60, and 120 min after release were filtered onto preweighed GF/F filters, which were dried and reweighed to determine particle mass. A logarithmic curve was fit to particle concentrations ($\text{mg POM/L} = -k \ln[\text{minute after release}] + \text{intercept}$) and the coefficient, k , was used as the measure of POM flux. Increasing values of k indicate faster rates of particle flux to the streambed. The mean fit of POM concentrations to these curves was $R^2 = 0.88$ ($N = 108$ streams), indicating this was a good method for quantifying POM flux.

Immediately after collection of POM samples, larvae were removed from the streams and placed into glass jars to measure their collective excretion rates of nitrogen (N) and phosphorous (P). These measurements were used to relate algal productivity to nutrient availability in the streams. Each jar (one per stream) contained 150 mL of autoclaved water and a piece of sterilized mesh netting for larval attachment. Water samples collected at the beginning and end of a 2-h in-

cubation were filtered through Whatman GF/C filters, placed on ice, and analyzed within 12 h for $\text{NH}_3\text{-N}$ and $\text{PO}_4\text{-P}$ (Nessler and Ascorbic acid methods, respectively; American Public Health Association 1985). Rates of nutrient excretion were calculated as final minus initial concentrations divided by incubation time. After collection of nutrient samples, larvae of each species were counted, dried for 24 h at 60°C , and weighed. These data were used to (1) calculate the biomass-specific rates of nutrient excretion by each of the three caddisfly species, (2) determine the final abundance of larvae in the streams, and (3) calculate final species evenness (as Simpson's index) for streams having two or more taxa in the colonist pool.

Data analyses

We separately modeled each of the three ecological processes (biofilm R , GPP, and POM flux) as a function of the fixed effects of species richness, disturbance, and the species richness \times disturbance interaction using mixed model ANOVAs that accounted for experimental blocking as a random effect (SAS 1996). Schwarz' Bayesian criteria were used to select covariance structures that accounted for any heterogeneity of variances across levels of species richness (Littell et al. 1996). A significant species richness \times disturbance interaction was taken as support for the hypothesis that disturbance altered the effect of suspension feeder species richness on an ecological process. When interactions were significant, the main effects of species richness were assessed within levels of disturbance. Probabilities of type I error were set at $\alpha = 0.05$.

Changes in GPP can result from either a change in algal biomass or a change in biomass-specific productivity (GPP/algal biomass). Therefore, for any treatment in which GPP exhibited a significant response to species richness, we (1) examined whether algal biomass and/or biomass-specific productivity also responded to changes in species richness (using mixed model ANOVAs with blocking as a random effect, SAS 1996), and (2) determined the Spearman rank correlation between these variables and GPP. Whenever algal biomass or biomass-specific productivity changed with species richness in a manner correlated to GPP, we modeled these response variables as a function of the N and P excretion rates of the caddisfly larvae (mixed model ANOVA using \log_{10} -transformed N and P excretion rates and blocking as a random effect, SAS 1996) to assess whether the recycling of nutrients could explain any significant portion of the variability in productivity between species richness treatments.

Measurements of GPP, biofilm R , and N/P excretion from the first experimental block were not included in the statistical analyses because unusually high concentrations of phosphorus were detected in the streams at the start of that experiment. This was most likely due to contamination of the holding tanks used to store

water prior to filling the laboratory streams. Because high ambient phosphorus could have potentially altered rates of productivity, respiration, and nutrient excretion, we decided to exclude these data prior to performing any statistical analyses. We did not, however, exclude measures of POM flux from the first block because we had no reason to believe this process could be altered by high P concentrations.

RESULTS

Species richness and the rates of ecological processes

The effect of suspension feeder species richness on biofilm respiration (R) did not change with disturbance regime (species richness \times disturbance, $F_{1,85} = 1.02$, $P = 0.32$), and there was no main effect of species richness on biofilm R ($F_{1,85} = 1.00$, $P = 0.32$). Disturbance did, however, alter the indirect effect of caddisfly species richness on gross primary production (GPP; species richness \times disturbance, $F_{1,85} = 9.77$, $P < 0.01$, Fig. 3A). In the absence of disturbance, there was a significant decline in GPP for every caddisfly species added to the streams ($t = -3.00$, $P < 0.01$, Fig. 3A). Streams with *Ceratopsyche bronta* or *Cheumatopsyche* sp. had the highest rates of GPP, but productivity was notably reduced in all streams having *Hydropsyche depravata* in the colonist pool (Fig. 3B). In contrast, in streams that were disturbed there was no relationship between species richness and GPP ($t = 1.42$, $P = 0.16$, Fig. 3A), and little variation between streams having different taxa/taxonomic combinations (Fig. 3C).

Biomass-specific productivity of the biofilm did not change with species richness in the absence of disturbance ($F_{1,39} = 0.87$, $P = 0.36$) and thus, could not account for trends in GPP in the undisturbed streams (Fig. 3A, B). However, algal biomass of the biofilm did decrease as species richness was increased (-0.24 μg chlorophyll a/cm^2 per additional caddisfly species, $F_{1,39} = 5.08$, $P = 0.03$), and there was a positive correlation between algal biomass and GPP in the absence of disturbance (Spearman $\rho = 0.51$, $P < 0.01$). Thus, the negative relationship between caddisfly species richness and GPP in the undisturbed streams (Fig. 3A, B) resulted from a reduction in algal biomass. Interestingly, the amount of algal biomass on tiles collected from the undisturbed streams paralleled changes in rates of N and P excretion by the caddisfly larvae (Fig. 4). A significant interaction between larval excretion of N and P explained $>50\%$ of all variation in algal biomass over the course of the experiment ($F_{1,3} = 12.68$, $P = 0.04$). *H. depravata* had the lowest rate of nutrient excretion of the three taxa studied (Fig. 5A), and undisturbed streams with *H. depravata* in the species pool consistently exhibited reduced rates of N and P excretion compared to streams having *Ceratopsyche bronta* and/or *Cheumatopsyche* (Fig. 5B, C). These data

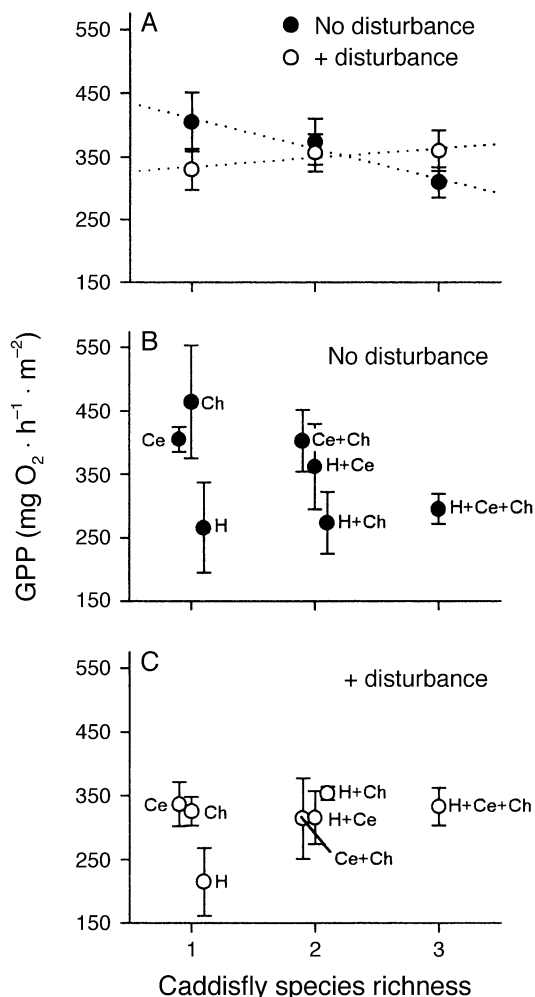


FIG. 3. (A) The indirect effect of caddisfly species richness on the gross primary production, GPP, of attached algae changed with disturbance regime ($P < 0.01$ for the species richness \times disturbance interaction). The slope relating GPP to species richness was < 0 in the absence of disturbance ($P < 0.01$) but not different from 0 in streams that were disturbed ($P = 0.16$). Mean values across all experimental blocks are shown for each taxon or combination in (B) undisturbed and (C) disturbed streams. Next to symbols are taxa that were in the colonist pools for that particular treatment (H = *Hydropsyche depravata*, Ce = *Ceratopsyche bronta*, Ch = *Cheumatopsyche* sp.). All data are the mean \pm 1 SE.

suggest that, as species richness was increased and *H. depravata* was added to the species pool of undisturbed streams, rates of nutrient excretion were reduced leading to lower algal biomass and productivity.

The effect of suspension feeder species richness on POM flux also differed between disturbed and undisturbed streams (species richness \times disturbance, $F_{1,96} = 5.71$, $P = 0.02$, Fig. 6A). In the absence of disturbance, species richness had no effect on the flux of POM from the water column to the benthic habitat ($t = -0.32$, $P = 0.75$, Fig. 6A). Two-species streams having *Hydropsyche depravata* in the colonist pool had the high-

est rates of POM flux, but all other taxa/taxonomic combinations had relatively similar rates (Fig. 6B). In disturbed streams, POM flux increased with increasing species richness ($t = 3.06$, $P < 0.01$, Fig. 6A). This positive relationship between species richness and POM flux did not result from the effects of any single taxon or taxonomic combination; POM flux was similar for all three individual species, and nearly identical for all of the two species combinations (Fig. 6C).

The effect of disturbance on community structure

The overall effect of disturbance on the caddisflies was to reduce larval abundance ($t = 8.30$, $df = 106$, $P < 0.01$ for a t test comparing all disturbed to all undisturbed streams, Fig. 7A) and increase the taxonomic evenness of species when they were together in the species pool ($t = -5.84$, $df = 70$, $P < 0.01$ for a t test comparing all disturbed to all undisturbed streams with two or more taxa, Fig. 7B). In streams that were not disturbed, 97% of the pore spaces (29 of 30) were occupied by larvae at the end of each experiment. The limited space that remained available for colonization appeared to result in competition between the larvae for suitable net sites. Displacement of small-bodied species was obvious in the undisturbed streams where two- and three-species systems were numerically dominated by the larger *Hydropsyche depravata* (Fig. 7C). This resulted in relatively low abundance of *C. bronta* and *Cheumatopsyche* (Fig. 7C) despite the fact that all taxa were equally represented in abundance in the col-

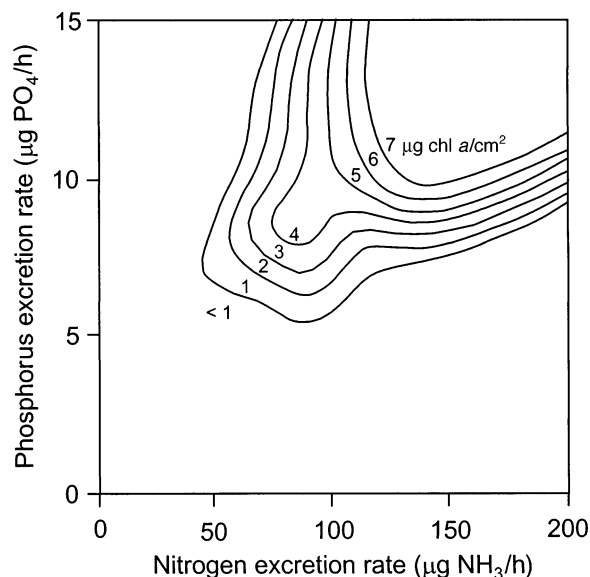


FIG. 4. Isoleths showing changes in algal biomass (as chlorophyll *a*) as a function of nitrogen and phosphorus excretion by caddisfly larvae inhabiting undisturbed streams. A significant interaction between these two nutrients ($P = 0.04$) explained $> 50\%$ of all variation in algal biomass throughout the study. Algal biomass was ultimately responsible for declines in GPP as species richness was increased in the undisturbed streams (i.e., Fig. 3A, B).

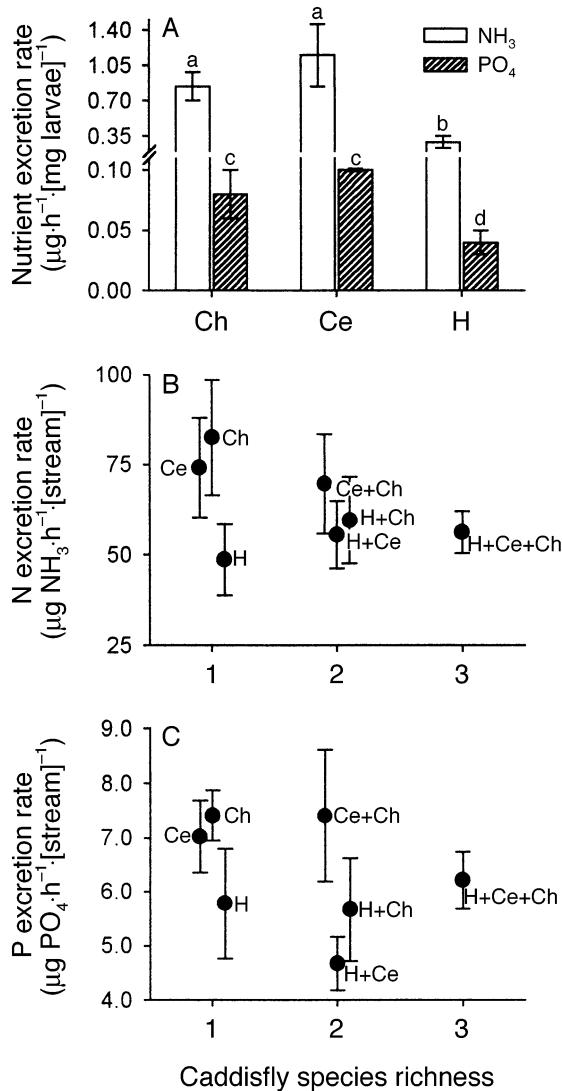


FIG. 5. (A) Biomass-specific rates of N and P excretion for caddisfly taxa calculated from measurements in single species, undisturbed streams. Bars labeled with different letters are significantly different from each other ($P < 0.05$ for LSD pairwise comparisons). Mean values of (B) N excretion and (C) P excretion in undisturbed streams are shown for each taxon or combination. Next to symbols are taxa that were in the colonist pools (H = *Hydropsyche depravata*, Ce = *Ceratopsyche bronta*, Ch = *Cheumatopsyche* sp.). All data are the mean \pm 1 SE.

onist pools (see Methods). In contrast, only 63% of the pore spaces (19 of 30) were occupied by larvae at the end of experiments in the disturbed streams. The high evenness of species (Fig. 7B), coupled with relative abundances that were comparable to that in the colonist pools (Fig. 7D) suggests there was little, if any, competitive displacement in the disturbed streams.

DISCUSSION

The differential effects of suspension feeder species richness on GPP and POM flux in the two disturbance

treatments support our hypothesis that the relationship between species richness and ecosystem functioning depends on whether populations are subject to a periodic mortality. Periodic mortalities can be induced on a community via any number of biotic or abiotic disturbances (e.g., grazing, predation, parasitism, fires, floods, etc.), most of which characterize ecosystems at a variety of spatial and temporal scales (Pickett and White 1985, Petraitis et al. 1989). Thus, our work suggests that disturbances may be key ecological factors

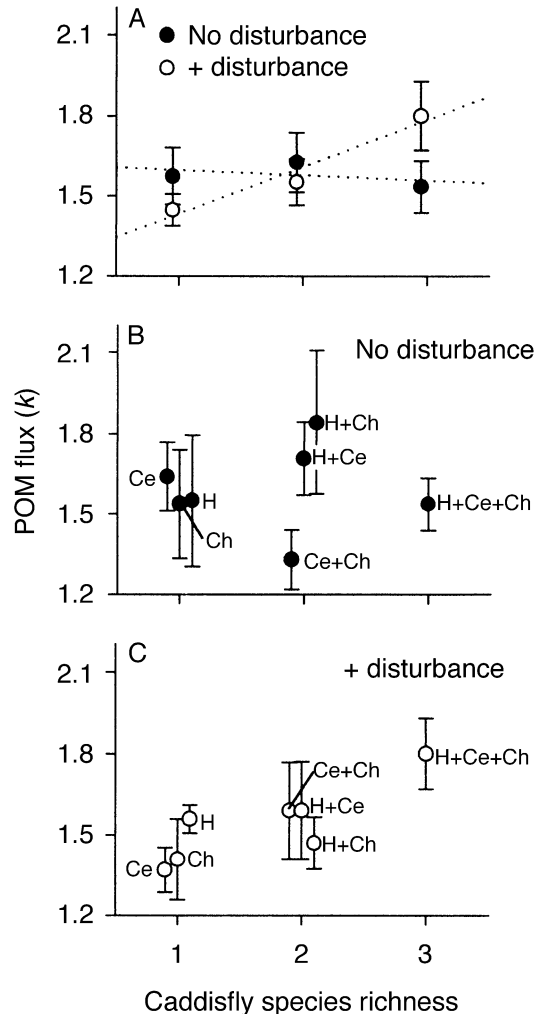


FIG. 6. (A) The effect of caddisfly species richness on the flux of particulate organic matter, POM, from the water column to streambed changed with disturbance regime ($P = 0.02$ for the species richness \times disturbance interaction). The slope relating POM flux to species richness was >0 in streams that were disturbed ($P < 0.01$) but not different from 0 in the absence of disturbance ($P = 0.75$). Mean values across all experimental blocks are shown for each taxon or combination in (B) undisturbed streams and (C) disturbed streams. Next to symbols are taxa that were in the colonist pools for that particular treatment (H = *Hydropsyche depravata*, Ce = *Ceratopsyche bronta*, Ch = *Cheumatopsyche* sp.). Data are the mean \pm 1 SE.

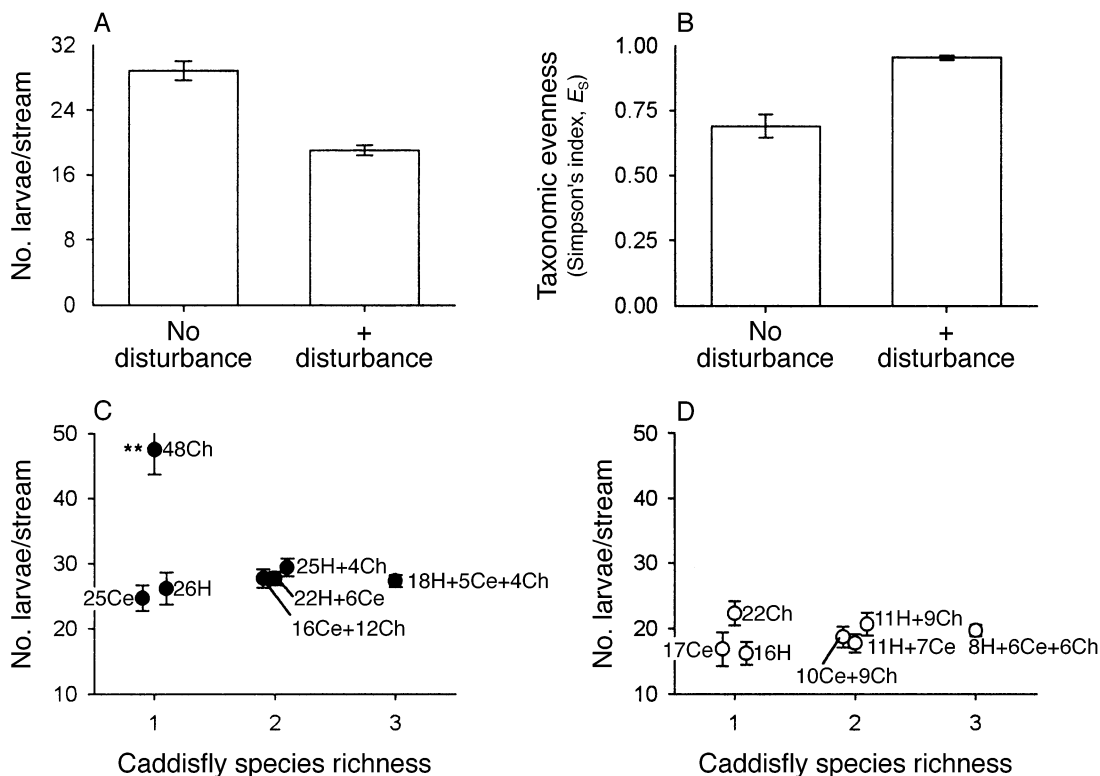


FIG. 7. (A) Larval abundance at the end of experimental blocks was significantly reduced in disturbed streams compared to undisturbed streams ($P < 0.01$). (B) The taxonomic evenness of species was higher in disturbed streams than in those that were not disturbed ($P < 0.01$). The mean abundance of larvae for each taxon or combination is shown for the (C) undisturbed streams and (D) disturbed streams. Next to symbols are taxa that were in the colonist pools (H = *Hydropsyche depravata*, Ce = *Ceratopsyche bronta*, Ch = *Cheumatopsyche* sp.) and the final abundance of each taxon. Data are the means ± 1 SE. Note that *Cheumatopsyche* was small enough that two larvae frequently colonized single pore spaces. This led to higher than mean abundance when this taxa was alone in the streams.

moderating relationships between biodiversity and ecosystem functioning.

There are at least three ways that disturbance could have altered the effects of suspension-feeder species richness on stream functioning in this study: (1) by reducing the probability that ecological processes were controlled by a single, dominant suspension-feeding taxon (i.e., suppressing the "selection-probability" effect; Huston 1997), (2) by altering how particulate resources were divided among co-occurring suspension feeder populations (i.e., complementary resource use; McNaughton 1993, Hooper 1998), or (3) by modifying the probability that suspension feeder diversity generated some unique physical or biological property that influenced functioning (i.e., an "emergent property"; Lawton 1994).

The selection-probability effect

When increasing species diversity also increases the chance of encountering a taxon with strong effects on ecological processes, a correlation between species richness and ecosystem functioning can result from the biological traits of that single species. This has been called the selection-probability effect by Huston (1997)

who, along with others (Aarssen 1997, Wardle 1999), considers it to be a statistical artifact of diversity. Tilman et al. (1997) and Loreau (2000) have called the same phenomenon the sampling effect, and consider it to be a valid mechanism by which diversity can influence ecosystem functioning. The important point from both views is that increasing diversity also increases the chance of a species-specific effect on ecological processes. This species-specific effect frequently manifests itself when increased diversity results in a competitively superior taxon being added to the species pool. As that taxon becomes dominant in a community, it comes to control the rates of ecological processes (Chapin et al. 2000, Loreau 2000).

One way the selection-probability effect could explain the results of our study is if the probability of dominance and control of ecological processes by a single caddisfly species was greater under one disturbance regime than another. We did find that disturbance altered the probability of dominance by a competitively superior caddisfly taxon. Abundance in the undisturbed streams was relatively high with nearly all of the pore spaces available for colonization occupied by larvae at the end of the experiment (Fig. 7A). The limited num-

ber of available net sites led to competition for space, and *Hydropsyche depravata* was able to outcompete the smaller species and dominate all two- and three-species streams to which it was added (Fig. 7C). These results are consistent with other studies having demonstrated that competitive interactions among caddisflies for suitable net sites are settled by body size (Jansson and Vuoristo 1979, Boon 1984, Englund and Olsson 1990, Matczak and Mackay 1990, Englund 1993).

Dominance by *Hydropsyche depravata* in the two- and three-species systems probably contributed to the negative relationship between caddisfly species richness and GPP in the undisturbed streams (Fig. 3A, B) by reducing the availability of nutrients required for algal growth. *H. depravata* had the lowest rates of nutrient excretion of any of the taxa studied (Fig. 5A); thus, undisturbed streams dominated by *H. depravata* had reduced rates of N and P excretion (Fig. 5B and C). It is likely that nutrient excretion by caddisfly larvae limited algal productivity during this study because (1) initial concentrations of N and P in water used to fill the streams were consistently undetectable, (2) larval excretion was the only obvious source of mineralized nutrients available for algal growth in the streams, and (3) we cannot identify other factors that might have limited productivity during the experiment; light was sufficient to saturate photosynthesis (see Methods) and there were no top-down controls on algae (e.g., herbivory). The possibility of nutrient limitation of algal productivity was supported by the finding that a significant interaction between larval excretion of N and P explained the majority of variation in algal biomass—the cause of declining GPP in the undisturbed streams.

Given that productivity was probably limited by nutrient availability, we think that as species were added to undisturbed streams, the likelihood of dominance by a superior competitor with low nutrient excretion led to reduced nutrient availability and decreased algal productivity. This is consistent with how the selection-probability effect results in ecological processes being controlled by a single, dominant species (Aarssen 1997, Chapin et al. 2000). The selection-probability effect would not, however, have operated in the disturbed streams where reduced abundance (Fig. 7A) minimized competition between the larvae for space. By limiting dominance of *Hydropsyche depravata*, disturbance suppressed the selection probability effect and altered the relationship between species richness and GPP.

Complementary resource use

The selection probability effect cannot explain trends in POM flux since this ecological process increased with species richness in disturbed streams (Fig. 6A) despite there being no dominant taxa. What then, led to the differential relationship between caddisfly species richness and POM flux in the disturbance treatments? Complementary use of resources is another

mechanism by which species diversity can influence the functioning of ecosystems (McNaughton 1993, Hooper 1998). This mechanism is based on the concept of “limiting similarity” which proposes that co-occurring species must differ by some minimum amount and use limited resources in “complementary” ways to coexist. When species divide resources in complementary ways, theory predicts that adding species to a system will increase the fraction of available resources used by organisms (Tilman et al. 1997). Cardinale et al. (2000) showed that by regulating species dominance, disturbance could theoretically alter complementary use of resources and, in turn, change the effect of species richness on the depletion of resources. Thus, a potential explanation for trends in POM flux (Fig. 6A) is that disturbance induced complementary use of POM among the suspension feeding taxa (e.g., via use of different size fractions).

It is important to note that in this study we assessed how species richness influenced the flux of a consumable resource (i.e., the rate of transfer of POM from one pool to another), not the total depletion of a resource from a single pool. Because theoretical predictions about complementary resource use have focussed on the latter (Tilman et al. 1997), we calculated a measure that is equivalent to the total depletion of resources from the stream water column. The flux of POM fit a logarithmic decay curve that approached an asymptotic minimum (see Methods); thus, the initial minus final concentrations of particles in the water (i.e., [POM] at 3 min – [POM] at 120 min) represents the total amount of POM depleted from the water. If changes in complementary resource use were responsible for the observed trends in POM flux, total POM depletion should have increased with species richness only in the disturbed streams (as in Fig. 8A). This was not the case. We modeled total POM depletion as a function of caddisfly species richness, disturbance, and the species richness \times disturbance interaction using a mixed model ANOVA with blocking as a random effect (SAS 1996). We found no species richness \times disturbance interaction ($F_{1,96} = 0.03$, $P = 0.87$) and no main effect of species richness ($F_{1,96} = 0.44$, $P = 0.51$). Thus, total POM depletion was not influenced by caddisfly species richness in either disturbance regime, and trends in POM flux could not have resulted from changes in complementary resource use.

The fact that total resource (i.e., POM) depletion did not respond to changes in species richness in disturbed streams while resource flux did respond illustrates an unexpected dependency of our conclusions on the temporal scale of observations. Note in Fig. 8B that observations confined to early time intervals (say, X_1 – X_5) would lead us to conclude that species richness influenced both the flux (i.e., rate of change) and total depletion of POM. Observations confined to later intervals, when resources were depleted to a constant minimum (e.g., $>X_7$), would lead us to conclude that spe-

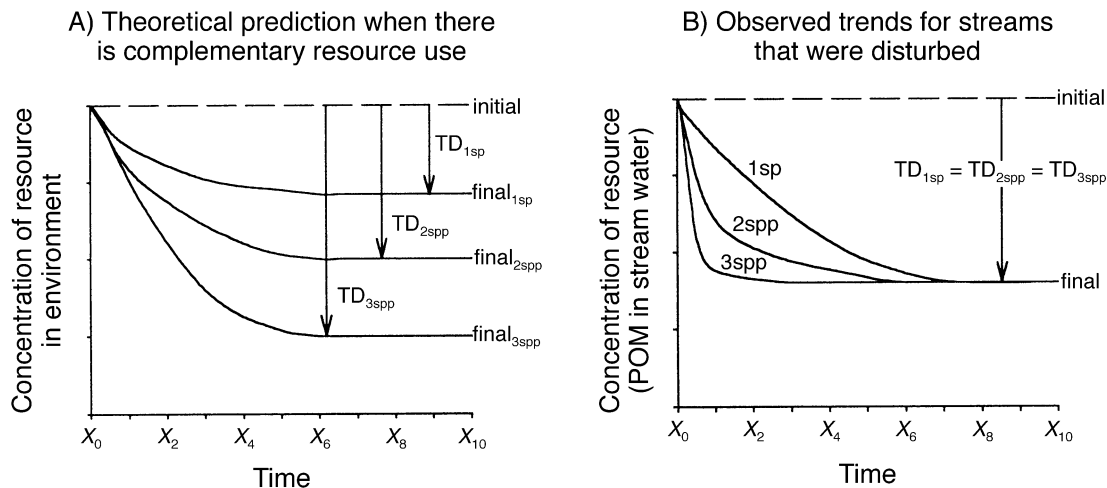


FIG. 8. When species use a resource in complementary ways, theory predicts that increasing species richness will increase the total depletion of that resource, TD, from the ecosystem. This prediction is shown in (A) for systems having one, two, or three species depleting some initial concentration of a resource over time. In contrast to this prediction, we found that (B) increasing the number of caddisfly species in disturbed streams increased the rate of depletion of particulate organic matter (POM, the resource consumed by these suspension feeders) but did not influence the final equilibrium levels of this resource.

cies richness had no effect on the flux or total depletion of POM. The asymptotic minimum concentrations of POM reached in this study were inevitable because we used streams that recirculated particles throughout the measurement period. It is unlikely, though, that such an asymptotic minimum is attained in natural stream ecosystems where renewal of organic matter from upstream precludes the depletion of this resource to levels that limit the fitness of suspension feeders (Georgian and Thorpe 1992, Monaghan et al. 2001). Therefore, we expect that altered species richness of suspension feeders in naturally disturbed stream ecosystems could influence both the rate of flux and, in turn, the total amount of particulate organic matter transferred from the water column to the benthic habitat (as in Fig. 8B, X_0 – X_5). Fig. 8B does, however, imply that the effect of species richness on ecosystem functioning will be temporally dynamic in any system where an initial concentration of a resource is depleted to some limiting concentration over time (e.g., the epilimnion of lakes after spring turnover, or forests following nutrient regeneration by fire).

While analysis of total POM depletion provides no evidence of complementary resource use, there is a potential limitation of our data. Total POM depletion from the stream water column was not only a function of direct larval consumption, but also a function of the physical deposition of particles. If physical deposition changed with species richness in a manner opposite from changes in larval consumption, then complementary resource use among the species could have been undetectable. We think this is unlikely because physical deposition in the sections of the streams not colonized by caddisflies was identical between treatments

(streams had identical physical characteristics; flow velocity, water depth, temperature, etc.). In the areas of the streams colonized by caddisflies, differences in the size and structure of larval catchnets between treatments might have differentially influenced physical deposition. Yet, because the sections of the streams colonized by larvae represented a small percentage of total area (<6% including return flow pipes), differences in physical deposition between treatments were likely quite small.

Emergent properties

An emergent property is one that cannot be predicted from an understanding of how individual parts of a system work in isolation (Salt 1979). Changes in species diversity have the potential to generate emergent physical or biological properties that lead to unpredictable changes in ecological processes. Unique biological properties may result if, for example, increasing species richness results in complex interspecific interactions (Wootton 1993, Billick and Case 1994). This is common in predator–prey systems where increasing the number of predator species leads to interaction modifications that facilitate consumption, in turn, causing multiple predators to impact prey populations in a manner that exceeds the summed effects of individual predators (Sih et al. 1998). Changing species richness can also introduce or eliminate biological structures with unique physical properties that regulate ecological processes. Indeed, the term “physical ecosystem engineer” has been applied to a broad array of species that, by their direct and indirect modifications of physical habitat, facilitate the flow of resources to other organisms (Jones et al. 1997).

We have evidence that a unique physical property resulted from the high species evenness maintained in the disturbed streams, and that this physical property contributed to the positive relationship between suspension feeder species richness and POM flux. In a subsequent study (Cardinale et al. 2002a), we examined how the feeding rates of larval caddisflies related to patterns of water flow around filtration nets when streams were colonized by either a single species, or by a high evenness of all three taxa. In streams with high taxonomic evenness, larval feeding rates were facilitated by unique changes in nearbed flow that accompanied increased diversity. Interspecific variation in net sizes tended to minimize current "shading" (i.e., the deceleration of flow from upstream to downstream neighbors) causing downstream larvae to capture and consume significantly more POM when in the presence of other species. This form of hydrodynamic facilitation led to short-term rates of POM consumption in high diversity streams that exceeded what could be predicted from the feeding rate of each species when alone (i.e., POM consumption increased with diversity in a nonadditive manner). Given this, we think that as species were added to disturbed streams in the current experiment, maintenance of high taxonomic evenness altered nearbed flow and facilitated rates of POM capture.

It is well known, in both freshwater and marine environments, that upstream neighbors can reduce flow and, therefore, the delivery of resources to downstream individuals in aggregations of benthic organisms (Hart 1986, Johnson 1990, Englund 1991, Okamura 1992, Sebens et al. 1997). There is also much evidence that near-bed hydrodynamics are dependent on the structural complexity of a benthic habitat (Nowell and Jumars 1984, Huettel and Gust 1992, Butman et al. 1994, Sebens et al. 1997). Taken together, it follows that biophysical complexity associated with species diversity could play an important role in regulating neighbor interactions and resource capture in aquatic benthic communities (Cardinale et al. 2002a). There is also reason to believe that analogous effects of diversity occur in terrestrial ecosystems. For example, Mulder et al. (2001) hypothesized that a positive relationship between bryophyte diversity and productivity during droughts resulted because greater complexity of vertical structure helped to "trap" water and facilitate plant survival. By maintaining a high taxonomic evenness, disturbances may increase the likelihood that species diversity will alter the physical environment in a manner favoring positive species interactions.

SUMMARY

We have used a simple experimental system to show how relationships between species richness and rates of ecological processes can depend on a system's disturbance regime. We found that disturbance (1) modified the direct effects of suspension feeder species

richness on resource fluxes by inducing an emergent physical property of diversity that favored facilitative interactions, and (2) altered the indirect effect of suspension feeder species richness on primary production by suppressing the probability of dominance by a taxon that had low rates of nutrient excretion. These findings support a growing number of studies suggesting that relationships between biodiversity and ecosystem functioning depend on how biotic and abiotic factors regulate the balance of positive and negative species interactions (e.g., Mulder et al. 1999, 2001, Waide et al. 1999, Cardinale et al. 2000, Klironomos et al. 2000, Naeem et al. 2000). Our experiment focused on a single form of nonselective disturbance that served to even out local species abundances. While this is a common way disturbance influences community structure, other types of disturbance (e.g., those which are selective or those in which recolonization of a disturbed site is limited by recruitment) can have qualitatively different effects. Thus, we expect the ecosystem-level consequences of changing biodiversity will depend on how multiple forms of disturbance act in concert to regulate community structure.

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