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Geographic patterns of diversity in streams are predicted by a multivariate model of disturbance and productivity

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Summary

1 Univariate explanations of biodiversity have often failed to account for broad-scale patterns in species richness. As a result, increased attention has been paid to the development and testing of more synthetic multivariate hypotheses. One class of multivariate hypotheses, founded in successional diversity theory, predict that species richness is jointly influenced by periodic disturbances that create new niche opportunities in space or time, and the production of community biomass that speeds displacement of inferior by superior competitors.

2 While the joint response of diversity to disturbance and productivity has gained support from theoretical and small-scale experimental studies, evidence that corresponding patterns of biodiversity occur broadly across natural systems is scarce.

3 Using a data set that employed standardized methods to sample 85 streams throughout the mid-Atlantic United States of America, we show that biogeographical patterns of primary producer diversity in stream ecosystems are consistent with the predictions of a multivariate model that incorporates disturbance frequency and community biomass production as independent variables. Periphyton species richness is a concave-down function of disturbance frequency (mean no. floods year⁻¹) and of biomass production (μg of biomass accrual $\text{cm}^{-2} \text{day}^{-1}$), and an increasing function of their interaction.

4 Changes in richness across the disturbance \times productivity response surface can be related to several predicted life-history traits of the dominant species.

5 Our findings complement prior studies by showing that multivariate models which consider interactive effects of community production and ecosystem disturbance are, in fact, candidate explanations of much broader patterns of richness in natural systems. Because multivariate models predict synergistic effects of ecological variables on species diversity, human activities – which are simultaneously altering both the disturbance regime and productivity of streams – could be influencing biodiversity more than previously anticipated.

Key-words: species diversity, disturbance, primary production, freshwater algae, periphyton, stream ecosystem functioning, flood, river

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Introduction

One of the enduring challenges in ecology is to identify those factors that explain patterns of biodiversity across large spatial scales (Hutchinson 1961; MacArthur &

Wilson 1967; Connell 1978; May 1986; Godfray & Lawton 2001; Hubbell 2001; Ricklefs 2004). Most hypotheses that account for geographical variation in diversity invoke single explanatory factors. For example, the Intermediate Disturbance Hypothesis (Connell 1978; Sousa 1984; Mackey & Currie 2001; Shea *et al.* 2004) predicts that the number of species in an ecosystem will be a unimodal function of the frequency of disturbance, because organisms face inherent trade-offs in their ability to compete for resources at low levels of disturbance and

their ability to recolonize habitats at high levels. The Productivity Hypothesis (Rosenzweig & Abramsky 1993; Waide *et al.* 1999; Mittelbach *et al.* 2001; Currie *et al.* 2004), on the other hand, predicts that species richness is a unimodal function of ecosystem productivity – more accurately, the availability of resources that limit production – which regulates the strength of species interactions and the local coexistence of competitors.

Each of these univariate hypotheses have had some success in explaining patterns of diversity, particularly in controlled experiments and observational studies where study units have been carefully selected to vary in just one explanatory factor (e.g. Buckling *et al.* 2000; Kassen *et al.* 2000; Rainey *et al.* 2000; Molino & Sabatier 2001; Chase & Leibold 2002; Scholes *et al.* 2005). However, ecologists have increasingly realized that models based on single causal factors are often inadequate descriptions of broad patterns of species richness in nature (Wootton 1998; Waide *et al.* 1999; Wilkinson 1999; Mackey & Currie 2001; Mittelbach *et al.* 2001; Roxburgh *et al.* 2004). When coupled with the recognition that potential causal factors often covary in nature, this has prompted much interest in merging hypotheses into more synthetic, multivariate explanations of biodiversity.

Some of the earliest attempts to merge hypotheses proposed that diversity is the result of a dynamic equilibrium between rates of community biomass production that hasten competitive exclusion, and the frequency or magnitude of disturbances that reduce the impact of competition on community dynamics (Huston 1979). However, as subsequent theory showed that disturbance does not, by itself, reduce the impact of competition on species population sizes (Chesson & Huntly 1997), the door was open for improvements. One improvement was proposed by Kondoh (2001), who used the patch occupancy models of Hastings (1980) and Tilman (1994) to explore the coupled impacts of disturbance and productivity on species richness. Like many of its predecessors, Kondoh's model predicted that the relationships of species richness to productivity and disturbance are both unimodal, but the level of one factor that maximizes species richness depends on the level of the second factor – an interaction that leads to patterns not easily anticipated from univariate models of diversity (Proulx & Mazumder 1998). An advance of this model was that it relied on more plausible mechanisms of species coexistence that require disturbance to create new niche opportunities in space and/or time. For example, new opportunities can result when patchy disturbance allows species to differentially express life history trade-offs, such as between their ability to compete for limiting resources, colonize open space or specialize on the exploitation of resource rich patches (MacArthur & Wilson 1967; Armstrong 1976; Tilman 1994; Pacala & Rees 1998; Amarasekare 2003). Importantly, the expression of these life-history traits is also a function of productivity, which influences the rate of biomass accumulation in open patches, dispersal of propagules across patches and, ultimately, the speed of

successional displacement of inferior by superior competitors. As a result, disturbance and productivity are predicted to jointly determine the variety of life-history traits that can be expressed in a system.

Several empirical tests of multivariate diversity theory have now shown clear interactive effects of disturbance and productivity (or resource supply) on species richness (e.g. Wilson & Tilman 2002; Kneitel & Chase 2004; Scholes *et al.* 2005). The results of these studies have been bolstered by meta-analyses of experimental manipulations of herbivory and nutrient supply in aquatic habitats that suggest the interactive effects of biotic disturbance and productivity on the richness of primary producers are likely to be general (Worm *et al.* 2002). In stream ecosystems, which are the focus of our research, an increasing number of studies have explored how disturbances (biotic or abiotic) interact with limiting resources to dictate the rate of biomass accumulation and the diversity of primary producers (Mulholland *et al.* 1991; Rosemond *et al.* 1993; Death & Winterbourn 1995; Pollock *et al.* 1998; Proulx & Mazumder 1998; Biggs *et al.* 1999). This work has prompted the development of conceptual models that predict how life-history traits of algal species change across disturbance \times productivity continua (McCormick 1996; Stevenson 1997; Biggs *et al.* 1998). Yet, even while a growing body of theory and small-scale empirical work lends support to multivariate models of diversity, there is relatively little convincing evidence that patterns of biodiversity in natural ecosystems are a joint function of a system's disturbance regime and level of biomass production. In part, this is because the interpretation of patterns in studies performed in natural systems is often clouded by inconsistent use of methodologies across sites. Even those studies that have successfully overcome this limitation (e.g. Death & Winterbourn 1995; Pollock *et al.* 1998; Biggs & Smith 2002) tend to be limited to a few sites in a relatively small geographical area.

Here we investigate whether species diversity and the life-history traits of primary producers across a broad array of natural stream ecosystems are consistent with a multivariate model that jointly considers the importance of disturbance and productivity. We analyse a data set where standardized methods were used to measure disturbance frequency (number of floods per year), primary production (the rates of biomass accrual of benthic periphyton) and species diversity (richness and evenness) of primary producers in 85 streams across a 3.6×10^5 km² area of the mid-Atlantic United States of America (Cardinale *et al.* 2005). Cardinale *et al.* (2005) used this data set to explore how algal diversity and biomass production covary across geographical regions having distinct hydrologic characteristics. Here we examine in more detail a potential explanation of their patterns by evaluating whether species richness varies across a disturbance/productivity response surface like that predicted by Kondoh (2001). This analysis is coupled with new data showing how species evenness, taxonomic composition and the life-history traits of dominant

species covary with stream flood frequency and rates of community biomass accrual.

Materials and methods

DISTURBANCE FREQUENCY

Of the numerous forms of disturbance that impact stream organisms, flooding is one of the most pervasive. High discharge events are known to reduce population sizes of nearly every major group of stream organism, not only because flow directly scours individuals from the stream channel, but also because sediment mobility is a significant source of mortality to flora and fauna (Resh *et al.* 1988; Allan 1995; Bond & Downes 2000). Here we define disturbance as a flood of bank-full magnitude or more which is likely to mobilize stream sediments and impose considerable mortality on benthic algae. We characterized the frequency of flooding in all stream ecosystems in the mid-Atlantic United States of America (Maryland, North Carolina, Pennsylvania, Virginia and West Virginia) that are gauged and monitored by the US Geological Survey (NWISWeb). Records of mean daily discharge were obtained for a 12-year period preceding the study (1 October 1989 to the date of sampling in 2001, updated from Cardinale *et al.* (2005) who used records only available to 30 September 1999). Streams having more than 365 days missing from the record, and which were too ephemeral or too deep to sample were eliminated from the data set (mean daily flow < 0.85 or $> 113 \text{ m}^3 \text{ second}^{-1}$).

For the 473 streams remaining, the mean number of floods per year was calculated using a flood frequency analysis of the annual maximum event series (Black 1991). A flood was defined as any discharge exceeding the 1.67-year recurrence interval – a definition that was chosen on both practical as well as biological grounds. Biologically, the size of this event is important because it is thought to represent a ‘bank-full’ discharge where physical forces are sufficient to reform the channel and rearrange the streambed (Leopold *et al.* 1964; Poff & Ward 1989; Leopold 1997). As the physical movement of substrates ranks among the most common cause of mortality to stream organisms (Resh *et al.* 1988; Allan 1995; Bond & Downes 2000), a discharge of this size almost certainly represents a significant disturbance to stream periphyton. Smaller discharge events can also move sediments and impose mortality on benthic organisms, but their characterization would be difficult, if not impossible across the large number of streams we studied (Lorang & Hauer 2003). Thus, we use a practical definition of a flood that can be reasonably considered to represent a major biological disturbance across a wide variety of streams.

PRODUCTIVITY AND DIVERSITY

A standardized assay was used to quantify the diversity and biomass production of benthic periphyton in 85

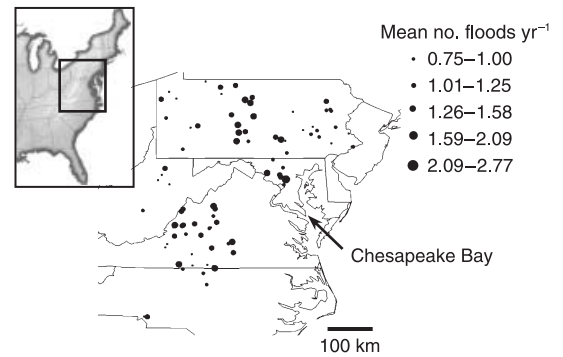


Fig. 1 Map showing location of 85 stream study sites throughout the mid-Atlantic United States of America. Streams were selected to represent a large gradient in the frequency of flooding based on analysis of long-term discharge records available for 474 streams in this region that are gauged and monitored by the US Geological Survey (see Methods).

streams for which estimates of flood frequency were available. Cardinale *et al.* (2005) used 83 of these streams to describe two discrete study groups that differed in six aspects of hydrologic variability. Here we focus on the continuum of flood frequency across the streams (Fig. 1), adding two new records that did not fall within the original hydrologic groupings (because samples from one of the hydrologic pairs could not be collected), but which extend the range of variables considered here.

In the summer of 2001 (28 June to 16 October), unglazed ceramic tiles (six sets, each with fifteen 5.29-cm^2 tiles connected in a 3×5 rectangular array) were staked flush with the surface of the streambed across two riffle habitats in each stream. Tiles were incubated for 15 days ($SD = 1$, range = 14–17), after which a randomly selected tile was collected from each of the six sets, and periphyton removed and preserved, as a composite sample, in glutaraldehyde. The density of all Bacillariophyceae, Cyanobacteria, Chlorophyceae, Euglenophyceae and Pyrrophyta were determined from material allowed to settle in a Utermöhl chamber. A minimum of 400 units (individuals, colonies or filaments) were identified from randomly selected transects at $480\times$ magnification. Diatom frustules were then cleaned by boiling in 30% hydrogen peroxide, mounted in Hyrax, and identified at $1500\times$. Individual cells were approximated to a geometric shape and, using dimensions from at least 10 individuals per species, the total biovolume of each population was determined (Hillebrand *et al.* 1999). Biovolume was converted to biomass assuming a specific gravity of 1.0, summed across taxa and divided by tile area and incubation period to derive the rate of periphyton biomass accrual ($\mu\text{g cm}^{-2} \text{ day}^{-1}$).

Biomass accrual is a common metric used to estimate productivity in aquatic ecosystems (Hall & Moll 1975), although several limitations should be noted. First, biomass accrual represents the sum of immigration, growth, death and emigration processes. It is likely that losses of biomass from cell death and sloughing were negligible in this study because incubation times were

kept short to approximate the exponential phase of biofilm growth (Stock & Ward 1989; Peterson & Stevenson 1992; Cardinale *et al.* 2001). We cannot, however, distinguish the influence of immigration from local cell division. Still, we specifically chose biomass accrual over other metrics because in aquatic systems of microalgae, biomass accrual is the only metric that allows one to examine species-specific contributions to biomass production, which is vital for interpreting patterns.

Although tile substrates are a standardized means of sampling periphyton, they are only useful to the extent that they provide an accurate depiction of species composition on natural substrata (Lowe *et al.* 1996). To assess whether the sampling tiles provided a reasonable approximation of species composition in the streams, we simultaneously sampled periphyton on $n = 6$ median sized natural particles ($d_{50} = 4-6$ cm, 2nd axis diameter) in a subset of 24 study streams chosen because they complemented a separate study of periphyton assemblages in Pennsylvania (Charles, unpublished data). For this comparison, we focused on the dominant group of primary producers (Bacillariophyceae), which represented > 90% of all taxa.

PREDICTIONS AND CRITICAL TESTS

Kondoh's (2001) model of successional diversity gives the qualitative prediction that species richness will be a concave-down function of disturbance frequency and of community biomass production, and an increasing function of their interaction. We tested this prediction by fitting our data to a second-order polynomial function of the form:

$$S = b_0 + b_1P + b_2D + b_3P^2 + b_4D^2 + b_5P \times D + \varepsilon \quad \text{eqn 1}$$

where D is the frequency of disturbance (mean no. floods year⁻¹), and P is periphyton biomass production on the sampling tiles ($\mu\text{g cm}^{-2} \text{day}^{-1}$). There was no significant correlation between flood frequency and rates of biomass accumulation ($r = 0.15$, $P > 0.10$); thus, the two variables were not confounded. As is true for many taxonomic groups (Willig *et al.* 2003; Hillebrand 2004), preliminary analyses revealed a latitudinal trend in periphyton species richness ($S = 87.57 - 1.61 \times \text{Latitude}$, $F = 23.48$, $P < 0.01$, $r^2 = 0.22$). Given this, we used the residual richness after accounting for the latitudinal trend as the dependent variable S . It is important to note that there was no correlation between stream latitude and disturbance frequency ($r = 0.03$, $P = 0.79$, also see Fig. 1), or between stream latitude and the rate of biomass production ($r = -0.06$, $P = 0.57$) that might generate a 'spurious' relationship (*sensu* Prairie & Bird 1989) between these variables and S . Thus, our conclusions are robust after accounting for latitudinal trends.

To examine trends in species composition across the productivity \times disturbance response surface, we

performed two complementary analyses. First, we modelled the evenness in final species biomass on the sampling tiles (as Simpson's index) as the dependent variable in equation 1. To interpret the curve fit we examined the dominant species in streams having strong influence over the polynomial coefficients, particularly b_3 and b_4 , which regulate curvilinearity. Second, we used a Principal Components Analyses (PCA) on the covariance matrix of species relative biomasses to identify dominant trends in species composition across the response surface. For this analysis we focused only on abundant and widespread species, including those found in ≥ 10 streams and representing $\geq 10\%$ of periphyton biomass in at least one of those streams. We found that the first three eigenvectors from the PCA explained 71% of all variation in relative biomass, and that these eigenvectors were strongly associated with the distributions of just four common algal species ($|\text{factor loadings}| > 0.60$). Thus, we summarize these results by simply showing trends in the relative biomass of these four taxa.

Results and discussion

GEOGRAPHIC PATTERNS IN SPECIES RICHNESS

With all 85 streams included in the statistical model, equation 1 explained a significant fraction of variation in species richness among the sampling tiles ($F = 3.87$, $P < 0.01$, $r^2 = 0.20$), but only coefficients for biomass production differed significantly from zero ($b_1 = 0.37 \pm 0.10$ mean and SE, $t = 3.90$, $P < 0.01$, $b_3 = -0.01 \pm 0.004$, $t = -2.63$, $P = 0.01$). A single stream (USGS gauge no. 01465798) was both a statistical outlier and had strong influence on model fit (studentized residual = 4, leverage = 0.8, open circle in Fig. 2a). More than 80% of the biomass at this site was dominated by the filamentous green alga, *Zygnema* sp. (open circle, Fig. 3a), which was found at this site and no other. With this data point excluded, the polynomial function remained a significant fit to the data, accounting for 30% of all variation in periphyton species richness (Table 1). There were significant quadratic trends for productivity ($b_3 = -0.02 \pm \text{SE } 0.004$, $t = -4.81$, $P < 0.01$) and disturbance frequency ($b_4 = -4.57 \pm 2.61$, $t = -1.75$, $P = 0.08$), and a positive term for their interaction ($b_5 = 0.60 \pm 0.17$, $t = 3.47$, $P < 0.01$). We used information criteria to assess whether statistical models with quadratic terms were a significantly better fit to the data than those without (the reader not familiar with information theoretic approaches to model selection can see Johnson & Omland 2004 for a summary). Akaike weights indicate that exclusion of b_3 and b_4 led to models that were highly improbable explanations of the data ($P < 0.01$), arguing the quadratic terms were necessary for satisfactory model fit. In support of this conclusion, we found that maximum richness occurred within the measured range of productivity given mean values of disturbance

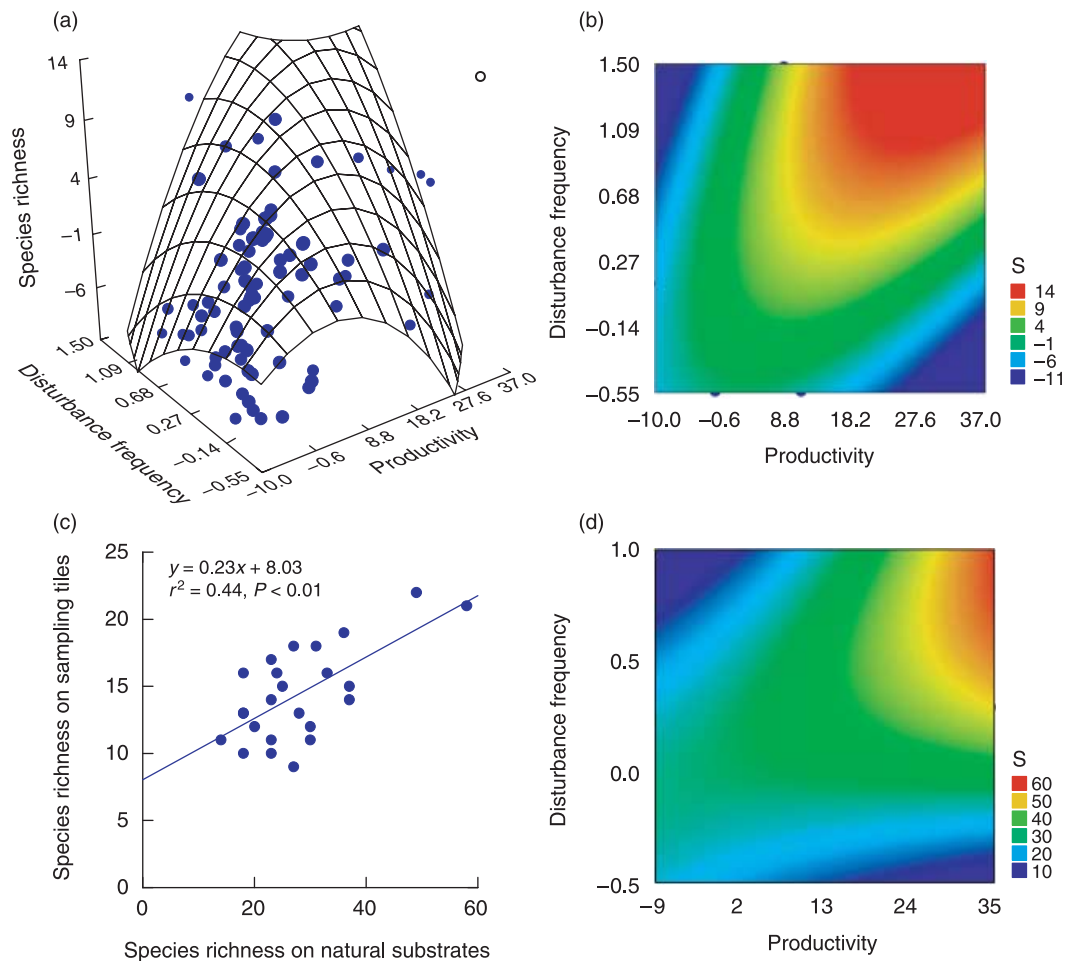


Fig. 2 Patterns of periphyton species richness across streams in the mid-Atlantic United States of America. (a) Species richness on the sampling tiles as a function of the rate of biomass production ($\mu\text{g cm}^{-2} \text{day}^{-1}$) and stream disturbance frequency (no. floods year $^{-1}$). The same data are presented as a two-dimensional contour plot in (b). Trends in (a) and (b) are fit with a quadratic smoothing function parameterized with polynomial coefficients in Table 1. Positive and negative values occur because richness is the residual after accounting for a latitudinal gradient in diversity (see Methods), and both productivity and disturbance were centred for analyses. Open circle represents the stream excluded from curve fitting (see Results). (c) The number of diatom species on sampling tiles as a function of diatom richness on natural substrata in a subset of 24 study streams. (d) Patterns of diatom richness on natural substrata as a function of biomass production of diatoms (measured from accumulation on tiles) and stream disturbance frequency.

(max S at $P = -b_1/2b_3 = 10.5$ for $S' = 0$ with D centred at mean = 0), and within the measured range of disturbance given mean values of productivity (max S at $D = -b_2/2b_4 = 0.32$ for $S' = 0$ with P centred at mean = 0). These results collectively indicate that patterns of periphyton species richness across these streams fit our predictions, being best explained as concave-down functions of productivity and disturbance frequency, and an increasing function of their interaction (Fig. 2a,b).

Analysis of diatom species richness on natural substrata collected from a subset of 24 study streams lends further support to the conclusions above. The number of diatom species on the standardized sampling tiles was positively, and linearly related to the number of diatom species on natural stream substrata, with one out of every 4–5 species being detected, on average (Fig. 2c). As occurred on the tiles, variation in diatom richness on natural substrata was best explained by an interaction between the productivity of diatoms and the

frequency of disturbance ($b_5 = 1.53 \pm 0.72$, $t = 2.13$, $P = 0.05$, $n = 24$, Fig. 2d). Unlike patterns on the tiles, quadratic terms in the statistical model were not significant, indicating no evidence of curvilinear relationships between richness and either productivity or disturbance. It is, however, unclear whether this inconsistency can be meaningfully interpreted since the range of these variables was constrained in the subset of 24 streams relative to the full data set (-10% for productivity, -66% for disturbance frequency). Either way, the results indicate that patterns of species richness are best explained by an interaction of disturbance and productivity (compare Fig. 2b–d).

CORRESPONDING PATTERNS IN SPECIES COMPOSITION

Much effort has gone into predicting the adaptive life-history traits of species expected to dominate

Table 1 Coefficients for the model $y = b_0 + b_1P + b_2D + b_3P^2 + b_4D^2 + b_5P \times D + \varepsilon$, where y = species richness (ANOVA, $F = 6.71$, $P < 0.01$, $r^2 = 0.30$), or evenness (ANOVA, $F = 2.90$, $P = 0.02$, $r^2 = 0.16$), P = periphyton biomass production ($\mu\text{g cm}^{-2} \text{ day}^{-1}$), and D = disturbance frequency (no. floods year $^{-1}$). P and D were centred for analyses, data for species richness represent the residuals after accounting for a latitudinal gradient (see Methods), and species evenness was transformed using the Box-Cox transformation, $E^{2.3}$, to meet statistical assumptions

Source	Species richness b_i (SE)	t	P	Species evenness b_i (SE)	t	P
Intercept	2.31 (0.75)	3.09	< 0.01	0.60 (0.04)	16.14	< 0.01
P	0.42 (0.09)	4.86	< 0.01	0.01 (0.004)	3.41	< 0.01
D	2.96 (1.84)	1.61	0.11	0.02 (0.09)	0.23	0.82
P^2	-0.02 (0.004)	-4.82	< 0.01	-0.007 (0.002)	-3.26	< 0.01
D^2	-4.59 (2.61)	-1.76	0.08	-0.22 (0.13)	-1.68	0.10
$P \times D$	0.60 (0.17)	3.46	< 0.01	0.01 (0.01)	0.92	0.36

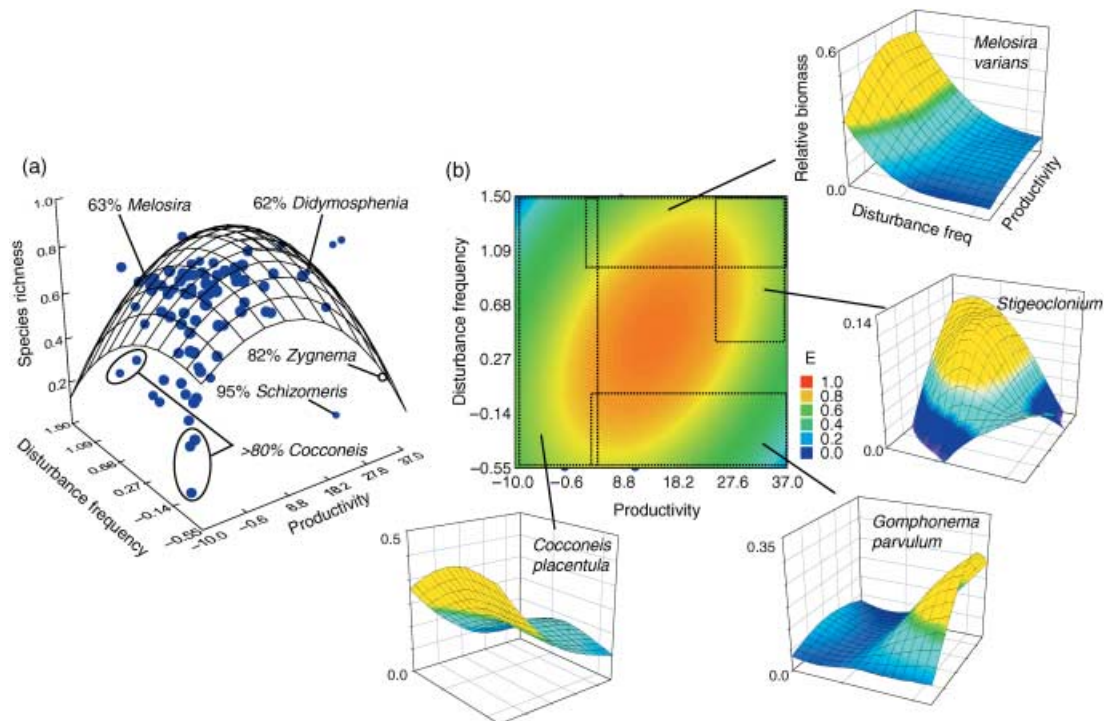


Fig. 3 Patterns in species composition. (a) The evenness of biomass among periphyton species on sampling tiles as a function of the rate of biomass production ($\mu\text{g cm}^{-2} \text{ day}^{-1}$) and stream disturbance frequency (no. floods year $^{-1}$). The same data are plotted as a two-dimensional contour plot in (b). In (a), the dominant species in streams having a strong influence on downward trends are noted at each corner. In (b), insets show the relative biomass (z -axis) of four common species as a function of productivity (x -axis) and disturbance frequency (y -axis). The combined distributions of these species explained 71% of all variation in dominance (see explanation of Principal Components Analysis in Methods). Scales of the x - and y -axes in each inset are the same as in main figure.

various combinations of disturbance and production in terrestrial plant assemblages (e.g. Grime 1979; Huston 1994), and analogous conceptual models have recently been developed for primary producers in stream ecosystems (McCormick 1996; Stevenson 1997; Biggs *et al.* 1998). The underlying assumptions of some of these models have been questioned on theoretical grounds (e.g. Chesson & Huntly 1997), but many give qualitatively similar predictions. When disturbance frequency is low relative to the rate of biomass accrual, conditions are expected to favour dominance by competitively superior species because (i) there is sufficient time for species to recruit to patches, even if they are slow growing or poor dispersers, (ii) local interactions have time to

influence community structure, and (iii) inferior competitors can be driven extinct from the system. In contrast, when disturbance frequency is high relative to the rate of biomass production, conditions favour dominance by species that are either adapted for dispersal, and therefore able to colonize and exploit the resources in spatial 'refuges' unoccupied by superior competitors, or are specifically adapted to resist disturbance and/or recover quickly.

We found that the evenness of algal species was highest at intermediate levels of productivity and disturbance frequency, but low at each of the four extremes (Fig. 3a, Table 1). At the low $P \times$ low D and low $P \times$ high D extreme, trends were influenced primarily by the diatom

Cocconeis placentula (Fig. 3a), which dominated the majority of streams characterized by low biomass accumulation (Fig. 3b and inset). *Cocconeis placentula* is often associated with high disturbance frequency because its adnate growth form confers resistance to scour by floods (Peterson 1996; Biggs *et al.* 1998). Studies have also associated this taxon with a broad range of stream productivity (Biggs *et al.* 1998), but while we found *C. placentula* in streams spanning the whole spectrum of biomass production, it was only a minor component of periphyton assemblages in streams with higher rates of accumulation. We suspect this is because, as an adnate growth form, *C. placentula* is unlikely to tolerate shading at the bottom of a periphytic mat and tends to be replaced by higher profile, often competitively superior species.

In support of this possibility, we found that trends at the high $P \times$ low D extreme were the result of dominance by the filamentous green alga *Schizomeris* sp. (bottom right of Fig. 3a), and the stalked diatom *Gomphonema parvulum* (Fig. 3b and inset). Both of these species are loosely attached growth forms that tend to be particularly sensitive to high velocity and the scour of floods (Hoagland *et al.* 1982; Burkholder *et al.* 1990; Biggs 1996; Peterson 1996). However, overstorey species such as these also tend to be superior competitors for light and nutrients and are typical of late-successional algal assemblages (Burkholder *et al.* 1990). *Gomphonema parvulum* is also particularly well known to tolerate organic pollution (Stevenson & Bahls 1999), which may further explain its dominance at the high $P \times$ low D extreme.

At the high $P \times$ high D extreme, trends were influenced by streams dominated by the diatoms *Didymosphenia germinata* and *Melosira varians* (Fig. 3a,b and inset), and by the filamentous green alga *Stigeoclonium* (Fig. 3b and inset). These taxa are often classified as late-successional species that dominate assemblages in eutrophic waters (Biggs *et al.* 1998; Kociolek & Spaulding 2003; Stoermer & Julius 2003). *Didymosphenia germinata*, which frequently grows as a mucilaginous mat (Kociolek & Spaulding 2003), and *Stigeoclonium*, which has basal cells that are highly resistant to shear (Biggs 1996), are well-adapted for persistence in flood prone environments. *Melosira varians*, on the other hand, is known to exhibit low resistance to scour disturbance (Biggs & Thomsen 1995; Passy 2002), but can reproduce rapidly to yield high biomass. Thus, we suspect that the prevalence of *M. varians* in frequently disturbed streams stems from its high resilience following space-clearing disturbance.

LIMITS TO INFERENCE

As a large-scale survey of biodiversity, it should be clear that we cannot link the documented patterns to any underlying theoretical model or biological mechanism to the exclusion of all other explanations. However, we think it is noteworthy that the biogeographical patterns

reported here are consistent with those of experimental tests (e.g. Wilson & Tilman 2002; Kneitel & Chase 2004; Scholes *et al.* 2005), meta-analyses (Worm *et al.* 2002) and mathematical theory (Kondoh 2001) detailing how disturbance and community biomass production interact to influence biodiversity. Our results are valuable because they suggest that inferences derived from more controlled, but less realistic avenues of research are applicable to much broader patterns of species richness in natural systems.

Our inferences do, however, have several limitations. First, algal species diversity and production were both characterized from short-term incubations of periphyton on artificial substrates. This method was chosen as a standardized means of sampling across a large number of streams having very different characteristics. Our intent was that the substrates would serve as passive samplers that portray patterns of diversity and rates of biomass accrual in open patches for the stream as a whole, but our conclusions are only valid to the extent that this assumption is true. For measures of species richness, the assumption was partly verified using independent samples of periphyton from natural substrata, which suggest we can have some confidence that the trends in species richness are robust. However, rates of biomass accrual on tile substrates are, at best, a limited characterization of primary production. Not only are we unable to account for certain loss terms that might influence the rate of biomass accrual (e.g. herbivory), we do not know if the rates of accrual are representative of those that occur naturally. Although it would have been ideal to measure the development of primary production on natural substrates following floods, 'tracking' storm events for 85 streams spanning 3.6×10^5 km² of the mid-Atlantic USA would have been impractical, if not impossible. It might have also been better to measure stream metabolism to obtain more direct estimates of production, but such methods suffer from not being able to distinguish between the contributing species. Thus, in the absence of practical alternatives, our use of sampling tiles to measure biomass accrual provides useful information that would be otherwise difficult to obtain.

Secondly, we chose to define disturbance as any discharge exceeding the 1.67 years recurrence interval, because this magnitude of event is commonly thought to represent a 'bank-full' flood where physical forces are sufficient to scour streambed sediments (Leopold 1968; Gordon *et al.* 1992). We think it is reasonable to assume that this definition does indeed characterize major, infrequent disturbances across the variety of sites that were studied, although it is also likely that each stream is subjected to smaller, more frequent events that scour algae from the streambed. It would have been preferable to obtain a direct measure of geomorphic disturbance at each site, but this requires the use of discharge/critical shear stress relationships that are often labourious to work out, or that must be assumed from theoretical relationships which generally do a poor job

of predicting sediment stability (Downes *et al.* 1998; Lorang & Hauer 2003). Thus, we were forced to define a flood as a discharge large enough to be safely considered a disturbance across a wide variety of stream types. Given our somewhat crude definition, it strikes us as particularly interesting that clear relationships still emerged between flood frequency, algal productivity and species richness. We suspect that improved methodology and more refined metrics of disturbance would only serve to make these relationships more apparent.

Conclusions and implications

Our study shows that patterns of periphyton species richness in streams throughout the mid-Atlantic United States of America are consistent with a multivariate model that predicts disturbance frequency and community biomass production will interact to influence community diversity (Kondoh 2001). We found that the relationship between species richness and biomass production was unimodal, but the level of productivity that maximized richness increased as a function of disturbance frequency. Similarly, the relationship between species diversity and disturbance frequency was unimodal, but the level of disturbance that maximized richness increased with increasing productivity. Changes in community composition along these environmental gradients suggest these patterns may have resulted from opposing effects of productivity and disturbance on species interactions. In streams where the frequency of floods was high relative to the rate of biomass production, periphyton assemblages were dominated by species specialized for coping with disturbance, such as adnate diatoms that are likely poor competitors, but whose small size and growth form makes them highly resistant to scour from high flow events. In streams where the frequency of floods is low relative to the rate of biomass production, assemblages were dominated by stalked and filamentous algal species that are especially prone to scour and have characteristics that imply low resilience (slow reproduction and/or poor dispersal), but which tend to be competitively superior because they grow upright above the periphyton canopy to sequester nutrients and light. Species richness was maximized along the positive diagonal of the disturbance \times productivity gradient, which theory argues is where the opposing effects of productivity and disturbance allow for the greatest expression of life-history traits.

When results of this study are interpreted alongside those of prior research, the balance of evidence suggests that the maintenance of species diversity in a given system is jointly determined by the frequency of disturbances that create new niche opportunities for species in space or time, and the rate at which biomass accrual leads to successional displacement of inferior by superior competitors. To the extent this conclusion is correct, it argues that univariate explanations of diversity (e.g. the Intermediate Disturbance and

Productivity Hypotheses) are antiquated, limited to too narrow a range of variables to represent generalities or, perhaps, altogether incorrect. Because multivariate models predict synergistic effects of ecological variables on species diversity, they further suggest that human activities – which are changing both the rates of disturbance and the productivity of ecosystems (Vitousek *et al.* 1997) – could impact biodiversity more than expected from prior ecological theory. In stream ecosystems, dams, urbanization and destruction of riparian zones are well known to alter the frequency of flooding (Poff *et al.* 1997), and excessive nutrient loading has increased the productivity of aquatic systems around the globe (Allan & Flecker 1993; Bennett *et al.* 2001). Attempts to mitigate the effects of altered disturbances rarely consider the concurrent impacts of eutrophication on productivity; similarly, attempts to mitigate eutrophication rarely consider how altered flow regimes change the frequency of disturbance. Multivariate models of diversity suggest that, for any attempt to mitigate human impacts on biodiversity, a significant but important challenge is that we conserve and/or restore both the natural levels of environmental variation that impose disturbance, and rates of resource supply that limit biomass production.

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