Are algal communities driven toward maximum biomass?

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In this continental-scale study, we show that in major benthic and planktonic stream habitats, algal biovolume—a proxy measure of biomass—is a unimodal function of species richness (SR). The biovolume peak is observed at intermediate to high SR in the benthos but at low richness in the phytoplankton. The unimodal nature of the biomass–diversity relationship implies that a decline in algal biomass with potential harmful effects on all higher trophic levels, from invertebrates to fish, can result from either excessive species gain or species loss, both being common consequences of human-induced habitat alterations. SR frequency distributions indicate that the most frequent richness is habitat-specific and significantly higher in the benthos than in the plankton. In all studied stream environments, the most frequent SR is lower than the SR that yields the highest biovolume, probably as a result of anthropogenic influences, but always within one standard deviation from it, i.e. they are statistically indistinguishable. This suggests that algal communities may be driven toward maximum biomass.

Keywords: diversity–productivity relationship; frequency distributions; NAWQA; phytoplankton; periphyton; species richness

1. INTRODUCTION

The epistemological paradox *the more we know the more we do not know* has rarely been as descriptive as in the ecological study of the species diversity–productivity relationship. There is a tremendous amount of literature devoted to this subject, but as the scope of investigations broadens to include new organismal groups, new systems and different scales, the commonalities among studies become fewer while the contingencies increase. The notion of unimodal functional response of species diversity to productivity was supported by research on vascular plants, macroalgae, phytoplankton, zooplankton and consumers in terrestrial, freshwater and marine systems (Rosenzweig & Abramsky 1993; Leibold 1999; Dodson *et al.* 2000; Mittelbach *et al.* 2001; Worm *et al.* 2002; Irigoien *et al.* 2004). Further inquiries into the nature of community–environment interactions revealed that the unimodal pattern holds for heterogeneous conditions, whereas in homogeneous environments the diversity–productivity relationship becomes linear or disappears (Guo & Berry 1998; Kassen *et al.* 2000; Hoffmann & Dodson 2005), possibly as a function of the size of the window of observations. Longer ecological gradients create heterogeneity of the environmental conditions and give enough 'space' to the community to display unimodal curves, whereas in short gradients we only see a small portion of the curve and it appears linear. Furthermore, the diversity–productivity relationship varies with spatial scales as in some studies the unimodal curve shifts to a linear pattern at larger scales (Mittelbach *et al.* 2001; Chase & Leibold 2002), while in other investigations this trend is reversed with scale (Gross *et al.* 2000). The history

of community assembly is also crucial: different successional sequences of the same species generate a variety of diversity–productivity relationships, including unimodal, linear, U-shaped and non-significant (Fukami & Morin 2003). Differences in diversity–productivity patterns across systems may arise from the different ways of measuring productivity, some of which are indirect and involve biomass or standing crop assessments rather than direct energy flow estimates (Tilman *et al.* 1996, 2001; Hector *et al.* 1999). A meta-analysis of 254 diversity–productivity studies revealed that the productivity measures affect the distribution of the diversity–productivity patterns in animal investigations; in plant studies (including algae) the relationships are robust, even though productivity estimates may be derived from abiotic surrogates such as rainfall or soil moisture (Groner & Novoplansky 2003).

Although it has been suggested that the diversity–productivity relationship is bidirectional and each component is both the cause and the consequence of the relationship (Loreau *et al.* 2001; Schmid 2002; Worm & Duffy 2003), until recently the pathway from diversity to productivity has received much less attention. The most commonly hypothesized response of productivity (biomass) to increasing diversity (species richness, SR) involves a saturating pattern where the initial increase in productivity eventually levels off (Hooper *et al.* 2005). However, positive linear, positive nonlinear and no relationship have also been documented (Hector *et al.* 1999; Waide *et al.* 1999). A recent investigation on the algal biomass accrual in streams from the mid-Atlantic US reported a positive relationship with SR in frequently disturbed watersheds, but not in streams of low discharge-related disturbance (Cardinale *et al.* 2005). In the present study,
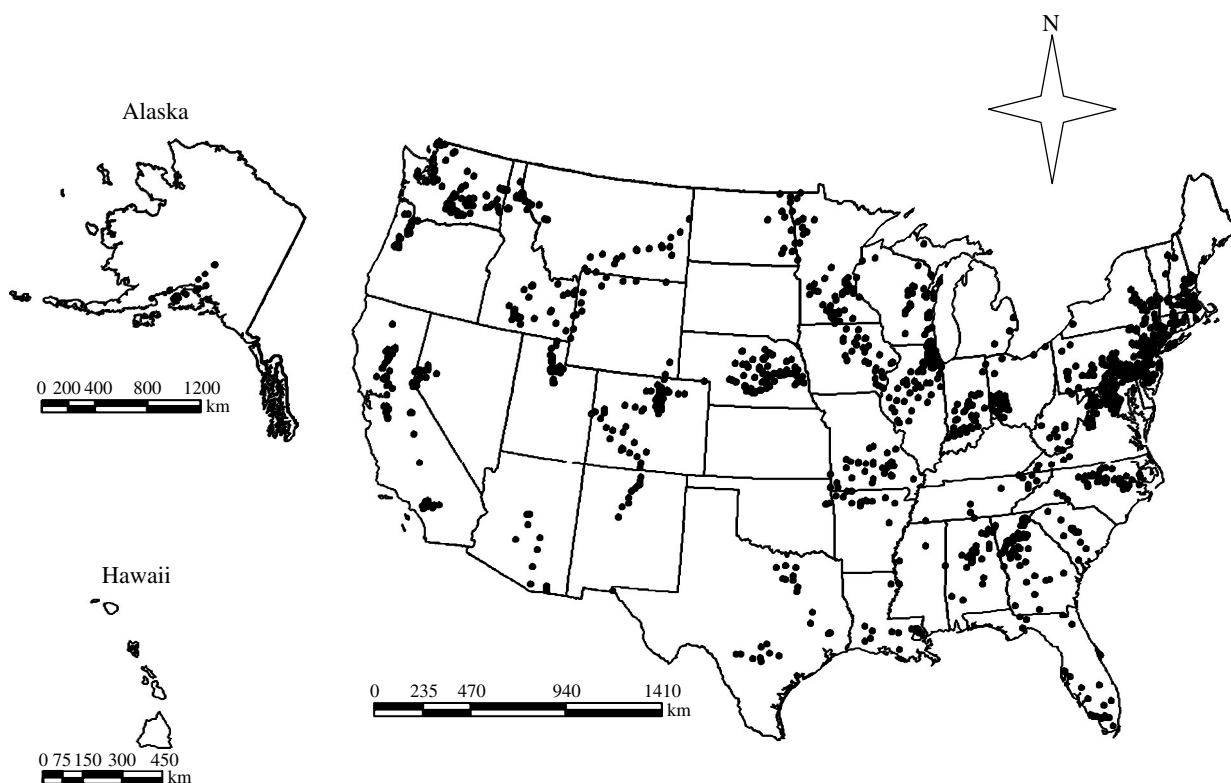
Figure 1. Map of the study area and sampling locations in the US.

we examine the algal communities from a large, systematic and well-designed survey of streams in the major US watersheds, carried out by the national water quality assessment (NAWQA) program. In our previous study of the NAWQA data, significant differences in algal taxonomic structure were discovered between benthic and planktonic habitats, which were attributed to differential niche differentiation (Passy & Legendre 2006). Niche differentiation, expressed in complementary resource utilization, is one of the key mechanisms explaining the diversity–productivity relationship (Waide *et al.* 1999; Loreau & Hector 2001; Symstad *et al.* 2003). Therefore, we expected this relationship to be habitat-dependent in the US running waters as well. More specifically, we asked the following questions: (i) what are the SR frequency distributions in the benthic and planktonic environments? (ii) what is the behaviour of algal biovolume, a proxy measure of biomass, along the SR gradient? and (iii) is the most frequent SR associated with the greatest biomass?

2. MATERIAL AND METHODS

(a) *Algal data*
The NAWQA dataset analysed here contains 4898 algal samples from 1553 locations in more than 50 major river basins and aquifers across the US, including sites in Alaska and Hawaii (figure 1). Three habitat types, defined by NAWQA, were quantitatively sampled for algae: richest targeted habitats (RTH), depositional-targeted habitats (DTH) and phytoplankton. The NAWQA dataset comprises 2730 RTH, 1700 DTH and 468 phytoplankton samples collected year round between March 1993 and September 2003.

RTH maintain the taxonomically richest community and encompass the following habitats: (i) shallow riffles in areas with coarse-grained substrates (epilithon); (ii) woody snags in reaches with fine-grained substrates (epidendron); and (iii)

macrophytes where riffles or woody snags are absent (epiphyton). In each study reach, epilithon was scraped with a brush from a predefined area on five cobbles in each of five different locations; if the substrate was gravel, epilithon was collected from 5 to 10 locations. All collections from a reach were composited and the total sampled area was calculated. Epidendron was scrubbed with a brush from a predefined area of woody snags collected from five locations in a reach and composited. The total sampled area was recorded. Macrophytes were carefully removed from five 50×50 cm square areas within a reach. Epiphyton was collected by agitation, brushing of the macrophytes and composited. The surface area of the sampled macrophytes was determined.

DTH microalgae are found in organically rich or sandy depositional areas along the stream margins, including epipelic and epipsammic habitats. Each habitat was sampled at five locations per study reach by inserting a 47 mm diameter Petri dish into the sediments and extracting the contents with a spatula. The five discrete collections were combined into a composite sample for each habitat. Phytoplankton is a community of suspended algae, collected from 1 l of water in nutrient-rich streams or 5 l of water in unproductive, nutrient-poor streams. More information on the habitats and sampling techniques can be found at http://water.usgs.gov/nawqa/protocols/OFR02-150/OFR02-150.pdf.

Sample processing and algal enumeration and identification, followed by assessment of algal biovolumes, were carried out by specialized phycology laboratories (for details visit http://diatom.acnatsci.org/nawqa/protocols.asp). In short, soft algae and total number of diatoms were enumerated in a Palmer–Maloney counting cell (RTH, DTH and phytoplankton) or Utermöhl sedimentation chamber (phytoplankton) until 300 living natural counting units (individual colony, filament or isolated cell) were encountered. Diatoms, whether single or in colonies, were always counted as individual cells. Diatom identification was carried out in permanent mounts after

acid-digestion of the raw samples. Biovolume was calculated for all taxa in a sample after approximation to simple geometric figures. The sum of biovolume of all algal specimens in a sample was standardized by the sampled area/volume and used in all analyses, considering that it represents one of the most accurate measures of algal biomass (Stevenson 1996).

(b) Statistical analyses

The SR frequency in each habitat was calculated and $\log_2$-transformed. Algal biovolume, measured as total sample cell biovolume, was $\log_2$-transformed and regressed against SR in three ways: (i) using the raw data; (ii) after averaging of $\log_2$ (biovolume) per SR class; and (iii) after finding the maximum value of $\log_2$ (biovolume) in each SR class. The rationale for using the average and maximum values was to extract the major trends from data that were inherently noisy. A similar approach for dealing with the noise in much smaller richness–biomass datasets was advocated in Schmid (2002), who analysed the relationship as the upper envelope enclosing the point scatter (Schmid 2002, fig. 1b).

The $\log_2$-SR frequency and the three measures of biovolume (raw, average and maximum) were fit with a parabola, which is equivalent to fitting a Gaussian curve to the original data,

$$\log_2(\hat{y}) = b_0 + b_1 x^k + b_2 x^{2k},$$

where $\hat{y}$ = expected frequency/biovolume, b_0, b_1, b_2 are parameters and x = SR; k = 1 or 0.5 in symmetric and positively skewed distributions, respectively. The optimum (u = value of x yielding the maximum frequency or maximum biovolume) and tolerance (t = one standard deviation, s.d.) were calculated as follows: $u = -b_1/(2b_2)$ and $t = 1/\sqrt{-2b_2}$ (ter Braak & Looman 1995). In positively skewed distributions, where u was derived from the square root of x, the actual value of x associated with the mode is equal to u^2.

3. RESULTS

SR frequency distributions exhibited unimodal patterns across the three habitats: the RTH and DTH curves were balanced, whereas the phytoplankton curve, which had $(SR)^{0.5}$ on the abscissa, was left truncated (figure 2a–c). The most frequent (SR) was the highest in DTH (52), followed by RTH (41) and phytoplankton (18). We conducted a contingency table analysis comparing the proportions of observations in these frequency classes in the three habitats (the contingency table included a fourth class containing all richness values other than 18, 41 and 52). The χ^2 test rejected the null hypothesis that SR frequencies were independent of habitat type and showed highly significant differences ($p = 0.017$).

The relationships between biovolume and SR were hump-shaped in all regressions in all habitats (figure 2d–f). The raw data were highly variable and generated weak ($R^2 = 0.04–0.15$) but highly significant relationships ($p < 0.000005$). Averaging the $\log_2$-biovolume data substantially decreased the variability per SR class and produced better fits ($R^2 = 0.37–0.49$). Notably, the fits of the raw and averaged data were statistically equivalent—all corresponding regression parameters from the two models (b_0 to b_2) were not significantly different (table 1). The unimodal nature of the biomass–richness relationship once again emerged when maximum $\log_2$-biovolume per species class was

analysed ($R^2 = 0.29–0.69$). Maximum $\log_2$-biovolume had the strongest relationship with SR in the benthos, whereas average $\log_2$-biovolume was best explained by SR in the phytoplankton.

The biovolume–SR relationships were symmetrical in the benthos with a maximum at intermediate to high SR (at SR = 50 in RTH and SR = 63 in DTH) and positively skewed in the phytoplankton, which had $(SR)^{0.5}$ on the abscissa and a maximum at a lower value of species richness (SR = 37; figure 2d–f). Average $\log_2$-biovolume exhibited SR optima that were very close to the optima of the raw data, i.e. the offset was between 3 and 6 richness classes. In the benthos, there was appreciable correspondence between maximum $\log_2$-biovolume and the raw data—the optima offset was 5 (RTH) and 8 (DTH) richness classes. Maximum $\log_2$-biovolume was a poor substitute of the raw data in the phytoplankton. In that habitat, SR explained a much smaller fraction of the variance in maximum $\log_2$-biovolume compared to the averaged data; the optima of the raw versus maximum $\log_2$-biovolume showed a substantial although not significant offset (14 richness classes; table 1). However, in all habitats the three estimates of SR optimum had overlapping confidence intervals, suggesting that they were statistically indistinguishable. In each habitat, the SR that yielded the highest biovolume, regardless of the regression method used for its estimation, was within 1 s.d. of the SR that was the most frequent (table 1, figure 2a–f).

4. DISCUSSION

Maximum biomass, measured as algal biovolume, was observed at much higher SR in the benthos than in the plankton. This phenomenon can be explained by the ecological differences between the two habitats in terms of structure of the environmental gradients and nature of interspecific interactions. The number and length of environmental gradients are expected to be much higher in the benthos, where the algal biofilm is subjected to strong vertical and in some instances horizontal nutrient, light, grazer and current velocity gradients (Stevenson 1996). Alternatively, the phytoplankton develops in the comparatively homogeneous environment of the well-mixed water column, where many of the aforementioned gradients do not exist or are much shorter. Hence, the ecological niches in the benthos, defined along the multiple environmental gradients observed there, are multidimensional, allowing a comparatively low degree of complementarity among species. More specifically, species with n-dimensional niches can theoretically coexist indefinitely when they occupy similar positions on all but one dimension (Hutchinson 1957). In the case where n is large, there can be substantial niche overlap among species; their similarity in resource acquisition and disturbance tolerance would translate in high taxonomic similarity among communities in that type of environment. Accordingly, the communities established in the benthos are expected to be species-rich but comparatively homogeneous in terms of higher taxonomic categories, i.e. the diversity of higher taxa such as genera, families, orders, etc. would be comparatively low. On the contrary, the phytoplankton habitat encompasses very few dimensions (n is small); this forces stronger differentiation among the species, which would occupy distinct and complementary
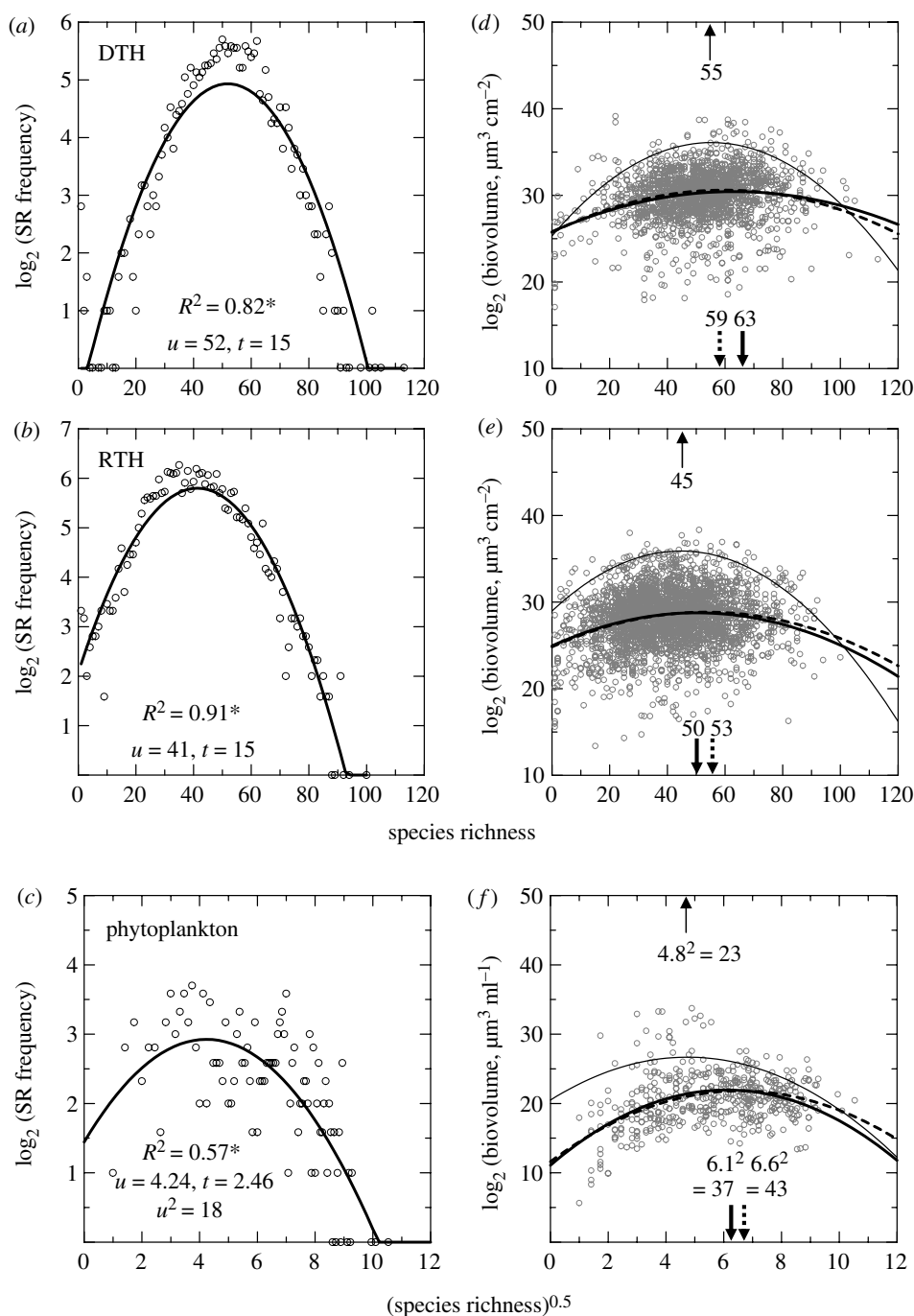
Figure 2. (*a–c*) Species richness frequency distributions in the three habitats, fitted by $\log_2(\hat{y}) = b_0 + b_1 x^k + b_2 x^{2k}$ ($k=1$ in DTH and RTH; $k=0.5$ in phytoplankton); $\hat{y}$, estimated species richness frequency; x, species richness; $^*p<0.000005$. Species richness frequency peaks are significantly different across habitats, $\chi^2 = 15.43$, $p=0.017$. (*d–f*) Biovolume per species richness in the three habitats, where the fitting functions were calculated from the raw $\log_2$ (biovolume) data (thick line), averaged $\log_2$ (biovolume) data (dashed line) and maximum $\log_2$ (biovolume) data (thin line). $p<0.000005$ in all analyses. The values of species richness associated with the biovolume modes are marked by arrows of corresponding line style.

positions along these dimensions. Strong niche differentiation is best achieved through alternative modes of nutrient sequestering and disturbance resistance, which are associated with divergence at the level of higher taxonomic categories. The phytoplankton communities are thus expected to have fewer but taxonomically more disparate species. These hypotheses are well supported by a recent investigation of the taxonomic composition of the NAWQA algal communities, which revealed that for the same SR, the diversity of all above species categories was significantly higher in the comparatively species-poor phytoplankton than in the species-rich benthos (Passy &

Legendre 2006). This means that an increase in SR in the phytoplankton was associated with the highest increase of new genera, families, orders, classes and phyla, i.e. the likelihood that each new species added to the community was a member of a different higher order taxon was the greatest. Conversely, an increase in SR in the benthos was greatly attributable to species that belonged to the same higher taxon, resulting in higher similarity among sites at all above-species levels. Therefore, many more but similar species can be packed along the multitude of long resource and disturbance gradients in the benthos, where the highest biovolume was attained at higher SR than in the

Table 1. Coefficients, 95% confidence intervals (CI) and coefficients of determination (R^2) of quadratic regression models of species richness versus frequency and species richness versus biovolume in the three habitats. (N, number of data points; AVG, average; MAX, maximum; $p < 0.000005$ for all relationships.)

habitat	$\log_2$ (frequency)	$\log_2$ (biovolume)	AVG $\log_2$ (biovolume)	MAX $\log_2$ (biovolume)
DTH				
N	98	1700	98	98
R^2	0.82	0.05	0.37	0.65
b_0	−0.69	25.81	25.72	25.32
95% CI	−1.20 to −0.18	24.89–26.74	24.68–26.77	23.96–26.68
b_1	0.22	0.15	0.16	0.39
95% CI	0.19–0.24	0.11–0.18	0.12–0.21	0.33–0.45
b_2	−0.0021	−0.0012	−0.0014	−0.0035
95% CI	−0.0023 to −0.0019	−0.0015 to −0.0008	−0.0018 to −0.0010	−0.0041 to −0.0030
u	52	63	59	55
t	15	21	19	12
RTH				
N	93	2730	93	93
R^2	0.91	0.04	0.45	0.69
b_0	2.07	24.94	24.83	28.97
95% CI	1.74–2.40	24.35–25.54	24.09–25.57	27.96–29.98
b_1	0.18	0.15	0.15	0.31
95% CI	0.16–0.20	0.12–0.18	0.08–0.13	0.26–0.36
b_2	−0.0022	−0.0015	−0.0014	−0.0035
95% CI	−0.0023 to −0.0020	−0.0018 to −0.0012	−0.0018 to −0.0010	−0.0040 to −0.0030
u	41	50	53	45
t	15	18	19	12
phytoplankton				
N	86	468	86	86
R^2	0.57	0.15	0.49	0.29
b_0	1.44	11.10	11.61	20.49
95% CI	0.58–2.31	8.97–13.23	9.57–13.67	16.35–24.63
b_1	0.70	3.56	3.11	2.61
95% CI	0.39–1.01	2.73–4.39	2.38–3.84	1.12–4.10
b_2	−0.0825	−0.2916	−0.2365	−0.2745
95% CI	−0.1086 to −0.0564	−0.3666 to −0.2166	−0.2979 to −0.1751	−0.3997 to −0.1494
u	4.24	6.10	6.57	4.75
t	2.46	1.31	1.45	1.35
u^2	18	37	43	23

phytoplankton. Further corroboration of this hypothesis was found in the analysis of diatom cell size distributions in the three habitats (S. I. Passy 2006, unpublished data), which revealed that species adjacent in size had significantly smaller biovolume differences in the benthos than in the phytoplankton. Species of similar sizes are considered ecologically equivalent; therefore the higher degree of biovolume similarity among species in the benthos suggests a higher degree of niche overlap than in the phytoplankton.

The nature of the interspecific interactions, facilitation versus competition, also differs between benthic and planktonic habitats. Facilitation is of widely recognized importance in the benthos, where succession and community establishment are contingent upon substrate preconditioning by pioneer species (Hoagland *et al.* 1982; Korte & Blinn 1983; Stevenson 1983). Facilitation enhances the efficiency of resource utilization and survival under stressful conditions and can thus elevate ecosystem productivity (Loreau & Hector 2001; Mulder *et al.* 2001; Cardinale *et al.* 2002). On the contrary, no such mechanism has been put forth in explaining

phytoplankton dynamics, which are governed primarily by negative interspecific interactions (Tilman 1982; Sommer 1985; Huisman *et al.* 1999, 2004; Litchman *et al.* 2004).

Top-down effects are also differential in the phytoplankton and benthos. For example, strong asymmetric grazing control in the phytoplankton eliminates sensitive species, allowing the exclusive proliferation of a few species with anti-grazer defences, which further increase their biomass through positive feedbacks (Irigoien *et al.* 2005). Grazer selectivity is much less pronounced in the benthos, where entire guilds, comprising understorey and motile species, can successfully avoid herbivory and even increase in abundance and primary production in the presence of grazers (Steinman 1996). Therefore, the discovery of maximum biomass at lower SR in the phytoplankton than in the benthos is not surprising. Facilitation in the benthos delays the negative effect of competition, which together with the weaker response to top-down controls, permits more species to coexist and produce maximum biomass.

Biovolume modes along the SR gradient differed between the two-benthic habitats. Algal communities in

RTH, exposed to stronger physical disturbance and shear stress, reached peak biovolume at intermediate SR, while in the sheltered soft-bottom DTH habitats, maximum biovolume was attained at high SR. High SR in the hard-substrate RTH environment is usually coupled with large physiognomic variability, including body plans and habits (unicellular to multicellular, prostrate to erect, filamentous to branched). Initial increase in SR is favourable for community growth because it facilitates subsequent colonization. Further increase in SR is associated with the establishment of multi-storey, cohesive and disturbance-resistant biofilm due to the coexistence of species with various profiles in a matrix of exopolymers. SR increase beyond this point would lead to stronger competition for nutrients and space, higher mortality and ultimately to community biovolume decline. DTH, on the other hand, is a peculiar community of primarily low-profile motile species, which can withstand frequent burial in the soft sediments. Similarly to RTH, initial increase in SR and accumulation of extracellular exudates would promote community growth by stabilizing the sediments. However, the negative effect of competition would be experienced at much higher SR than in RTH for two reasons: first, the nutrient limitation in DTH is weaker because algae receive nutrients from the sediment and the water column, whereas in RTH the water column is the exclusive nutrient source (Burkholder 1996), and second, the motile species in DTH can escape stressful conditions and biotic interactions.

The nonlinear response of biovolume to SR implies different underlying mechanisms along the SR gradient. There is ample research pointing to positive species interactions (complementarity or facilitation) and sampling effect (the likelihood that a highly productive species is a member of the community) as the mechanisms driving the positive relationship between biomass and SR (Fridley 2001; Loreau *et al.* 2001; Tilman *et al.* 2001; Hooper *et al.* 2005).We are not aware of any observation on biomass or productivity decline at higher SR and consequently of any theoretical work on the nature of such a relationship. We hypothesize that negative species interactions, involving increased competition due to niche overlap, govern the dynamics of species-rich communities. This process is accelerated in the phytoplankton, where the negative effect of high diversity was expressed at much lower SR than in the benthos due to the low capacity of the short environmental gradients in the plankton to accommodate species coexistence and the diminished role of positive interspecific interactions.

A unimodal biovolume–diversity response curve was an unexpected outcome of this analysis in view of the large body of evidence suggesting an increase in biomass at higher diversities (Tilman *et al.* 1997, 2001; Gessner *et al.* 2004; Hooper *et al.* 2005). The reason for this discrepancy, we think, is methodological and not conceptual. Our knowledge to-date is derived primarily from experimental studies, manipulating a limited number of species in terrestrial systems over short periods of time (Tilman *et al.* 1996; Hector *et al.* 1999). The only other comprehensive study of the freshwater stream periphyton found positive or no relationships between biomass production and algal SR (Cardinale *et al.* 2005). Absence of significant correlation between SR and biomass was also documented in the periphyton of freshwater lakes and brackish coastal areas (Hillebrand 2003). However, these periphyton studies were conducted using artificial substrates, which tend to underestimate the natural epilithic communities, especially the taxonomic composition of green algae and cyanobacteria (Cattaneo & Amireault 1992). As a result, the SR gradient on artificial substrates is truncated and cannot represent the whole spectrum of variation in production. So, the evidence from studies on artificial substrates cannot be taken as contradicting our findings of a unimodal relationship in natural communities.

Our treatment of the biomass–diversity relationships in stream periphyton and phytoplankton is based on one of the most comprehensive datasets worldwide. It comprises 1553 distinct localities where 4898 samples were collected from natural substrates along environmental gradients on a continental scale; thousands of algae, aggregated in communities of two to over a hundred species, were identified in these samples. Most locations were sampled several times over the course of 10 years, a length of time which is orders of magnitude longer than the generation time of freshwater algae, spanning days to weeks. Our findings suggest that in stream ecosystems there is a biodiversity threshold, corresponding to the mode of the biovolume–SR curve, on both sides of which the curve exhibits different behaviour. Above this threshold, an increase in SR, which is a common community response to anthropogenic alterations of nutrient supply and light such as eutrophication and deforestation, may result in decreased biomass. Phytoplankton, where community biovolume peaks at the lowest SR of the three habitats, would suffer the strongest biomass decline with richness increase. In contrast, DTH with a biovolume maximum at the highest SR in all habitats, would be least affected by species additions above the threshold. On the other hand, a decrease in species diversity below the biovolume mode, which can be caused by natural or anthropogenic forces such as organic pollution, acidification or the use of pesticides, will bring about reduction in biomass with the fastest rate in the phytoplankton, and the slowest in DTH.

The notion that ecosystems are organized for high diversity and productivity is not new. Natural selection, through its influence on species competition and mutualism, has been invoked as the mechanism that controls this process, e.g. ecological dominants are replaced by new and better fit successors, more capable of exploiting the environment and promoting higher productivity, from which all ecosystem's members benefit (Leigh & Vermeij 2002). Nevertheless, the evidence that ecosystems are organized for high biomass has been somewhat circumstantial so far. This includes the observed tendency of ecosystems to lose biodiversity and productivity in response to random changes and the increase of biodiversity and productivity in macroevolutionary time (Leigh & Vermeij 2002). Here, we present direct support for ecosystem organization toward maximum biomass from a rigorous analysis of continental algal biodiversity patterns. In all habitats, the SR that yielded the highest biovolume was not the most frequent, probably as a result of human-induced environmental modifications, but it was always within one standard deviation of the frequency maximum. This remarkable association of SR, frequency and biovolume suggests that algal communities may be driven toward maximum biomass.

In conclusion, this is the first continental study on the relationship between biomass and diversity showing that biomass is a unimodal function of SR, which is a challenge to a long tradition in ecology regarding SR as dependent on biomass. The implications of this discovery for environmental research, conservation and management are considerable because it demonstrates how a decline in algal biomass with potential detrimental effects on all higher trophic levels, from invertebrates to fish, can result from either excessive species gain or species loss. Our results suggest that stream ecosystems may be more vulnerable than previously thought since any deviation from an optimal number of species, with either anthropogenic or natural origin, will have profound and negative impact on their primary production.

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Worm, B., Lotze, H. K., Hillebrand, H. & Sommer, U. 2002 Consumer versus resource control of species diversity and ecosystem functioning. *Nature* **417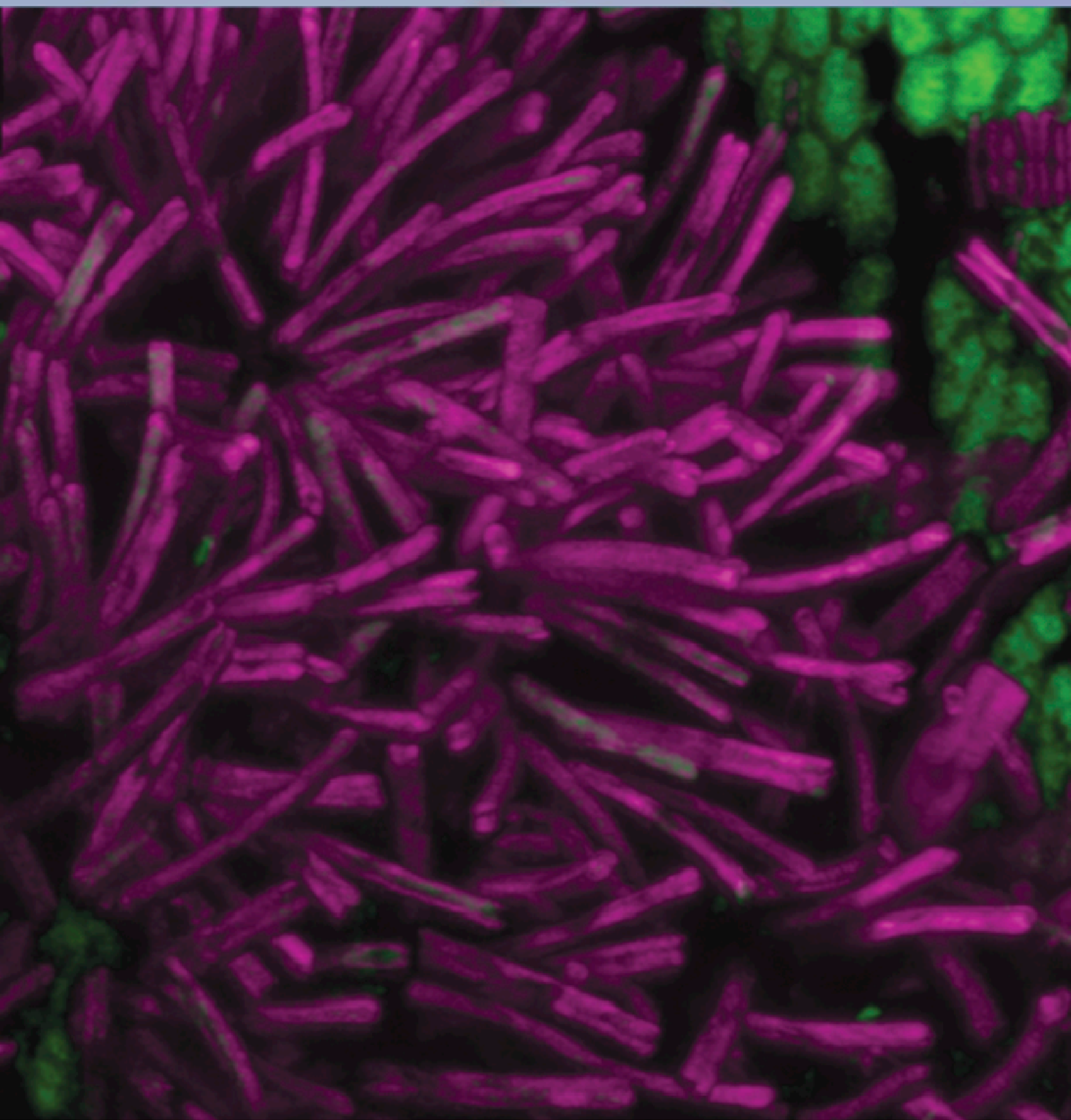**, 848–851. (doi:10.1038/nature00830)