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RESEARCH PAPER

Power law relationships among hierarchical taxonomic categories in algae reveal a new paradox of the plankton

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ABSTRACT

Aim In this continental-scale study, the biodiversity of benthic and planktonic algal communities was explored. A recent analysis of extinct and extant tree communities by Enquist *et al.* (2002) showed that richness of higher taxa was a power function of species richness, invariant across temporal and spatial scales. Here we examined whether the relationships between algal richness at hierarchical taxonomic levels conform to power laws as seen for trees, and if these relationships differ between benthic and planktonic habitats.

Location Streams from more than 50 major watersheds in the United States.

Method A total of 3698 samples were collected from 1277 locations by the National Water-Quality Assessment Program. Three types of stream habitat were sampled: richest targeted habitats, depositional targeted habitats, and phytoplankton. The relationships between taxonomic richness at the species level vs. all higher categories from genus to phylum across the three habitats were examined by ordinary least squares (OLS) regressions after ln-transformation of all variables. The slopes, b, of these regressions represent the exponents of the power functions that scaled the richness of higher taxonomic levels (T) to species richness (S) in the form: $T \propto S^b$.

Results Algal richness at hierarchical taxonomic categories (genus to phylum) is a power function of species richness. The scaling exponent of this function, which captures the diversification of higher taxa, i.e. the rate of increase of their richness with the increase of species richness, is significantly different across environments.

Main conclusions The differential algal diversification in the three studied habitats emphasizes the fundamental role of the environment in structuring the communities of simple organisms such as algae. The finding that the diversification of higher taxa is greater in the seemingly homogeneous planktonic environment, when compared to benthic habitats, encompassing an array of ecological niches, poses a new paradox of the plankton.

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Keywords

Algae, benthos, biodiversity, diatoms, NAWQA, phytoplankton, periphyton, power law, scaling, species richness.

INTRODUCTION

Phylogenetically, algae are hard to define. They form a heterogeneous polyphyletic mixture of organisms spanning two kingdoms and nine phyla (Graham & Wilcox, 2000). Ecologically, algae have very similar resource and habitat requirements, allowing them to establish cohesive communities of strongly interacting species with a major role in primary production in aquatic environments (Stevenson *et al.*, 1996). How algal communities are structured taxonomically, to what extent algal biodiversity patterns are habitat-specific, and how algae in plankton and benthos differ, are still open questions in ecology. Analysis of the global

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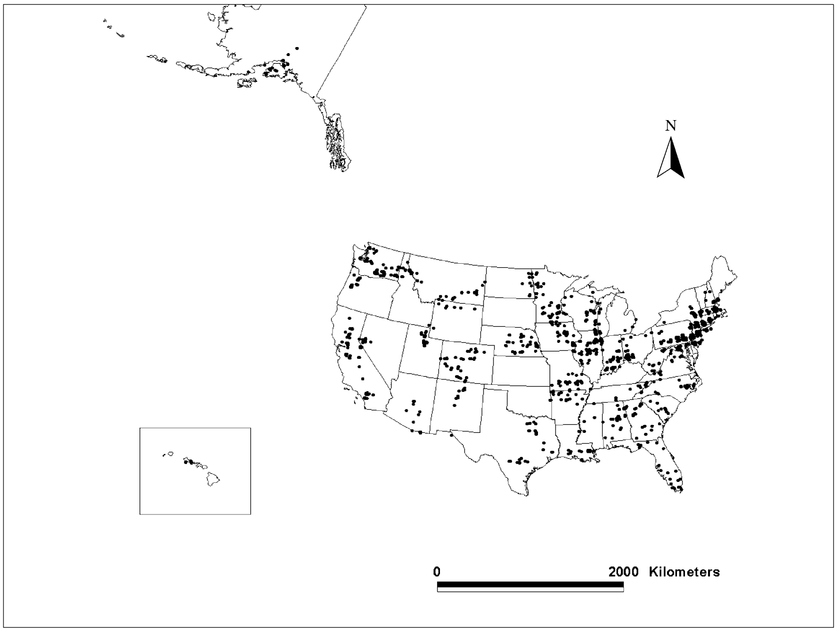

Figure 1 Sampling locations in the United States.

biodiversity of extinct and extant tree communities (Enquist *et al.*, 2002) showed that richness of higher taxa was a power function of species richness. The scaling exponent was invariant across continental and historical scales, suggestive of globally operating ecological processes, overriding local variations of environment and evolutionary history. More recently, studies on ecto- and endoparasitic assemblages documented similar power relationships between richness at the species vs. higher taxonomic levels (Mouillot & Poulin, 2004; Krasnov *et al.*, 2005). Biodiversity is one of many other phenomena in biology, physics and chemistry that exhibit universal scale-invariant behaviour, expressed mathematically by power functions (Gisiger, 2001; Brown *et al.*, 2002). However, unlike trees, algae are evolutionarily primitive organisms with simple body plans, short generation times, rapid population dynamics, and fast community turnover rates. Unlike terrestrial systems, aquatic ecosystems are subjected to a strong control of physical disturbances of varying frequency and intensity (Giller *et al.*, 2004). Algae have a much closer association with the environment than more complex organisms — disturbances trigger community shifts, which are quickly established via short but multiple generations. Therefore, the taxonomic structuring of algal communities may not conform to the relationships described for trees.

For more than 40 years, phytoplankton species richness has challenged the basic postulate of ecological theory that the number of co-existing species cannot exceed the number of limiting resources in equilibrium. During this time scientists have viewed environmental homogeneity as a hindrance to species diversity and the apparent homogeneity of open waters supporting hundreds of plankton species as a paradox (Hutchinson, 1961). Experimental research put forth variable resource ratios and supply, as well as fluctuating light intensities, as possible explanations of the paradox (Tilman, 1982; Sommer, 1985; Flöder *et al.*, 2002). Theoretical investigations pointed to demographic and environmental stochasticity (Anderies & Beisner, 2000); competition models (Huisman & Weissing, 1999) have demonstrated that chaotic fluctuations in species abundances allow the co-existence of multiple species far exceeding the number of limiting resources, even in a constant environment. Unlike lacustrine planktonic flora, stream phytoplankton is drawn from various sources, including benthic washouts as well as inputs from lakes, ponds, impoundments, and backwaters along the stream course. Thus stream phytoplankton may comprise planktonic and benthic species, but despite these differences in the source of immigrants and propagules, there is a substantial floristic overlap between phytoplankton of rivers and lakes (Reynolds *et al.*, 1994 and the references therein). True phytoplankton develops and maintains substantial populations in slow-flowing lowland streams and large rivers with sufficient residence time of the water mass (Allan, 1995).

Here we analysed the data from a large, well-designed survey of planktonic and benthic algae from rivers and streams within the major watersheds in the United States. The questions we asked were: (1) do the relationships between algal richness at hierarchical taxonomic levels conform to power laws as seen for trees; and (2) do these relationships differ between planktonic and benthic habitats?

METHODS

Algal data

The algal data set analysed here contained 3698 algal samples from 1277 locations (Fig. 1). It was generated by the National Water-Quality Assessment (NAWQA) Program, monitoring the water chemistry, hydrology, land use, stream habitat, and aquatic life in more than 50 major river basins and aquifers across the United States. Three habitat types, defined by NAWQA, were sampled quantitatively for algae: richest targeted habitats (RTH), depositional targeted habitats (DTH), and phytoplankton. The NAWQA data set comprised 2032 RTH, 1212 DTH, and 454 phytoplankton samples collected between March 1993 and September 2001. RTH and DTH samples were taken from a known area of stream bottom. Phytoplankton was collected from a known volume of water. RTH maintain the taxonomically richest community (2360 species), developing on stones and macrophytes in riffle areas and snags on sandy substrates in areas of relatively high current velocities. DTH (1976 species) are found in soft-bottom depositional areas of slow current. Phytoplankton (1298 species) is a community of suspended algae.

Sample processing and algal enumeration and identification were carried out by specialized phycology laboratories. Rigorous taxonomic reviews of the algal counts by expert taxonomists at the Patrick Center for Environmental Research, Academy of Natural Sciences in Philadelphia, ensured taxonomic consistency and precision. For detailed descriptions of the sampling habitats, techniques, and protocols visit http://water.usgs.gov/nawqa/protocols/OFR-93-409/alg1.html and http://water.usgs.gov/nawqa/protocols/algprotocol/.

Statistical analyses

The relationships between taxonomic richness at the species level vs. all higher categories from genus to phylum across the three habitats were examined by regression analyses using the following statistical model:

$$y_{ij} = a + b_1x_{i1} + b_2x_{i2} + b_3x_{i3} + \varepsilon_{ij}$$

where y_{ij} = ln-higher taxon richness in $i = 1, 2, \ldots, 3698$ samples from environments $j = \{1, 2, 3\} = \{\text{DTH, RTH, phytoplankton}\}$, x_{i1} = ln-species richness in DTH, x_{i2} = ln-species richness in RTH, x_{i3} = ln-species richness in phytoplankton, ε_{ij} = error term. The slopes, b_j, of these regressions represent the exponents of the power functions that scaled the richness of higher taxonomic levels (T) to species richness (S) in the form: $T \propto S^{b_j}$.

The actual slope values (b_j) for the three habitats and five taxonomic categories were compared to values obtained from a random neutral model, which played the role of a null hypothesis to assess the significance of the observed relationships. Under that model, each species is drawn at random from a metacommunity; it has the same chance of reaching each locality and surviving into it, all species having equal competitive ability. This is similar to other neutral models that are often considered for community analysis (Bell, 2001; Hubbell, 2001; He, 2005); the only difference is that in this analysis all species had an equal likelihood of being included in the pseudo-community, which was not dependent upon their abundance. For algae, which have cosmopolitan distributions, dispersal across the US territory poses no problem in geological time (Fenchel & Finlay, 2004), so we were mainly testing the existence of species assemblages resulting from non-neutral interactions and environmental influences against the neutral survival of species in the local communities. The simulation study helped us determine if the actual slope values estimated by regression could have been obtained by assembling randomly species from the three metacommunity species pools. In practice, a simulation consisted of constructing, for each sampling unit, a counterpart community whose species, in the same numbers as in the NAWQA sample, were drawn at random from the available continental species pool in the particular habitat (RTH, DTH, or phytoplankton). Then the number of genera, families, etc. were counted in that pseudo-community and used as a point in a simulated relationship comparing ln(Species) to ln(Genera), ln(Species) to ln(Families), etc. The species were drawn without replacement because in the real samples the data are of the presence–absence type, each species being counted only once in a sampling unit. A simulated data table contained as many pseudo-samples as there were in the real table, i.e. 2032 in RTH, 1212 in DTH, and 454 in phytoplankton. Linear regressions were computed for each simulated table, using the model described in the previous paragraph. Five thousand such simulated data tables of the three habitats were produced. From the results, the mean regression slopes were computed, as well as the empirical 95% confidence intervals for the slopes. The range of values that incorporated the middle 95% of the simulated slopes was used as nonparametric empirical estimates of the confidence intervals for the simulated slopes.

RESULTS AND DISCUSSION

The relationships between richness at the species and all above-species levels followed power laws in all studied habitats (Fig. 2). This is not a surprising result, considering the nature of hierarchical taxonomic classifications, which impose constraints on the variation of the higher categories as a function of species richness. The exponents of the power functions, derived from the respective ln–ln regressions, declined steadily and significantly from generic to class richness (Fig. 3a, Table 1); only the slopes of class and phylum against species richness were not significantly different from each other. Within each taxonomic category, the regression slopes were significantly different across the three habitats ($P < 0.05$) but they were much closer in the two benthic communities (Fig. 3a; Table 1). The regression slopes were the highest in phytoplankton and the lowest in DTH, i.e. the community of suspended algae had the highest scaling exponent of higher taxon diversification, and the community in depositional habitats of low velocity, the lowest (Figs 2 and 3a). This means that an increase in species richness in the phytoplankton was coupled with the highest increase of new genera, families, orders, classes, and phyla, i.e. each new species added to the community had the highest probability of being a member of a different higher taxon. Conversely, an increase in species richness 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.

This pattern was not due to inconsistencies between phytoplankton and benthic algal taxonomy or differential habitat-fidelity. Hypothetically, taxonomic inconsistencies may arise from differential distribution of algal groups across habitats, e.g. phytoplankton, dominated by diatoms where the splitting of genera is common and benthos with prevalence of green algae,

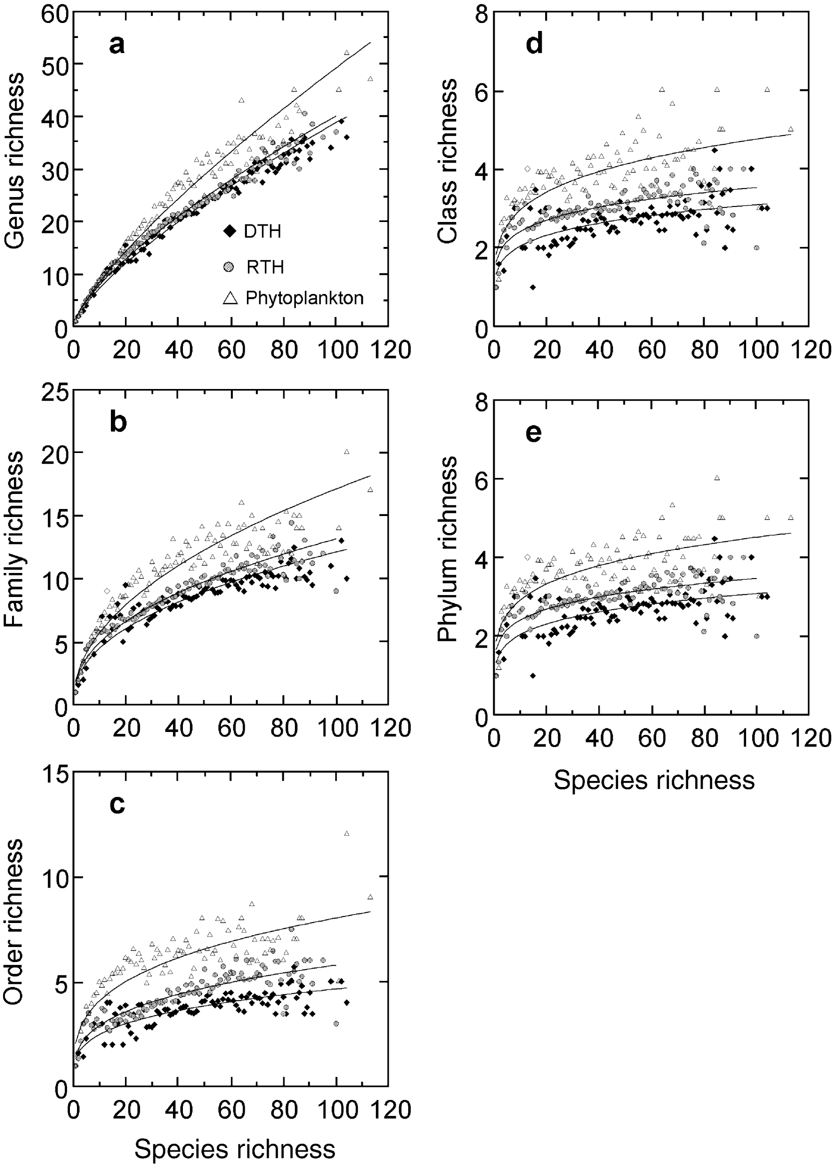

Figure 2 Power law relationships between species richness and the average richness of all higher-order taxonomic categories across the three studied habitats. For clarity, higher taxa richness was averaged for each species richness class. Particular exponents and R^2-values are given in Table 1. DTH = depositional targeted habitats; RTH = richest targeted habitats.

which have much more conservative taxonomy. This was clearly not the case with our data set, where all three habitats were dominated by the same algal groups, with diatoms being the most abundant everywhere. Moreover, analysis of species presence–absence data revealed that the number of unique species, i.e. confined to a given habitat, was low and comparable across habitats. Thus only 15%, 19%, and 26% of all species in DTH, phytoplankton, and RTH, respectively, were unique, indicating that in each habitat the majority of species was also found in other habitats, i.e. all habitats were equally prone to the vagaries of taxonomy. There was also no risk of artefacts generated by different taxonomic treatment of the habitats. Again hypothetically, if benthos samples were identified according to a conservative school of taxonomy and related taxa were lumped into common genera, the exponent estimates in the benthos would be low; alternatively, if phytoplankton samples were analysed following newer taxonomic trends of recognizing new genera, families, etc. from existing ones, the exponent estimates in the phytoplankton would be high. This was also not a problem with this data set because only a few recognized phycology laboratories carried out all identifications of both phytoplankton and benthos, thus introducing the same type and amount of human error to both habitat assessments. The slope differences between benthic and planktonic communities cannot be attributed to differences in the scale of observation, because in both habitats only local communities were investigated where species can interact physically with one another either directly in competing for light, nutrients, and space, or indirectly by providing food for the grazers.

All regression slopes derived from real communities were much smaller than the 95% confidence intervals of the slopes from the randomly assembled communities, indicating that the differences in taxonomic structuring of real and randomized communities were highly significant (Table 1, Fig. 3b). These differences, however, were least pronounced in the phytoplankton, suggesting the highest likelihood of finding most of the higher taxa by random draw of species from the available pool.

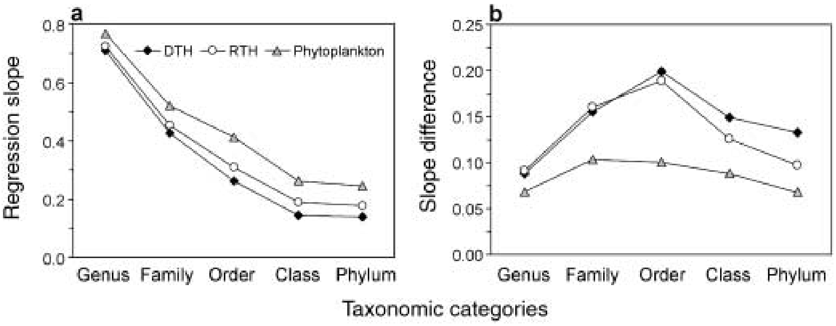

Figure 3 (a) Slopes of ordinary least squares (OLS) regressions of species richness against higher taxa richness in real communities. (b) Slope difference between randomized and real communities across the same taxonomic categories. All slope differences were significantly different from zero (see Table 1), indicating that the real communities were significantly different from randomly assembled communities. DTH = depositional targeted habitats; RTH = richest targeted habitats.

Table 1 Slopes, 95% confidence intervals (CI), and coefficients of determination (R^2) of linear ln–ln regression models of species richness vs. richness of higher taxonomic categories in the three habitats and the randomized communities (5000 randomizations). Underlined slopes within a habitat are not significantly different from each other at $P < 0.05$. N = number of samples, DTH = depositional targeted habitats, RTH = richest targeted habitats. $P < 0.000005$ for all relationships. *The CIs of these slopes are overlapping but their significance was confirmed by nested models regression analysis at $P < 0.000001$.

	Species–Genus	Species–Family	Species–Order	Species–Class	Species–Phylum
Habitats ($N = 3698$) R^2	0.903	0.627	0.304	0.184	0.168
DTH ($N = 1212$)					
b_1	0.708*	0.427	0.261	0.145	0.138
95% CI	0.701–0.716	0.416–0.438	0.244–0.279	0.128–0.161	0.122–0.154
Mean b_1 (randomization)	0.796	0.582	0.460	0.294	0.271
Empirical 95% CI (randomization)	0.791–0.802	0.573–0.591	0.448–0.473	0.281–0.306	0.259–0.284
RTH ($N = 2032$)					
b_2	0.723*	0.454	0.310	0.187	0.178
95% CI	0.715–0.730	0.443–0.466	0.292–0.328	0.170–0.204	0.161–0.195
Mean b_2 (randomization)	0.813	0.615	0.499	0.312	0.275
Empirical 95% CI (randomization)	0.808–0.819	0.606–0.625	0.486–0.512	0.299–0.326	0.262–0.289
Phytoplankton ($N = 454$)					
b_3	0.767	0.520	0.413	0.261	0.244
95% CI	0.758–0.776	0.507–0.533	0.392–0.434	0.242–0.281	0.225–0.263
Mean b_3 (randomization)	0.835	0.623	0.513	0.349	0.311
Empirical 95% CI (randomization)	0.829–0.842	0.613–0.633	0.499–0.527	0.335–0.362	0.298–0.324

Here we show that the biodiversity patterns of algal communities in streams differ between planktonic and benthic habitats: as species richness increases the richness of higher taxa increases at a significantly higher rate in the phytoplankton than in the benthos. This poses a new paradox of the plankton: the homogeneous environment of open running waters promotes the greatest biodiversity at higher taxonomic levels compared to the heterogeneous benthic habitats. Organismal patchiness, indicative of the scale of environmental homogeneity, measures in hundreds of metres in the plankton (Ludovisi *et al*., 2005) and only in centimetres to a few metres in the benthos (Sinsabaugh *et al*., 1991; Passy, 2001). Better mixing of algae, with unlimited dispersal within the large patches of homogeneous environment in the plankton, can explain the higher similarity between real and randomized communities in this habitat. In contrast, the dispersal of benthic algae may be hindered at various instances, e.g. during dislodgement from their substrate or entering the plankton when they experience increased mortality (Wetzel, 2001), or in finding a suitable and unoccupied substrate to establish viable populations. In conditions of impeded dispersal, local factors would control the benthic communities, as suggested by dissimilarity with their respective randomized communities, which was much higher than in the phytoplankton. However, mixing cannot explain the differences in taxonomic diversification among the three communities. RTH and DTH slopes showed similar departures from the respective pseudo-communities' slopes but remained significantly different from each other. Therefore, a process other than mixing must generate the observed patterns in the real communities of the three habitats.

High environmental variability offsetting the competitive exclusion is an insightful explanation of the original paradox of the plankton (Hutchinson, 1961; Tilman, 1982; Sommer, 1985; Flöder *et al*., 2002). High environmental homogeneity forcing a stronger niche differentiation in the phytoplankton is a plausible explanation of the paradox described here. A key difference between planktonic and benthic habitats is the structure of their environmental gradients, which determine the niche properties of the resident species and consequently their co-existence. In the

Table 2 Exponents (b_{1-3}), 95% confidence intervals (CI), and coefficients of determination (R^2) of the species–genus and species–family power functions in real and randomized communities of algae (this study) and trees (Enquist *et al.*, 2002). The intercept was constrained to zero in all regressions. N = number of samples, DTH = depositional targeted habitats, RTH = richest targeted habitats. $P < 0.000005$ for all relationships in this study.

Algae (this study)	Species–Genus	Species–Family
$N = 3698$ R^2	0.903	0.626
DTH, $N = 1212$		
b_1	0.806	0.559
95% CI	0.804–0.809	0.555–0.562
b_1 mean (randomization)	0.859	0.682
95% CI (randomization)	0.857–0.860	0.680–0.684
RTH, $N = 2032$		
b_2	0.827	0.595
95% CI	0.825–0.829	0.592–0.615
b_2 mean (randomization)	0.880	0.723
95% CI (randomization)	0.879–0.881	0.721–0.724
Phytoplankton, $N = 454$		
b_3	0.875	0.666
95% CI	0.871–0.880	0.659–0.674
b_3 mean (randomization)	0.905	0.735
95% CI (randomization)	0.902–0.907	0.730–0.738
Trees, North America, $N = 57$ (Enquist *et al.*, 2002)		
R^2	0.973	0.931
b_1	0.938	0.825
95% CI	0.93–0.95	0.81–0.84
b_1 mean (randomization)	0.981	0.887
95% CI (randomization)	0.981–0.981	0.887–0.889

well-mixed plankton, the resource and disturbance gradients are short and comparatively few, while in the highly compartmentalized, heterogeneous benthos, there are multiple and steep gradients of nutrient depletion, light attenuation, and current velocity and grazer disturbance (Stevenson *et al.*, 1996). Therefore, co-existence along the few short gradients in the plankton would occur as long as species have complementary mechanisms for sequestering resources or avoiding stress, whereas in the benthos adaptations for a different level of the gradient will suffice. For example, only 1% of the light that reaches the benthic biofilm, i.e. the light that has not been absorbed by the phytoplankton, may penetrate as deeply as 5–6 mm into the biofilm (Hill, 1996), generating a steep light attenuation profile in the benthos, which can support a number of species differing in their shade tolerances (Johnson *et al.*, 1997). Alternatively, co-existence along the short light attenuation gradient in the phytoplankton can occur if algae utilize different parts of the light spectrum or exhibit large differences along the other resource (or disturbance) gradients. The simplicity of the gradient structure in the plankton would enforce stronger niche differentiation in this habitat, which is associated generally with large differences in life history strategies and mechanisms for resource acquisition, maintaining buoyancy, and avoiding grazing (Reynolds, 1998; Wetzel, 2001; Smayda, 2002; Salmaso, 2003; Stomp *et al.*, 2004). Higher taxonomic levels in algae correspond to gross differences in morphological, biochemical, physiological, and life history characteristics with a great impact on niche differentiation. Such characteristics include cell size, multicellularity, cell wall composition, photosynthetic and accessory pigment composition, storage products, motility, dormancy, allelopathy, as well as mechanisms for nitrogen fixation and carbon concentration. Life history strategies may vary between single life forms as found in diatoms or multiple life forms as observed in dinoflagellates. Higher taxonomic disparity results in alternative adaptations for common stress experienced by algae, e.g. sinking is counteracted by the development of gas vacuoles in cyanobacteria, long spines or colonial habits in diatoms, and motility in dinoflagellates, all of which are common members of the phytoplankton. Thus, 31 exclusively polyphyletic functional groups spanning several phyla of planktonic algae were described for a few ecological conditions in lakes and rivers (Reynolds *et al.*, 2002). The most common species and superior competitors for silicate and phosphate in the Lake Michigan phytoplankton belong to different diatom genera (Tilman, 1981).

In theory, the existence of multiple gradients in the benthos would allow the coexistence of species with large niche overlaps as long as they have complementary positions along at least one gradient. With all other conditions being equal, high niche similarity is found in taxonomically similar species, whose slight differences in body plans or physiology (at the congeneric level) can separate them along a single gradient. For instance, a current velocity gradient spanning approximately 0.5 m of stream bottom (as found in RTH) triggered a shift from *Fragilaria capucina*- to *F. crotonensis*-dominated communities under constant ambient light and nutrients (Passy, 2001). Put into the framework of recent views on the role of phylogeny in community organization (Webb *et al.*, 2002), the simple gradient structure in the plankton would promote community assembly via phylogenetic repulsion, i.e. exclusion of phylogenetically similar species, while the diversity of environmental gradients in the benthos would enforce communities governed by phylogenetic attraction, i.e. clumping of phylogenetically similar species.

Higher taxa increase with species richness differed in the two benthic habitats: it was lower in DTH, where algae frequently become buried in the unstable substrates and the selection favours motile species pertaining to a few diatom genera (Bahls, 1993). Furthermore, algal communities in depositional habitats can be exposed to sediment-borne contaminants for extended periods of time. This imposes further constraint on potential colonizers — only species tolerant to pollution can proliferate in such environments and adaptations to stress, such as pollution, are conserved typically within a genus. For example, the vast majority of species of the predominantly benthic genera *Eunotia* and *Nitzschia* are tolerant to acid and organic pollution, respectively. Therefore, habitat filtering occurs in DTH under environmental stress (physical disturbance or chemical contamination) when stress-resistant species have an advantage but also a great likelihood of belonging to a small set of tolerant genera (phylogenetic attraction).

We compared our results to those of Enquist *et al.* (2002) for trees (Table 2). Because these authors used regression through the origin, we performed our computations and simulations again using the same method. The power function exponents for generic and familial richness vs. species richness observed in algal communities across the United States were significantly lower than the respective exponents reported for North American tree communities (Enquist *et al*., 2002). This suggests that along the species richness gradient, higher taxa richness increased at a slower rate in algae than in trees, contributing to lower taxonomic diversity and higher similarity among algal communities than tree communities. The tree data set was collected from 0.1-ha closed-canopy forest plots (Enquist *et al*., 2002) which, considering the size of the study objects relative to the size of the sampling unit, must be fairly homogeneous within the tree assemblage in terms of the abiotic environment. Therefore, the higher rates of biodiversity increase with species richness observed in trees (Enquist *et al*., 2002) suggest even stronger niche differentiation in the terrestrial habitat than in the phytoplankton.

In conclusion, the behaviour of higher taxa richness as a function of species richness across all studied habitats conformed to power laws, as expected. The role of the environment, however, was evident in the communities of the simpler algae where power functions generated statistically different exponents across habitats. This suggests that there was an environmental constraint on the taxonomic composition of algal communities, which selected for higher biodiversity at all above-species levels in the phytoplankton and at the species level in the benthos. In this study we regarded an old concept, such as the paradox of the plankton and a new concept, such as the taxonomic scale invariance of biological communities. Only in the synthesis of these concepts were we able to gain original insight into the global patterns of biodiversity.

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BIOSKETCHES

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Pierre Legendre is interested in understanding the processes that determine the spatial structure of natural communities and control beta diversity. He has developed a number of statistical methods to answer questions that arise in this research framework.

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