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Niche dimensionality and herbivory control stream algal biomass via shifts in guild composition, richness, and evenness

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Abstract. We developed a framework for the hierarchical pathways of bottom-up (niche dimensionality) and top-down control (herbivory) on biomass of stream algae via changes in guild composition (relative abundance of low profile, high profile, and motile guilds), species richness, and evenness. We further tested (1) the contrasting predictions of resource competition theory vs. the benthic model of coexistence on how the number of added nutrients constrains species richness, (2) the relationship between species richness and evenness, and (3) the biodiversity–ecosystem-function paradigm. Implementing a combination of field and lab experiments that manipulated for the first time in benthic algae herbivory and/or niche dimensionality, i.e., the number of added nutrients (NAN), including nitrogen, phosphorus, iron, and manganese, we made the following discoveries. First, important predictors of guild composition were herbivory (field) and NAN (lab); of richness, NAN (field) and NAN and guild composition (lab); of evenness, guild composition (field and lab) and herbivory (field); and of biomass, guild composition, NAN, and richness + evenness (field and lab). Herbivory increased the proportions of the low profile and motile guilds but decreased the proportion of the high profile guild. In the absence of grazing, greater proportions of the high profile guild resulted in elevated richness and biomass but diminished evenness, whereas in the presence of grazing, these relationships generally disappeared. Second, both experiments confirmed the prediction of the benthic model that species richness increases with NAN, a pattern inconsistent with resource competition theory. Third, supplementation with manganese and/or iron increased algal richness, indicating that micronutrients, which have generally been overlooked in stream ecology, added dimensions to the algal niche. Fourth, the richness–evenness relationship, observed only in the absence of herbivory, depended on the size of the species pool. It was positive at richness lower than 49 species (lab), implying complementarity and facilitation, while at higher richness (field and lab), this relationship was negative, consistent with negative interspecific interactions. Finally, the greater dependence of biomass production on guild composition and NAN than on richness and evenness suggests that more comprehensive, environmentally explicit, and trait-based approaches are necessary for the study of the biodiversity–ecosystem-function paradigm.

Key words: algal and diatom guilds; biodiversity–ecosystem-function paradigm; evenness; fertilization; herbivory; niche dimensionality; resource competition theory; trait-based approach.

INTRODUCTION

Biodiversity, encompassing species richness and evenness, is a fundamental property of biological communities, determining their functions and ability to provide services to humans, such as food production, regulation of water quantity and quality, and pest and human disease control (Díaz et al. 2006, Cardinale et al. 2012, Naeem et al. 2012). According to the biodiversity–ecosystem-function paradigm, species-rich communities maintain greater functionality, including higher biomass production (Naeem et al. 1994, Hooper et al. 2005, Cardinale 2011, Tilman et al. 2014, Duffy et al. 2017). The influence of evenness on biomass is less straightforward as both high evenness and high dominance have been linked to greater production, depending on whether complementarity (facilitation or niche partitioning) or selection (the dominant species is highly productive), respectively, is the major pathway of biomass production (Hillebrand et al. 2008, Lehtinen et al. 2017). In turn, species richness and evenness are governed by resource availability and herbivory (Hillebrand

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2003, Hillebrand et al. 2007). However, it is less clear to what extent nutrient niche dimensionality (as opposed to nutrient enrichment) alone and in conjunction with grazing controls species richness and evenness, and consequently ecosystem function, and whether this control is direct or indirect via shifts in traits. To address these uncertainties, we propose a trait-based framework, linking bottom-up (number of added nutrients) and top-down factors (herbivory) with changes in traits (guild composition) and subsequent effects on species richness, evenness, and biomass (measured here as density and biovolume per area; Fig. 1). We test this framework with field and lab experiments with benthic stream algae and describe its background in more detail below.

Producer richness is a function of habitat niche dimensionality, determined in part by community spatial structure and the number of limiting or non-limiting resources. In communities with simple spatial structure, where each individual accesses resources independently of others, species richness increases with the number of limiting resources, according to resource competition theory (Tilman 1982; Fig. 1). The reason is that, under multiple resource limitation, there are more possibilities for trade-off, i.e., if each species is a superior competitor for a different limiting resource, competitive exclusion is prevented. Thus, in lake phytoplankton and grasslands, increasing the concentrations of multiple nutrients (making them non-limiting) leads to biodiversity loss (Interlandi and Kilham 2001, Grover and Chrzanowski 2004, Harpole and Tilman 2007). Conversely, in communities, such as photosynthetic biofilms, with complex three-dimensional structure due to overgrowth, niche dimensionality is defined by the number of non-limiting resources (Passy 2008). According to this “benthic model” of coexistence, species trade off tolerance to nutrient limitation for beneficial spatial position in the overstory, where access to nutrients and light is unrestricted. When resources are in short supply, mostly tolerant understory species can grow and the overall species richness is low. At higher numbers of added nutrients, richness increases because multiple overstory species, sensitive of nutrient limitation, overgrow the understory species, which nevertheless continue to persist due to tolerance of nutrient limitation. Thus, the biofilm development from a single story to a multistory matrix with the addition of nutrients is associated with an increase in both species richness and biomass. While there is ample experimental research on the effect of niche dimensionality on biodiversity and biomass in grasslands (Harpole and Tilman 2007, Harpole et al. 2016, Borer et al. 2017), to our knowledge, there is no manipulative research in freshwater biofilms, despite their marked deviation from the grassland patterns, demonstrated at a continental scale (Passy 2008). This limits our capability to predict how future changes in nutrient supply with the ongoing oligotrophication (Jeppesen et al. 2005, Minaudo et al. 2015) and eutrophication (Stoddard et al. 2016) of lakes and rivers will impact biodiversity and functionality of algae, which are an important carbon source for higher trophic levels (Finlay 2001, Brett et al. 2017).

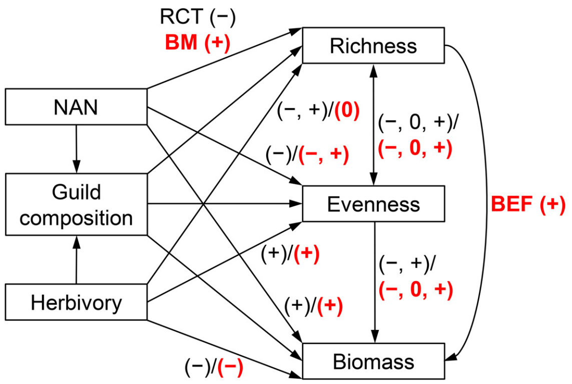

Fig. 1. Framework capturing the hierarchical effects of bottom-up (number of added nutrients, NAN) and top-down factors (herbivory), guild composition, and community structure (species richness and evenness) on function (biomass production). The influence of NAN on richness is postulated to be negative by resource competition theory (RCT) but positive by the benthic model (BM). A negative effect of NAN on evenness has been reported in grasslands. Evenness has a negative influence on biomass under selection but positive effect under complementarity (see Introduction for details). According to the biodiversity–ecosystem-function (BEF) paradigm, richness has a positive impact on biomass. Previously reported relationship directions are given in plain text, while directions observed in this study are shown in boldface red (negative −, positive +, and no relationship 0). Guild composition is represented by three variables (relative abundances of low profile, high profile, and motile guilds); therefore, no directional relationships are identified. All effects are hypothesized to be causal (unidirectional arrows), except for the richness–evenness relationship, often viewed as correlative (e.g., Soininen et al. 2012) (bidirectional arrow). The effects of each hierarchical level and the covariance between and among hierarchical levels were assessed by variance partitioning (Figs. 7, 8).

Herbivory is a major biotic constraint in aquatic ecosystems with an impact on richness, evenness, and biomass (Feminella and Hawkins 1995, Steinman 1996, Hillebrand et al. 2007, Hillebrand 2009). The effects of herbivory on producer biodiversity are generally opposite to those of nutrient enrichment (Worm et al. 2002, Hillebrand 2003) and shift in direction across ecosystems (Hillebrand et al. 2007). Specifically, in terrestrial habitats, eutrophication decreases richness because it stimulates plant growth and causes the shading and eventual elimination of species that are inferior competitors for light (Dybzinski and Tilman 2007, Hautier et al. 2009). In contrast, herbivory increases plant richness because it removes plant biomass and alleviates light limitation (Borer et al. 2014). In freshwater environments, on the other hand, richness responds positively to fertilization but negatively to herbivory (Steinman 1996, Hillebrand et al. 2007).

The inconsistency in richness response between terrestrial and freshwater ecosystems can be explained with the benthic model. Specifically, high nutrient supply in aquatic environments, such as the benthos, promotes establishment of speciose eutrophic overstory guilds (i.e., high profile and motile) with unimpeded access to both nutrients and light (Passy 2007, Lange et al. 2011, 2016, Stenger-Kovács et al. 2013, Hlúbiková et al. 2014), thus precluding the necessity to trade off an ability to capture nutrients for an ability to utilize light. However, since these species (particularly the high profile guild) are more vulnerable to grazing due to extended growth (Steinman et al. 1991, Lamberti et al. 1995, Steinman 1996, Hillebrand 2003), their consumption by herbivores brings about a decline in both richness and biomass but to a different degree. Species richness tends to decrease less with grazing (Liess and Hillebrand 2004, Alberti et al. 2017) because tolerant understory species are grazer resistant, while sensitive overstory species can still be present, even if they cannot accumulate considerable biomass, e.g., by maintaining basal growth (Lamberti et al. 1995, Steinman 1996). Biomass, on the other hand, can be severely reduced by herbivory (Feminella and Hawkins 1995, Gruner et al. 2008, Alberti et al. 2017), shown to cause a logarithmic decline in algal standing crop (Lamberti et al. 1995) and prevent nuisance levels of filamentous algae (high profile guild) under eutrophication (Anderson et al. 1999, Sturt et al. 2011).

Unlike richness, evenness is generally a negative function of nutrient enrichment but a positive function of herbivory (Hillebrand et al. 2007). In grasslands, the number of added nutrients had a negative impact on a diversity index, which scales positively with both richness and evenness (Harpole et al. 2016). Thus, the environmental responses of richness and evenness are discrepant in some systems but similar in others, leading to a variable correlation between the two diversity metrics (Stirling and Wilsey 2001, Bock et al. 2007, Soininen et al. 2012).

Using a set of field and laboratory experiments, we examined the biotic responses of stream algae to bottom-up vs. top-down controls, as defined in the proposed framework (Fig. 1). We hypothesized that higher numbers of added nutrients will promote the establishment of high profile and motile guilds, while retaining the low profile guild and thus leading to greater species richness, evenness, and biomass. A compositional shift from preponderance of the low profile guild to dominance of the high profile and motile guilds is expected along the gradient of number of added nutrients. Herbivory will select primarily against the high profile guild and will consequently reduce richness, evenness, and biomass. Within this framework, we further tested in the presence and absence of grazing (1) the opposing predictions of resource competition theory and the benthic model about the influence of the number of added nutrients on species richness (Passy 2008), (2) the relationship between species richness and evenness, and (3) the biodiversity–ecosystem-function paradigm.

MATERIALS AND METHODS

Field experiment

On 27 January 2012, we deployed 96 agar-filled clay dishes (1.6 cm in height and 8 cm in diameter) in a canopy-free reach of the Llano River, Texas, USA (30.47° N, 99.78° W). The clay dishes were retrieved after 42 d, which provided sufficient time for establishment of mature, late-successional biofilms. To prevent cross-fertilization among treatments from lateral diffusion, only dishes of the same treatment were glued to a 40.64 × 20.32 × 4.45 cm concrete step stone and positioned at the stream cobble bottom in a random fashion. There were 16 nutrient treatments: control (unenriched agar), N (0.11 mol/L $NaNO_3$), P (0.11 mol/L KH_2PO_4), Fe (0.007 mol/L $FeCl_3 \cdot H_2O$ + 9.91×10^{-4} mol/L $Na_2 \cdot EDTA \cdot 2H_2O$), and Mn ($4.45 \times 10^{-3}$ mol/L $MnCl_2 \cdot 4H_2O$), and all their combinations. The nutrient treatments generated a gradient of number of added nutrients ranging from 0 (control) to 4 (N, P, Fe, and Mn added). In addition, two grazer treatments, i.e., the above 16 combinations with or without 0.4% malathion, assessed the grazer effect. All 32 treatments had three replicates each.

Ambient nutrient levels in the Llano River during the field experiment were 575.4 ± 113.1 μg/L NO_3, 0.8 ± 1.7 μg/L PO_4, 3.9 ± 1.8 μg/L Fe, and 1.8 ± 3.1 μg/L Mn (mean ± standard deviation). Current velocity near the substrates at the time of deployment was 76.2 ± 1.1 cm/s, while discharge, as measured from a nearby USGS gage in Junction, Texas, averaged 2.20 ± 0.05 m^3/s during the field experiment. Average pH and specific conductivity were 8.15 ± 0.04 and 399.81 ± 1.39 μS/cm, respectively.

Lab experiments

Since malathion in the field experiments controlled only insect grazers, to assess biofilm responses to number of added nutrients in complete absence of macroinvertebrate herbivores, we carried out two lab microcosm experiments in February–March 2011 and September–October 2011. The microcosms were 24 circular round dishes, holding 4.5 L of water. In each microcosm, modified COMBO medium was recirculated at a current velocity of 8 cm/s by an IKA RW-20 digital overhead stirrer (IKA Works, Wilmington, North Carolina, USA). The medium was prepared by mixing carbon-filtered water with $NaNO_3$ (14.0 mg/L N), K_2HPO_4 (1.55 mg/L P), EDTA + $FeCl_3 \cdot H_2O$ (0.21 mg/L Fe), and all their combinations or left as control (all of the aforementioned nutrients were excluded). There were eight different nutrient treatments with three replicates each, resulting in a number of added nutrients ranging from 0 (control) to 3 (N, P, and Fe added). Metal halide 250 W lamps provided illumination of ~200 $\mu mol \cdot m^{-2} \cdot s^{-1}$ for 14 h daily. The bottom of each microcosm was lined with natural stone tiles. The microcosms were inoculated on day one of the experiment with benthic algae collected from physicochemically diverse streams in the Dallas-Fort Worth metroplex. Samples of fully developed, late-successional biofilms (prior to natural sloughing) were collected at day 40 and 60 in the two runs, respectively, by scraping three random tiles per microcosm. A detailed description of the experiments is given in Larson et al. (2015).

Algal processing, identification, and guild assignment

The collected algae were fixed with 4% formaldehyde. Using a Palmer-Maloney cell, soft algae units (a unit was defined as a cell for unicellular algae, a colony, or 25 μm of a filament) were counted in 30 random fields. After processing with acids, sample material was mounted with Naphrax (PhycoTech, Inc., St. Joseph, Michigan, USA) for diatom identification. At least 400 diatom frustules were counted per sample. Algal densities (units/cm^2) were converted to biovolume ($\mu\mathrm{m}^3/\mathrm{cm}^2$).

Guild assignment into low profile, high profile, motile, and planktonic followed Passy (2007), Passy and Larson (2011), and Rimet and Bouchez (2012). The low profile guild grows close to the substratum, the high profile guild extends into the biofilm matrix, and the motile guild can move across the substratum and within the biofilm. Low profile species are tolerant to nutrient limitation and resistant to grazing, while high profile and motile guilds have higher nutrient demands and the high profile guild is also more sensitive to grazing. The planktonic guild is not an integral part of the benthos and in this study, it was represented by very few species with low total biomass (i.e., one to four species across experiments with average proportional density and biovolume < 1%). For these reasons, the planktonic guild was not included in any analyses.

Statistical analyses

Total richness (*S*), Pielou's evenness (*J*), ln-transformed biomass (density and biovolume), and richness and proportion of total density for each guild were calculated for all samples. Using SYSTAT 13 (SYSTAT Software, Inc., San Jose, California, USA), relationships among these variables were examined with quadratic regressions after centering of the predictors on their mean. Backward selection was employed to select only significant variables ($P < 0.05$). Specifically, each dependent variable in Fig. 1, i.e., proportional abundance of low, high, and motile guilds, species richness, evenness, and biomass, was regressed against each of its predictor sets (Table 1). Given that the non-manipulated predictors covaried (the manipulated predictors were fully factorial and did not covary), we implemented variance partitioning with the vegan R package (version 2.5-2) to calculate the pure and covariance effects of each predictor set (Legendre and Legendre 2012). Thus, guild proportions were considered functions of NAN and herbivory, *S* and *J* depended on NAN, herbivory, guild composition, and their two-way covariances, and biomass was constrained by NAN, herbivory, guild proportions, community properties (*S* and *J*), and their two- and three-way covariances.

RESULTS

The number of added nutrients in both experiments and grazing in the field experiment had strong impacts on guild composition and community properties (Table 1, Figs. 2, 3). The two most abundant guilds in the field experiment were low profile and high profile (Fig. 2a–c), while in the lab experiments, high profile and motile (Fig. 3a–c). These guilds had distinct responses to NAN, which were also dependent on grazing in the field experiment. The low profile guild in the non-grazed field treatments and the motile guild in the lab experiments decreased with NAN, while the high profile guild increased. In the presence of grazing in the field, the response of the low profile guild to NAN was weak and of the high profile guild, non-existent.

Total species richness increased with NAN but was not affected by grazing (Figs. 2d, 3d). Richness of the three guilds was not sensitive to grazing either (*t* tests, $P > 0.05$) and increased with NAN but at different rates (Appendix S1). High profile and motile guild richness increased faster with NAN than low profile guild richness. Community evenness had a variable response to NAN in the field and the lab, which was also constrained by grazing (Figs. 2e, 3e). Biomass increased with NAN or showed a hump-shaped response in the grazed field treatments (Figs. 2f, g, 3f, g).

In the field, species richness and biomass decreased at greater proportions of the low profile guild, but increased with high profile guild proportion (P_{High}), particularly in the non-grazed treatments (Appendix S1). Evenness strongly declined with P_{High} in the non-grazed treatments (Appendix S1). In the lab experiments, richness and biomass too increased with P_{High} but declined with motile guild proportion (P_{Motile}, Appendix S1). Evenness peaked at intermediate P_{High} and P_{Motile} (Appendix S1).

In the field, richness and evenness were negatively related in non-grazed communities but not related in grazed communities, while in the lab, evenness was a unimodal function of richness (Fig. 4). In the field, biomass increased with richness but decreased with evenness in the absence of grazing, whereas in the presence of grazing, evenness was a nonsignificant predictor of density and a positive predictor of biovolume (Fig. 5). In the lab, biomass increased with richness (Fig. 6) but was not affected by evenness.

Guild proportions in the field were more strongly constrained by grazing ($R^2 = 0.23–0.51$) than by NAN ($R^2 = 0.00–0.08$; Fig. 7a–c). Variance partitioning revealed that richness was primarily determined by pure

TABLE 1. Regression models and statistics for all response variables in Fig. 1 against each of their respective predictor sets.

Response variable and predictor set	Model	R^2	Adj R^2	P-value
Field experiment (n = 96)				
P_{Low}				
NAN	$-0.29\mathrm{NAN}$	0.08	0.07	0.004
Herbivory	$0.60\mathrm{Herbivory}$	0.36	0.36	<0.00001
P_{High}				
NAN	$0.21\mathrm{NAN}$	0.05	0.03	0.038
Herbivory	$-0.71\mathrm{Herbivory}$	0.51	0.50	<0.00001
P_{Motile}				
NAN	NS			
Herbivory	$0.49\mathrm{Herbivory}$	0.24	0.23	<0.00001
Richness				
NAN	$0.73\mathrm{NAN} - 0.22\mathrm{NAN}^2$	0.59	0.58	<0.00001
Herbivory	NS			
Guild comp.	$-0.53P_{\mathrm{Low}}{}^2 + 0.73P_{\mathrm{High}}{}^2$	0.14	0.13	0.0007
Evenness				
NAN	$-0.24\mathrm{NAN}$	0.06	0.05	0.019
Herbivory	$0.69\mathrm{Herbivory}$	0.47	0.47	<0.00001
Guild comp.	$-0.44P_{\mathrm{Low}} - 0.18P_{\mathrm{Low}}{}^2 - 1.14P_{\mathrm{High}} - 0.20P_{\mathrm{High}}{}^2 - 0.18P_{\mathrm{Motile}}{}^2$	0.84	0.83	<0.00001
ln(density)				
NAN	$0.47\mathrm{NAN} - 0.34\mathrm{NAN}^2$	0.33	0.32	<0.00001
Herbivory	$-0.41\mathrm{Herbivory}$	0.17	0.16	0.00003
Guild comp.	$-0.60P_{\mathrm{Low}}{}^2 + 0.46P_{\mathrm{High}} + 0.72P_{\mathrm{High}}{}^2 + 0.25P_{\mathrm{Motile}}{}^2$	0.48	0.46	<0.00001
$S + J$	$0.45S - 0.39J$	0.40	0.39	<0.00001
ln(biovolume)				
NAN	$0.52\mathrm{NAN} - 0.30\mathrm{NAN}^2$	0.36	0.35	<0.00001
Herbivory	$-0.33\mathrm{Herbivory}$	0.11	0.10	0.001
Guild comp.	$-0.52P_{\mathrm{Low}} - 0.43P_{\mathrm{Low}}{}^2 + 0.52P_{\mathrm{High}}{}^2$	0.43	0.41	<0.00001
$S + J$	$0.38S - 0.20S^2 - 0.27J$	0.35	0.33	<0.00001
Lab experiments (n = 48)				
P_{Low}				
NAN	NS			
P_{High}				
NAN	$0.64\mathrm{NAN}$	0.40	0.39	<0.00001
P_{Motile}				
NAN	$-0.69\mathrm{NAN}$	0.47	0.46	<0.00001
Richness				
NAN	$0.77\mathrm{NAN} + 0.19\mathrm{NAN}^2$	0.64	0.62	<0.00001
Guild comp.	$0.30P_{\mathrm{Low}} + 0.77P_{\mathrm{High}}$	0.51	0.49	<0.00001
Evenness				
NAN	$0.32\mathrm{NAN}$	0.10	0.08	0.029
Guild comp.	$-0.42P_{\mathrm{High}}{}^2 - 0.52P_{\mathrm{Motile}} - 0.31P_{\mathrm{Motile}}{}^2$	0.65	0.63	<0.00001
ln(density)				
NAN	$0.72\mathrm{NAN} + 0.26\mathrm{NAN}^2$	0.59	0.57	<0.00001
Guild comp.	$-0.18P_{\mathrm{High}}{}^2 - 0.86P_{\mathrm{Motile}} + 0.48P_{\mathrm{Motile}}{}^2$	0.89	0.88	<0.00001
$S + J$	$0.65S$	0.43	0.41	<0.00001
ln(biovolume)				
NAN	$0.72\mathrm{NAN} + 0.24\mathrm{NAN}^2$	0.57	0.55	<0.00001
Guild comp.	$-0.85P_{\mathrm{Motile}} + 0.32P_{\mathrm{Motile}}{}^2$	0.87	0.86	<0.00001
$S + J$	$0.79S - 0.25J$	0.50	0.48	<0.00001

Notes: The predictor sets included number of added nutrients, NAN (NAN + NAN^2), Herbivory (presence or absence of grazers), Guild composition (comp.; $P_{\mathrm{Low}} + P_{\mathrm{Low}}{}^2 + P_{\mathrm{High}} + P_{\mathrm{High}}{}^2 + P_{\mathrm{Motile}} + P_{\mathrm{Motile}}{}^2$), and Richness ($S$) + Evenness ($J$) ($S + S^2 + J + J^2$). Following backward stepping procedure, only significant predictors were included in the final model, shown here. The regression coefficients are standardized.

Adj, adjusted; P_{Low}, proportion of low profile guild; P_{High}, proportion of high profile guild; P_{Motile}, proportion of motile guild; NS, not significant ($P \geq 0.05$).

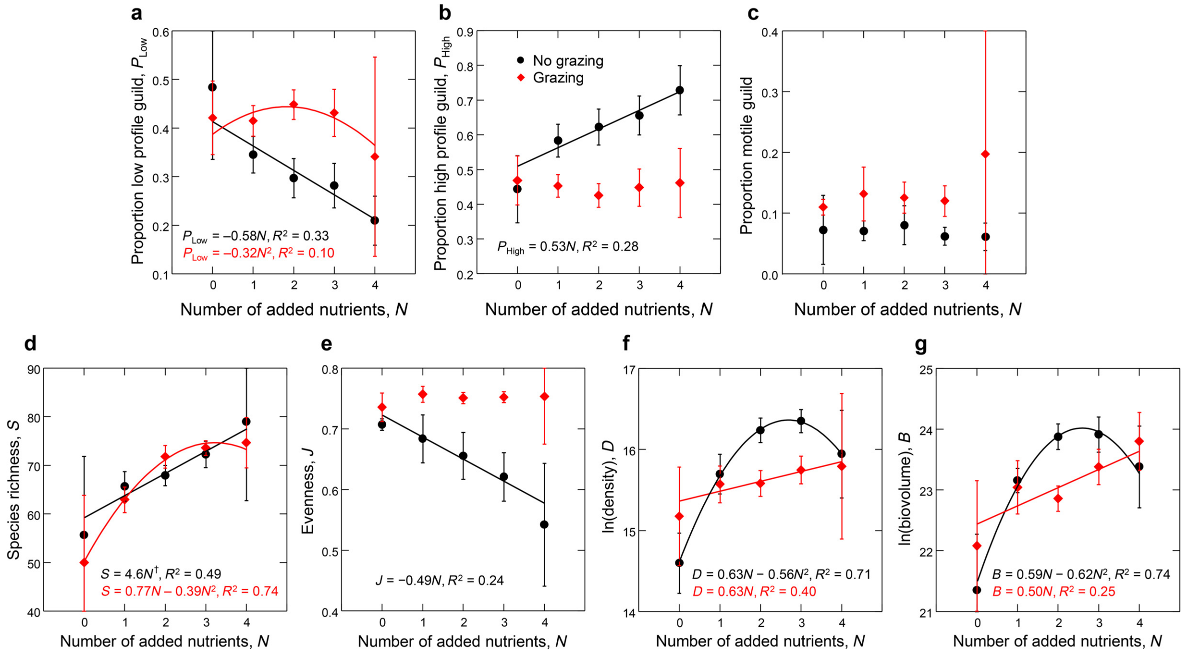

FIG. 2. Responses of (a–c) guild proportions, (d) species richness, (e) evenness, and (f and g) biomass to number of added nutrients across grazed vs. non-grazed communities in the field experiment. Error bars indicate the 95% confidence interval. Regression fits, models, and statistics are shown in the panels for all significant relationships ($P < 0.05$). Standardized regression coefficients are given in all regressions but d, non-grazed treatments, where the non-standardized coefficient is shown (marked with †) to allow direct calculation of how many species are added to the community with each nutrient; $n = 96$ samples. Density was measured as units/cm^2, biovolume as μm^3/cm^2.

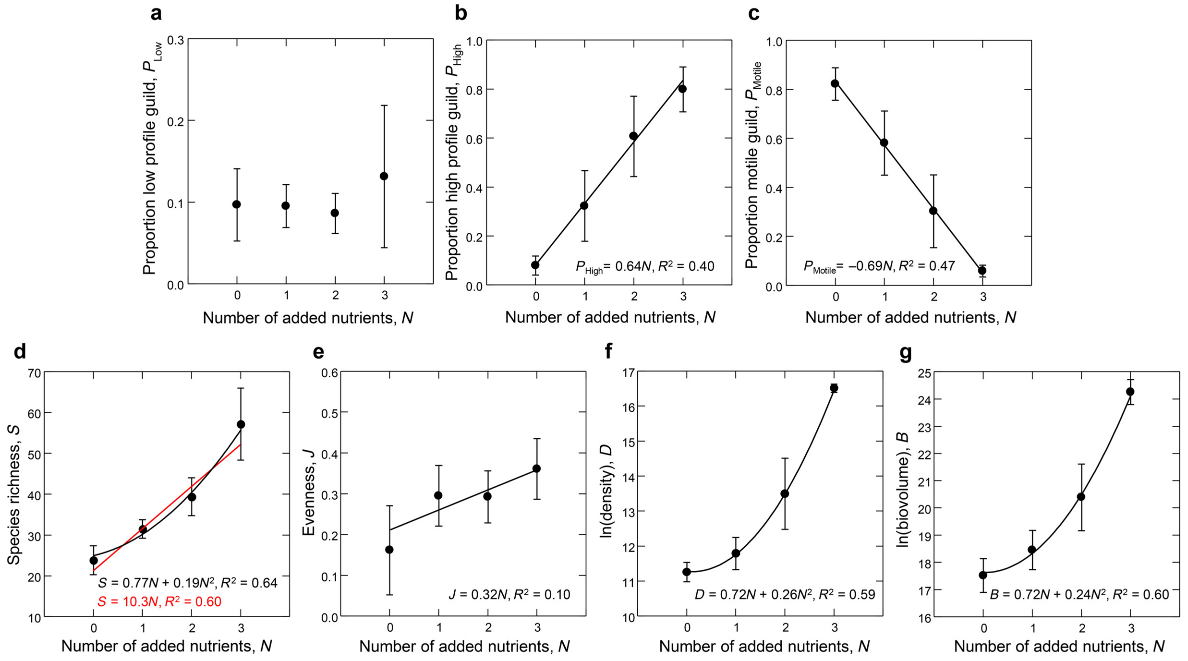

FIG. 3. Response of (a–c) guild proportions, (d) species richness, (e) evenness, and (f and g) biomass to number of added nutrients in the lab experiments. Error bars indicate the 95% confidence interval. Regression fits, models, and statistics are given in the panels for all significant relationships ($P < 0.05$). The regression coefficients are standardized. In panel d, the quadratic model (in black) provides a slightly better fit than the linear model (in red), but the linear model is also shown (with a non-standardized coefficient) for comparison with the non-grazed communities in Fig. 2d; $n = 48$ samples.

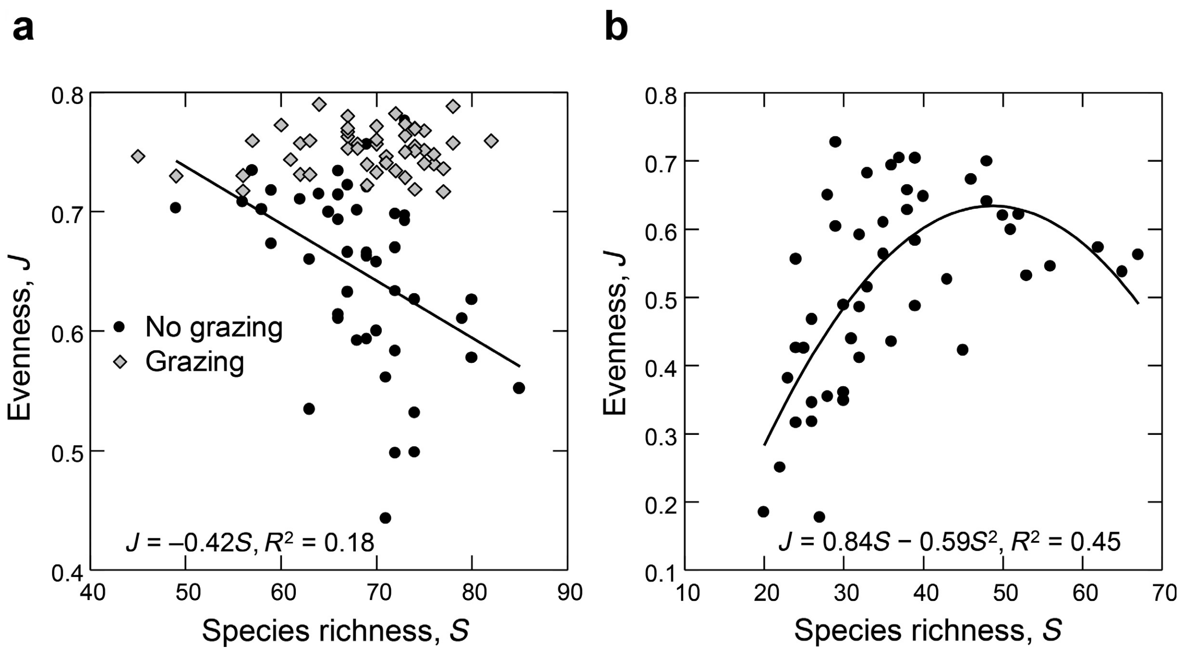

FIG. 4. Relationship of species richness and evenness in the (a) field experiment and (b) lab experiments. Regression fits, models, and statistics are given in the panels only for significant relationships ($P < 0.05$). The regression coefficients are standardized. Although the relationship between species richness and evenness is likely correlative, it is assessed here with regression to capture potential nonlinearities.

NAN ($R^2 = 0.52$), while evenness, by the covariance of guild composition with grazing ($R^2 = 0.45$), followed by pure guild composition ($R^2 = 0.33$; Fig. 7d, e). The variability in biomass (density and biovolume) was well captured by the pure and covariance terms of all predictors ($R^2 = 0.65–0.68$; Fig. 7f, g). Guild composition had the strongest overall effect ($R^2 = 0.43–0.48$), followed by $S + J$ ($R^2 = 0.35–0.40$), NAN ($R^2 = 0.33–0.36$), and grazing ($R^2 = 0.11–0.17$; Table 1). Most of the explained variance in biomass was contributed by pure guild composition ($R^2 = 0.16–0.21$), followed by the covariance of NAN and $S + J$ ($R^2 = 0.11–0.14$), the covariance of NAN, guild composition, and $S + J$ ($R^2 = 0.13$), the covariance of grazing, guild composition, and $S + J$ ($R^2 = 0.09–0.13$), and pure NAN ($R^2 = 0.07–0.10$). The remaining terms had little to no effect on biomass.

In the lab, richness was determined primarily by the covariance of NAN and guild composition ($R^2 = 0.45$), followed by pure NAN ($R^2 = 0.17$; Fig. 8a). Evenness was controlled mostly by guild composition ($R^2 = 0.54$; Fig. 8b). The three predictor sets explained nearly perfectly the variability in biomass ($R^2 = 0.91$; Fig. 8c, d). Guild composition was the strongest predictor of biomass ($R^2 = 0.87–0.89$), followed by NAN ($R^2 = 0.57–0.59$), and $S + J$ ($R^2 = 0.43–0.50$; Table 1). Variance partitioning indicated that biomass was determined primarily by the covariance of NAN, guild composition, and $S + J$ ($R^2 = 0.42–0.46$), followed by pure guild composition ($R^2 = 0.34–0.35$).

DISCUSSION

This study is the first to manipulate a comparatively large number of nutrients (three to four) in natural and artificial streams in order to assess the impact of niche dimensionality on algal guild composition, biodiversity, and biomass. Elucidating the shared and independent effects of niche dimensionality, herbivory, and guild composition on algal community structure and function in stream ecosystems is also novel. Below, we discuss in more detail the functional, biodiversity (including the richness-evenness relationship), and biomass responses to hierarchical causation, as given in our model (Fig. 1).

Functional responses

Prior knowledge on diatom guild responses to herbivory, derived from manipulation of a single grazer or correlative studies, suggests weak grazer influences on guild abundance and diversity (Lange et al. 2011, Göthe et al. 2013, Vilmi et al. 2017). Here, we applied a broad-spectrum insecticide, malathion, to suppress the insect grazer community in the field and followed the responses of guilds, comprising all algae but not just diatoms. We demonstrated that herbivory had no effect on guild richness, but was the dominant force behind guild composition. The high profile guild benefited from grazer exclusion, while the low profile and motile guilds achieved significantly greater proportions in the presence of grazers. These results confirmed that the three guilds

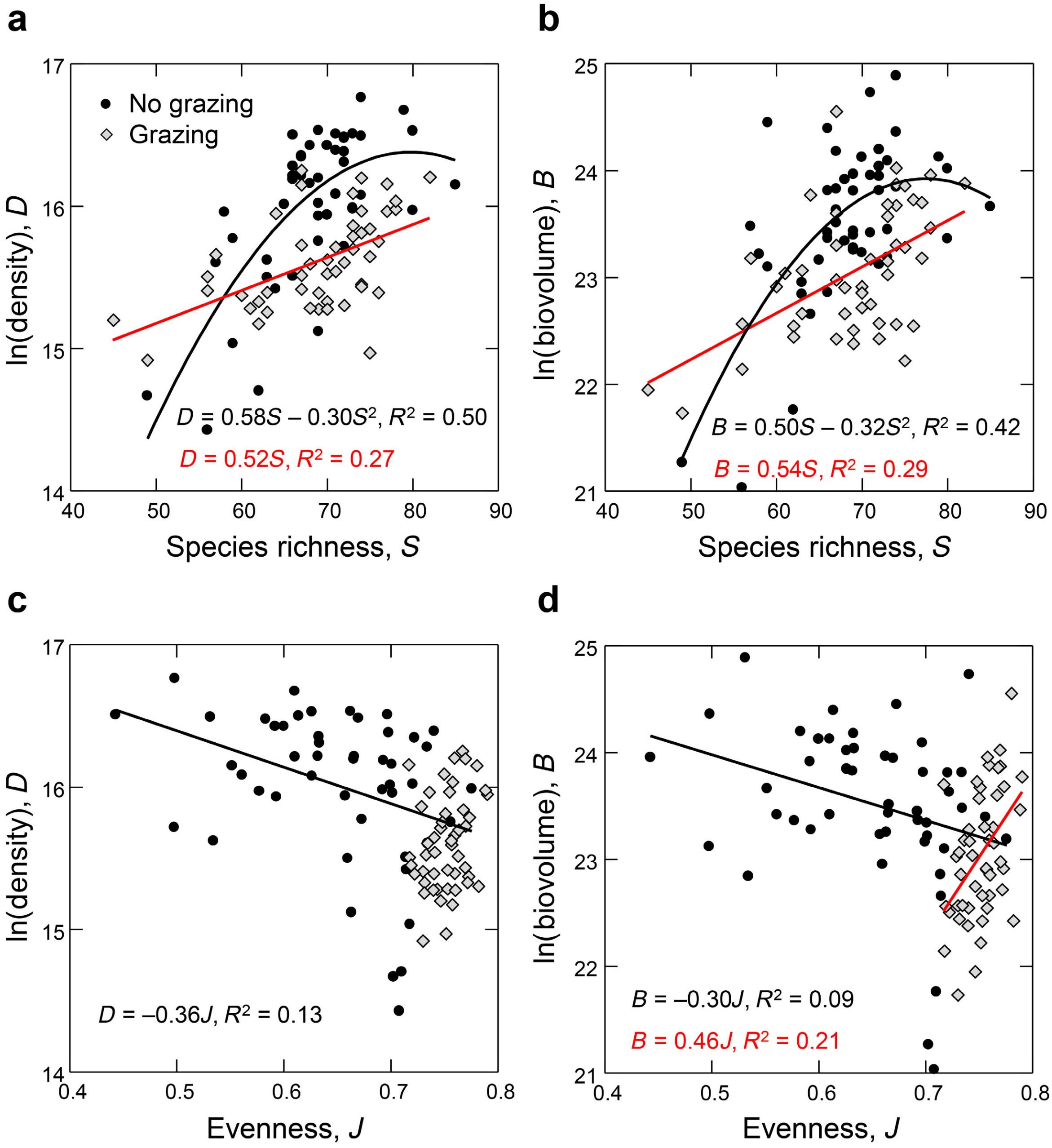

FIG. 5. Relationships of species richness with (a) density and (b) biovolume and of evenness with (c) density and (d) biovolume across grazed (in gray and red) vs. non-grazed communities (in black) in the field experiment. Regression fits, models, and statistics are given in the panels for all significant relationships ($P < 0.05$). The regression coefficients are standardized. The number of samples in each grazing treatment is 48.

exhibit differential sensitivity to disturbance, as originally proposed (Passy 2007). Diatom guilds have gained popularity in biomonitoring of water pollution (Berthon et al. 2011, Marcel et al. 2017) and we too show here distinct responses of algal guilds to nutrient additions. However, we caution that the overriding effect of herbivory on guild composition may hamper bioassessment efforts and future biomonitoring programs should develop metrics that are based on guild richness, which may be less sensitive to grazing.

Biodiversity responses

Species richness was a function of niche dimensionality and guild composition. Herbivory had no effect on species richness, but it modified its response to niche

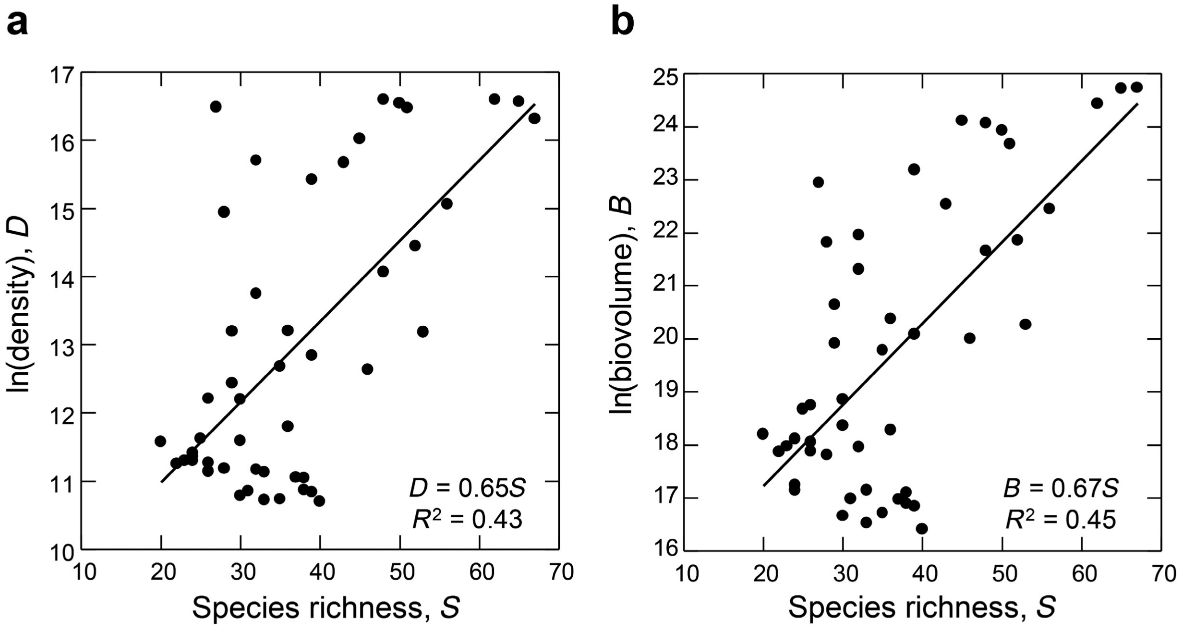

FIG. 6. Relationships of species richness with (a) density and (b) biovolume in the lab experiments ($P < 0.05$ for both relationships). The relationships of evenness with density and biovolume were not significant and, therefore, not shown here. Regression fits, models, and statistics are given in the panels. The regression coefficients are standardized. The number of samples is 48.

dimensionality. In the absence of herbivory (in the grazer-free field treatments and in the lab experiments), we observed a steep increase in species richness with the number of added nutrients, i.e., between about 5 and 10 species per added nutrient, respectively. In the presence of grazing in the field, species richness too increased with the number of added nutrients but saturated at three added nutrients. Notably, one of the nutrients manipulated in the lab (iron) and two of the nutrients manipulated in field (iron and manganese) were micronutrients and maximum richness was reached at the highest number of added nutrients (in the absence of grazing). This result indicates that micronutrients add dimensions to the algal niche and, therefore, supports an emerging paradigm in stream ecology, viewing producer communities as being constrained by both micro- and macronutrients, but not just by macronutrients, as believed for decades (Larson et al. 2015). Given the high impact of the number of added nutrients on community organization in streams (Larson et al. 2016 and this study), we advocate broadening the scope of fertilization research in lotic ecosystems, which so far has focused primarily on the overall enrichment effect, ignoring the influence of niche dimensionality.

We tested the predictions of resource competition theory vs. the benthic model. Our findings were generally consistent with the benthic model (Passy 2008), forecasting a positive relationship of species richness with the number of added nutrients. However, while continentally the increase in average species richness was about two species per added nutrient (Passy 2008), here we detected more accelerated rates of increase, which were further dependent on herbivory. This discrepancy is likely due to factors, such as herbivory, temperature, current velocity, and light, which differed widely in the continental study but were controlled or kept constant here. Considering the strong but variable rates of richness increase with niche dimensionality, future research should investigate the environmental and biotic origins of this variability.

Our results disagree with the prediction of resource competition theory for a negative effect of the number of added nutrients on species richness (Tilman 1982) and with observations in lacustrine phytoplankton (Interlandi and Kilham 2001, Grover and Chrzanowski 2004) and grasslands (Harpole and Tilman 2007, Harpole et al. 2016, Borer et al. 2017), confirming this prediction. An investigation of coastal phytoplankton communities, showing a richness increase with total nitrogen and phosphorus, too reported inconsistency with resource competition theory (Lehtinen et al. 2017). Thus, the evidence from some aquatic systems suggests that this theory may be valid for more limited environmental settings than previously thought.

As discussed, according to the benthic model, at low niche dimensionality tolerant understory species predominate, while at high niche dimensionality, tolerant understory and sensitive overstory species coexist, leading to a greater community richness (Passy 2008). Our observations in both natural and artificial streams partially support this notion. When no nutrients were added, species from all three guilds had comparably low richness. However, with added nutrients, richness of the

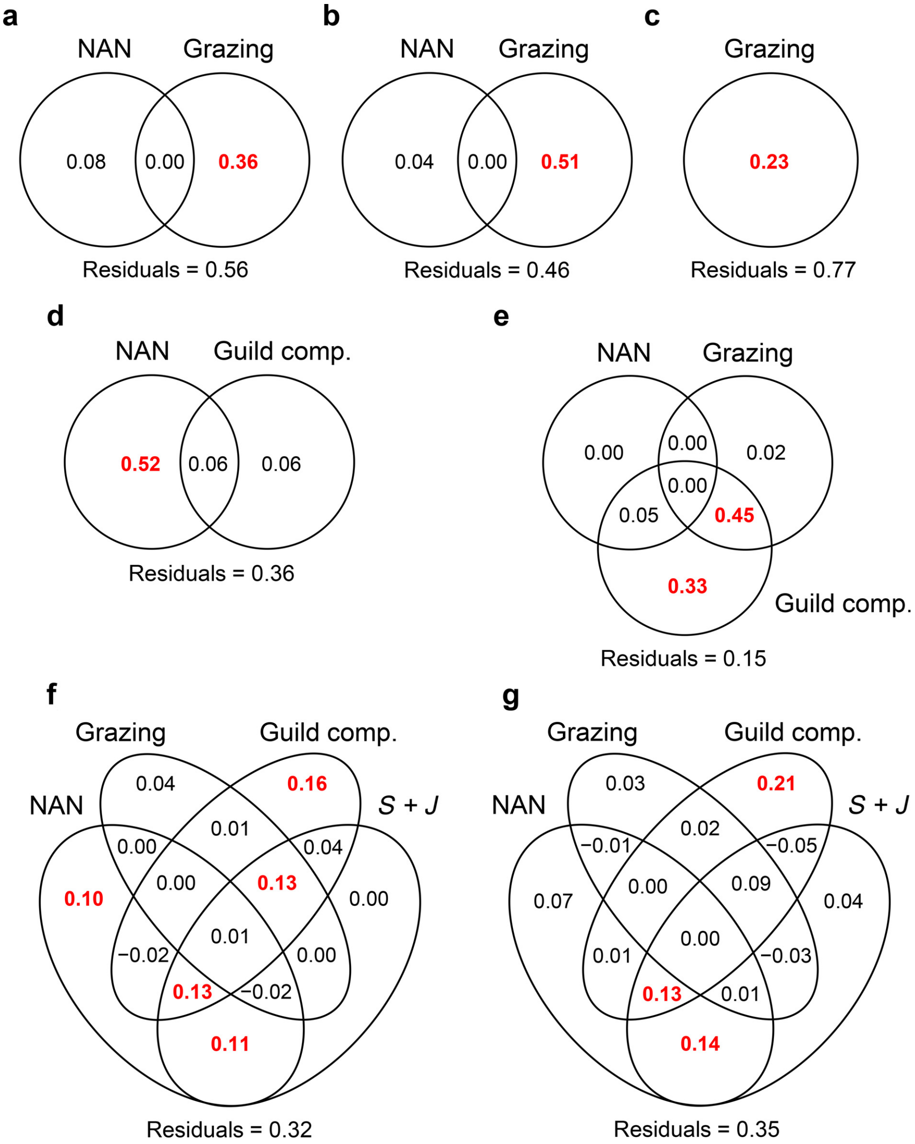

FIG. 7. Variance partitioning for the field experiment of (a) low profile guild proportion, (b) high profile guild proportion, (c) motile guild proportion, (d) species richness, (e) evenness, (f) density, and (g) biovolume showing the pure (circles or ovals) and covariance effects (circle- or oval intersections) of the predictor sets, as given in Table 1. The numbers represent adjusted R^2. For emphasis, higher adjusted R^2 values, i.e., ≥0.10, are boldfaced in red. Only significant predictor sets ($P < 0.05$) are included. NAN, number of added nutrients; comp., composition.

overstory guilds, i.e., the high profile and the motile guild, increased at a faster rate than richness of the understory low profile guild, regardless of grazing, thus revealing coexistence rather than competitive exclusion, as hypothesized.

Richness and evenness exhibited discrepant and variable responses to niche dimensionality, grazing, and trait composition, which led to a variable richness-evenness relationship. Niche dimensionality increased richness, as expected, but had either no effect or negative effect on evenness (depending on grazer presence), contrary to our prediction. These patterns are similar to the positive richness response but negative evenness response to fertilization (Hillebrand et al. 2007). Nevertheless, they further illuminate that not just macronutrient levels but also the poorly investigated number of added nutrients (both micro- and macronutrients) has a substantial impact on algal biodiversity. Grazing had no influence on richness but significantly increased evenness. This result only partially agrees with meta-analyses of periphyton (Liess and Hillebrand 2004) and freshwater communities in general (Hillebrand et al. 2007), showing a negative effect of grazers on richness but a positive effect on evenness. Finally, in both experiments, richness was

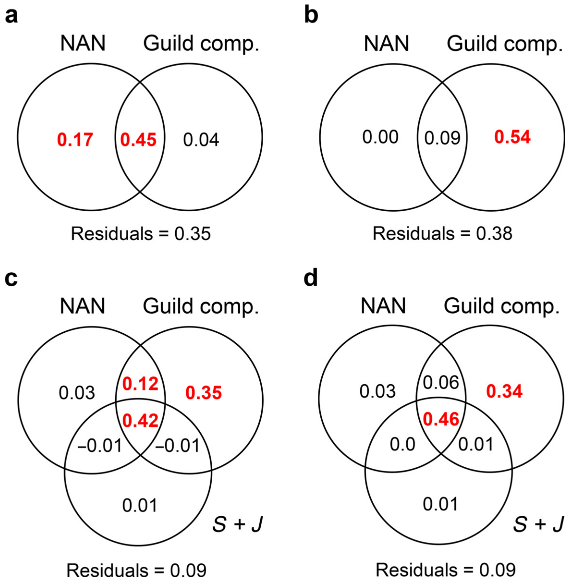

FIG. 8. Variance partitioning for the lab experiments of (a) species richness, (b) evenness, (c) density, and (d) biovolume showing the pure (circles) and covariance effects (circle intersections) of the predictor sets, as defined in Table 1. The numbers represent adjusted R^2. For emphasis, higher adjusted R^2 values, i.e., ≥0.10, are boldfaced in red. Only significant predictor sets ($P < 0.05$) are included. NAN, number of added nutrients; comp., composition.

more strongly controlled by number of added nutrients, while evenness, by guild composition and its covariance terms, indicating that interspecific interactions may have a more prominent role in determining evenness compared to richness.

Richness–evenness relationship

The richness–evenness relationship exhibited a negative trend (field, grazer-free treatment), no trend (field, grazing treatment), and a hump shape with a peak at 49 species (lab). The divergence between the patterns observed in the field in the absence of grazing and in the lab, where no grazing occurred, could be explained with differences in richness. Richness was significantly greater (*t* test, $P < 0.00001$) in the field (mean of 69 species) than in the lab (mean of 37 species), most likely because the lab microcosms were closed systems with no immigration after initial inoculation. However, at the region of richness overlap between the two experiments (49–67 species), the richness–evenness relationship was negative in both.

Thus, in the absence of grazing, the relationship between richness and evenness switched from positive at lower richness (<49 species) to negative at higher richness. A similar pattern was reported for the richness–evenness correlation across plants, animals, and fungi, transitioning between positive and negative at a threshold of 100 species (Stirling and Wilsey 2001). These observations imply that positive interspecific interactions (e.g., complementarity and facilitation), may predominate at lower richness and give rise to an increasing evenness. Conversely, negative interspecific interactions (e.g., competition and allelopathy) at higher richness, may cause a decline in evenness. These interactions were offset in the presence of grazing, when evenness was high along the richness gradient and the relationship between the two metrics disappeared. The variability in the richness–evenness relationship in this study mirrors numerous other observations in both terrestrial and aquatic systems, showing positive, negative, or nonexistent trends (Stirling and Wilsey 2001, Soininen et al. 2012). However, by adopting a manipulative approach, we determined that, in stream algae, this variability was driven by herbivory and the size of the species pool, which was constrained by the level of dispersal. Considering that stream ecosystems vary greatly in terms of both herbivory and dispersal with lower stream orders subjected to limited dispersal and low grazing and higher stream orders, to mass effects and low to high grazing (Vannote et al. 1980, Heino et al. 2015, Jamoneau et al. 2018), we expect the richness–evenness relationship to depend on stream order, but further research is necessary to test this prediction.

Biomass responses

We explored the biodiversity–ecosystem-function relationship from the perspective of the proposed framework. Although we did not manipulate species richness directly, which would have been unfeasible in the species-rich periphyton (with total richness of 105–180 species across the different experiments), we varied species richness indirectly by introducing a gradient of number of added nutrients. In both field and lab experiments, biomass (density and biovolume) was a positive function of species richness, consistent with the prediction of the biodiversity–ecosystem-function paradigm. However, biomass was also strongly dependent on the remaining predictor sets with guild composition having the most pronounced overall and pure effects. Marked influence of trait composition on community functions, often exceeding that of richness, has been well documented in plants and aquatic consumers (Díaz and Cabido 2001, Lecerf and Richardson 2010, Cadotte 2017). Here we show that, in stream algae, the relative proportion of just three guilds captured 68–97% of the explained variance in density and 63–95% of the explained variance in biovolume across the field and lab experiments. These numbers largely surpassed the contributions of species richness to the explained variance in density (37–45%) and biovolume (38–48%) in the two experiments. Thus, our results emphasize the primary role of guild composition in biomass production of aquatic producers and suggest potentially high functional redundancy among algal species.

The number of added nutrients, contributing 47–63% and 54–60% to the explained variance in density and biovolume, respectively, also outperformed species richness. So far, research on the relative impacts of nutrients vs. species richness on biomass production has generated inconsistent results. A global analysis of planktonic algae, grasslands, and forests found that species richness tended to have a greater effect on biomass production than nutrients (Duffy et al. 2017). In contrast, a meta-analysis of plant biomass production showed that the addition of multiple nutrients had a much larger influence than species richness (Hooper et al. 2012). Our findings add substantially to this body of knowledge by providing novel information on how niche dimensionality, i.e., the number rather than the amount of nutrients, contributes to biomass production relative to species richness and species richness + evenness. Notably, adding evenness as an explanatory variable improved the richness model for the field but not for the lab study, indicating that the two diversity metrics may have independent effects on biomass under some circumstances.

In the field study, both the evenness–density and evenness–biovolume relationships were negative in the non-grazed communities but nonexistent or positive, respectively, in the grazed communities. This suggests that the mechanism of biomass production may depend on grazing. In the absence of grazing, the proportion of the high profile guild increased with the number of added nutrients, concurrent with an increase in biomass and a decrease in evenness, i.e., a few productive high profile species proliferated under elevated nutrient supply and contributed the most to biovolume (up to about 80% of total biovolume). The positive evenness–biovolume relationship in the presence of grazing, where high profile species decreased and the low profile and motile species increased in relative abundance, implies a more complementary resource utilization. Similarly, in a plant experiment, low trait dissimilarity with prevalence of tall species was linked to selection, but high trait dissimilarity, involving multiple traits, to complementarity (Cadotte 2017). A laboratory study with stream algae demonstrated a shift from complementarity at heterogeneous current velocities to selection at a homogeneous current velocity (Cardinale 2011). Current velocity in our field study was relatively uniform but grazing apparently created niche opportunities for guilds that were less competitive for resources (low profile and motile) but more resistant to grazing, which may have triggered a switch from selection in the absence of grazing to complementarity in the presence of grazing.

Simple univariate approaches of studying the relationship between species richness and biomass, which have been widely used for decades, were criticized because they generate inconsistent results and fail to account for the complexity of mechanisms controlling both richness and biomass (Adler et al. 2011). Our framework addresses this deficiency and by examining richness and biomass as functions of niche dimensionality, herbivory, and guild composition, reveals to what extent their correlation is driven by both abiotic and biotic factors. In summary, this investigation experimentally proves an alternative model to resource competition theory for the behavior of algal richness along the gradient of number of added nutrients; demonstrates that the algal niche is defined by both macronutrients and micronutrients; and provides mechanistic explanations for the variability in the richness–evenness relationship and the accumulation of biomass in the freshwater benthos.

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