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Benthic algal community composition across a watershed: coupling processes between land and water

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Abstract One of the main goals of ecology is to understand how the abiotic environment influences the biotic characteristics of the ecosystem. Various processes at multiple scales interact to affect the physical and chemical environments that are experienced by organisms, which ultimately influence community composition. We aimed to understand the processes that control benthic algae community composition within a watershed. We investigated the impact of both land cover and physiochemical variables on benthic algal community composition. We sampled benthic algae along with multiple habitat and water chemistry parameters within three microhabitats across eight sites along the mainstem of the Kiamichi River in southeastern Oklahoma. We used the benthic light availability model to assess the amount of light reaching the bottom of the stream. Additionally, we conducted a GIS analysis of the watershed to determine the land cover affecting each of these sites. Several of the in-stream site-scale variables that were measured (e.g., conductivity, pH and canopy cover) were strongly correlated with both position within the watershed and percent agriculture within the watershed. The physiochemical parameters that were correlated with watershed position and land cover were then used to understand the linkage with algae community composition. Algae genera composition was strongly correlated with both light reaching the bottom of the stream and conductivity. Our results suggest a hierarchy of factors that determine species composition and show the dependence of community composition on differing light regimes.

Keywords Benthic light availability model (BLAM) · Algal community · Land cover · Spatial scale · Non-metric multidimensional scaling (NMDS)

Introduction

Across ecological systems, there are multiple, hierarchical determinants of species composition including climate, geology and chemistry. These larger-scale patterns influence fine-scale habitat features which ultimately influence the conditions an organism experiences in their environment. This hierarchy is especially apparent in river ecosystems (Burcher et al. 2007; Frissell et al. 1986) because these ecosystems integrate the landscapes they drain (Hynes 1975) and respond to changing terrestrial conditions (Likens et al. 1978). For example, discharge, solute and seston

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load interactively respond to land cover and landscape physiography at the watershed scale, while stream hydraulics, light and organic inputs tend to be more sensitive to reach-scale geomorphology and the condition of the riparian zone (Allan 2004; Snelder and Biggs 2002). Thus, stream communities are affected by land cover through multiple mechanisms operating over a range of spatial and temporal scales (Allan 2004; Burcher et al. 2007; Snelder and Biggs 2002; Winemiller et al. 2010). The distinction between the factors that have direct and indirect effects allows us to better predict those effects by establishing linkages between cause and effect of proximate factors that influence species composition (Burcher et al. 2007). Because of this, overarching affects such as landscape structure, shading and anthropogenic impacts directly influence underlying chemical parameters and physical habitat structure, which ultimately, in conjunction with biotic interactions, influences community composition.

Biomass of algae is in part controlled by light availability and the productivity. The species composition of benthic algae is often an important regulating factor determining macroinvertebrate species composition. Both the species composition and abundance of benthic algal communities in streams are a result of both biotic and abiotic factors that operate at several geographic scales as reviewed in Stevenson (1997). Benthic algae species composition has often been used as an indicator of environmental stress or is characteristic of particular habitat types (Greenwood and Lowe 2006; Reavie et al. 2010; Stelzer and Lamberti 2001; Taylor et al. 2004), especially diatoms (Dixit et al. 1992; Hill et al. 2003; Lawson 1999; Potapova and Charles 2002, 2007; Smucker and Vis 2011; Stevenson et al. 2008; Weilhoefer and Pan 2006; Zampella et al. 2007). Furthermore, conductivity of freshwaters has been shown to explain most of the variation in diatom assemblages in the USA (Potapova and Charles 2003) in addition to spatial factors across biogeographic regions (Potapova and Charles 2002).

Qualitative predictions have been made regarding general longitudinal patterns of light availability and species composition of aquatic invertebrates in rivers (Vannote et al. 1980), but explicit tests of these predictions are scarce (but see Julian et al. 2008c). In the framework of the river continuum concept (RCC), light availability is predicted to increase in a downstream direction as the river increases in width, but with benthic light availability dissipating with increased turbidity in downstream reaches. Studies of timber harvest which leads to greater light availability show distinct changes in algae flora with diatoms composing most of the periphyton prior to logging, and a shift toward large mats of green algae following harvest (Hansmann and Phinney 1973). However, the influence of basin-scale disturbances such as timber harvest on diatom species community is also explained in part by higher N, P, turbidity and conductivity in harvested watersheds (Naymik et al. 2005). While the effect of light (both shading and optical water quality) on benthic primary productivity has been investigated (Julian et al. 2008c), no study has investigated the specific role of light availability on algal species composition. This critical gap exists because light has not been widely recognized as a limiting resource in riverine ecosystems in comparison with nutrients and habitat.

Local habitat features such as substrate effects on algae composition and richness may vary in importance depending on scale. It would appear that at large geographic scales, the importance of substrate is minimal in influencing species diversity of stream diatoms (Potapova and Charles 2005). However, smaller-scale studies have found an influence of substrate on diatom species composition (Soininen and Eloranta 2004; Tuchman and Stevenson 1980) perhaps related to protection from grazing due to substrate roughness (Bergey and Weaver 2004). Thus, understanding the distribution and the features underpinning their occurrence is dependent upon the scale of interest.

Following the hierarchical framework proposed by Stevenson (1997) and the cascade concept outlined in Burcher et al. (2007), we test the determinants of benthic algae genus composition to understand the large-scale patterns that dictate local-scale conditions. Although many studies have utilized algal species identification, many have also shown the utility of genus-level assays in assessing stream condition (Hill et al. 2003; Wang et al. 2005). Researchers have shown that ion concentrations in the water determine algae species composition, specifically diatoms (Potapova and Charles 2003). Here we investigate factors that determine algae community assemblage within a stream and how these factors vary longitudinally along the stream continuum. This study investigates the dependence of physicochemical and biotic characteristics on land cover-associated factors at the watershed scale. We were particularly interested in how benthic light availability varied across the river continuum and how it influenced benthic algae community composition. Our results suggest a hierarchy of factors that determine species composition and indicate the dependence of community composition on differing light regimes.

Materials and methods

Study area

We sampled eight sites between June 8 and June 11, 2012, throughout the Kiamichi River in southeastern Oklahoma, USA (Fig. 1). The Kiamichi River, a tributary of the Red River in the Mississippi drainage, begins in the Ouachita Uplands and flows 197 km through a narrow, mainly ridge-and-valley watershed (3686 km^2). The mean monthly discharge between 1973 and 2014 at the most upstream site (USGS 07335700) was 1.7 m^3 s^{-1} and the mean monthly discharge near the most downstream sampling site (USGS 07336200) between 1983 and 2014 was 37.1 m^3 s^{-1}. This river flows through the Ouachita highland region and is known for its high fish and mussel biodiversity (Matthews et al. 2005). The study area is dominated by forest cover, and agriculture is primarily cattle and chickens. The river is typically shallow, with warm water temperatures during the summer and more moderate temperatures and flow during the remainder of the year (Table 1).

Physiochemical parameters

We used a calibrated YSI Professional Plus multiparameter sonde (YSI, Yellow Springs, OH, USA) to measure temperature, specific conductivity, pH and dissolved oxygen at each site. A Hach 2100Q portable turbidimeter (Hach, Loveland, CO, USA) was used to determine nephelometric turbidity units (NTU) at each site. We measured depth (m) and stream width (m) at each of the algae collection points. While we do not have water chemistry data for our sites in 2012, we collected triplicate water samples twice (June and July) in 2010 for total dissolved nitrogen and phosphorus determination at each of these sites except for the most upstream site. Additionally, we measured total dissolved nitrogen and phosphorus at one of these sites (site 7) in July 2011 and noted little difference in nutrient concentrations between 2010 and 2011. Site 1, the most upstream site,

Fig. 1 Algae collection sites along the Kiamichi River. Site 1 is the most upstream site, and site 8 is the most downstream site

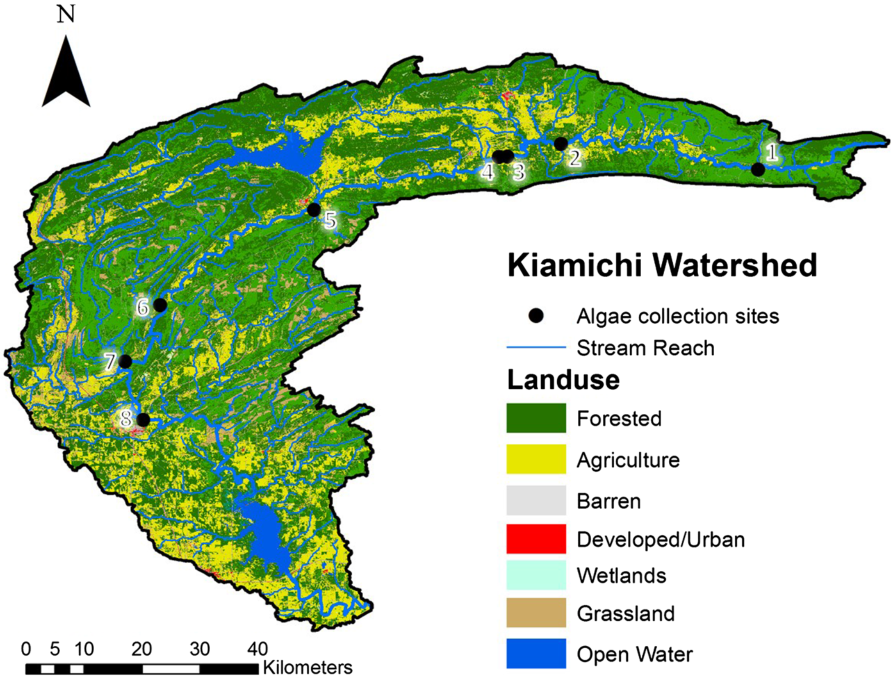

Table 1 Water chemistry variables (mean), light availability (mean) and watershed land cover for each sample site

Parameter	Site							
	1	2	3	4	5	6	7	8
Watershed area (km^2)	124	489	809	815	1860	2044	2299	2891
Temperature (°C)	24.41	26.91	30.18	30.42	29.23	27.34	32.55	30.47
pH	6.68	6.78	6.97	6.94	6.99	6.91	7.56	7.45
Conductivity (μS cm^{-2})	27.0	45.1	53.5	55.0	69.83	61.1	56.5	64.7
Dissolved oxygen (mg/L)	6.81	6.96	7.40	6.90	6.92	6.41	8.89	8.58
Total dissolved nitrogen (mg/L)	0.242	0.294	0.346	0.343	0.343	0.324	0.357	0.342
Total dissolved phosphorus (mg/L)	0.041	0.044	0.033	0.033	0.039	0.033	0.034	0.030
Turbidity (NTU)	2.60	9.49	12.20	10.1	11.20	9.83	5.38	7.67
Shading coefficient (s)	0.68	0.66	0.85	0.75	0.78	0.78	0.81	0.86
% Urban	2.26	2.66	3.06	3.07	2.64	2.67	2.59	2.73
% Forest	95.16	85.46	76.29	75.91	70.91	71.27	72.43	70.41
% Grassland/shrubs	0.78	2.27	4.80	4.86	6.82	6.81	7.57	8.12
% Agriculture	1.77	9.15	14.55	14.86	15.23	15.07	13.58	15.54
% Wetland	0.03	0.35	1.00	1.00	1.27	1.29	1.21	1.08

was only sampled once in July 2010. Samples were field filtered, acidified, and analyzed for total dissolved nitrogen and phosphorus (following persulfate digestion) within 28 days of collection using a Lachat QuikChem FIA+ 8000 Series flow injection analyzer (Hach Company, Loveland, CO, USA).

Algae sampling and identification

We designated the three main habitat types found in the Kiamichi River for sampling all sites: mid-channel, riffle and water willow (*Justicia americana*) areas. Within each habitat type, we sampled three rocks of varying sizes to try to minimize the effect of varying hydrologic disturbance on algae colonization: a small (2–16 mm), a medium (16–64 mm) and a large (64–250 mm) rock was sampled in each habitat type. We used a soft-bristled brush in water to remove algae from the entire rock, and the resulting slurry was collected and preserved in 3 % glutaraldehyde. In the laboratory, >300 cells were identified to genus and counted at 100× magnification for each individual sample, which resulted in ~1000 cells identified and counted for each habitat/site. Counts were used to calculate relative abundances (proportions) of algal genera and the distribution of algal groups (green algae, Chlorophyta; diatoms, Bacillariophyceae; and blue-green algae, Cyanobacteria) at each site.

Canopy data and light modeling

We used the benthic light availability model (BLAM; Julian et al. 2008b) to determine the amount of photosynthetically active radiation (PAR) available to the benthic algae community. BLAM (Julian et al. 2008b) calculates the amount of PAR at the stream bed (E_{bed}) by incorporating the terrestrial and aquatic controls on benthic light availability. The first-order control on light availability is above-canopy PAR (E_{can}) in mol m^{-2} day^{-1}, where one mol equals 6.02 × 1023 photons. E_{can} is the total PAR (as irradiance) available to the river before any shading from topography or riparian vegetation. We obtained E_{can} measurements from a nearby Oklahoma mesonet station (http://www.mesonet.org/) for the week prior to sample collection. We took the average PAR across these days which was equivalent to the daily average PAR for the study period.

Topography and shading decrease the intensity of PAR that reaches the water surface of a stream, reducing E_{can}–E_s. The ratio of E_s:E_{can} is the shading coefficient (s), where s decreases with increased shading. We used the "canopy photo method," where a hemispherical canopy photograph is overlaid by the sunpath to calculate how much solar radiation is transmitted through openings in the canopy (Fig. 2). Most other methods used to quantify stream shade (e.g., clinometer and densiometer) can underestimate transmitted PAR by as much as 85 % (Chazdon and Pearcy 1991), while the canopy photograph method has been used successfully to quantify stream shading (Taylor et al. 2004). At each site, digital hemispherical canopy photographs were taken using a Nikon Coolpix 4500 with a fisheye lens. Three canopy photographs were taken at each site above each algae collection point (the three habitat types). For each photograph, we processed and analyzed each photograph with gap light analyzer (GLA) software according to Frazer et al. (1999) to obtain E_s and s with parameters set in GLA as shown in Table 2.

Reflection at the air–water interface decreases the intensity of PAR that enters the water column, reducing E_s–E_0. The ratio of E_0:E_s is the reflection coefficient (r) and was estimated using Fresnel's formula (Kirk 1994). Once light enters the water column, it is attenuated exponentially with depth at a rate defined by the diffuse attenuation coefficient (K_d). We estimated K_d from turbidity (T_n) measurements, where $K_d = 0.17T_n$ (Julian et al. 2008b). The PAR at depth (y) on the streambed (E_{bed}) in mol m^{-2} day^{-1} at one location in time is:

Fig. 2 Canopy photograph from sample site 1

Table 2 Parameters used in gap light analyzer program

Parameter in GLA	Defined as
Period	April 15–September 30
Projection	Polar
Orientation	Horizontal
Time step	1 min
Azimuth regions	36
Zenith regions	9
Solar constant	1300 W/m^2
Cloudiness index	0.5
Sky-region brightness	UOC model
Clear-sky transmission coefficient	0.65

$$E_{bed} = (E_{can} \times s \times r)e^{-K_d y}$$

E_{bed} was derived for each individual canopy photograph and then averaged to determine site E_{bed}. The E_{bed} predictor integrates total light availability, shading by the stream, water turbidity and average depth.

Land cover

We derived watershed areas for each sampling point using the Spatial Analyst Toolkit in ArcMap 10.0 (Environmental System Research Institute, Redlands, CA, USA) with a 30-m digital elevation model (DEM) from the National Elevation Dataset. Then, we obtained land cover (30-m resolution) for the USA from the 2006 National Land Cover Database (Homer et al. 2004). Grids were lined up, and for each site, we derived the watershed land cover. Land cover classifications included forest, agriculture, grassland, urban, wetland/open water and barren.

Data analysis

We investigated the structure and correlation structure within the abiotic data and land cover data with Spearman rank correlation similar as Burcher et al. (2007). To determine our sampling efficiency, we looked at the species–area curve. We also examined the most abundant genera using a log abundance plot using the mvabund package in R v3.1.2.

We used an analysis of similarity (ANOSIM) to determine whether there were significant differences in algal communities across the three habitat types sampled and/or across sites. Analysis of similarities provides a way to test whether there is a significant difference between two or more groups of sampling units (Clarke 1993). We removed algae genera in which only one cell was counted, and then, each sample was transformed into proportions. ANOSIM was calculated using Bray–Curtis distances with 999 Monte Carlo permutations. Each test in ANOSIM produces an R-statistic, which contrasts the similarities of sites within a habitat with the similarities of sites among habitats or vice versa.

To determine differences in algae across the sample sites and the variables that controlled algae community composition, algae data from all habitats were combined for each site due to algae communities not being different across the habitat types. Variation of algae assemblages across the sites were summarized using non-metric multidimensional scaling (NMDS), a multivariate ordination technique commonly used in ecological community analysis (Tabachnick and Fidell 2007). We used algal relative abundances to calculate Bray–Curtis dissimilarity indices among the sites. NMDS projects each site into a species-defined ordination space with two or more dimensions based on their ranked dissimilarity. The goodness of fit for the NMDS projections was measured as a stress value which quantifies the deviation from a monotonic relationship between the distance among sites in the original Bray–Curtis dissimilarity matrix and the distance among sites in the ordination plot.

We aimed to determine the relationships between land cover, location in the watershed and physiochemical parameters and their control on algal community composition. Following the NMDS, we wanted to understand the hierarchy of the data in the form of a conceptual diagram. We used the envfit function in the vegan package (Oksanen et al. 2011) in Rv3.1.2 to do a post hoc analysis of the physiochemical variables (i.e., conductivity, pH, temperature, light availability and nutrient concentrations) that may be contributing to algal community assemblage. The envfit function finds the direction in k-dimensional ordination space that has maximal correlation with an external variable and assesses the significance of the variables using permutation tests. All analyses were performed using the R software package (R Development Core Team 2012).

Results

Algae genera and predictors

We collected 49–66 algae genera at each of our samples sites and 85 genera total. We accumulated genera richness as we accrued more samples; however, this accumulation reached an asymptote (Fig. 3). The most common genera across all sites were *Gomphonema*, followed by *Navicula* and *Scenedesmus* (Fig. 4). Our ANOSIM indicated that there were no significant differences in algae genera assemblage structure across the three habitat types sampled at the sites ($R^2 = 0.02, p = 0.28$), but there were differences across the sites ($R^2 = 0.49, p < 0.001$). Because there were no differences among habitat types, we combined all data for each site into total proportion of algae assemblage. When we ran our NDMS on the combined algae proportions, NMDS explained over 99 % of the variation in the algae genera data structure with low stress (stress = 0.06; Fig. 5). NMDS axis one was negatively related to the abundance of many of the green algae taxa (i.e., *Chaetophora*, *Chlamydomonas*, *Chlorella* and *Mallomonas*) and positively related to several blue-green taxa (*Aphanocapsa*, *Microcystis*, and *Rhizoclonium*; Fig. 5). We found that NMDS axis two was negatively related to several diatom taxa (e.g., *Ellerbeckia*, *Kirchneriella*, *Melosira*, *Nitzschia* and

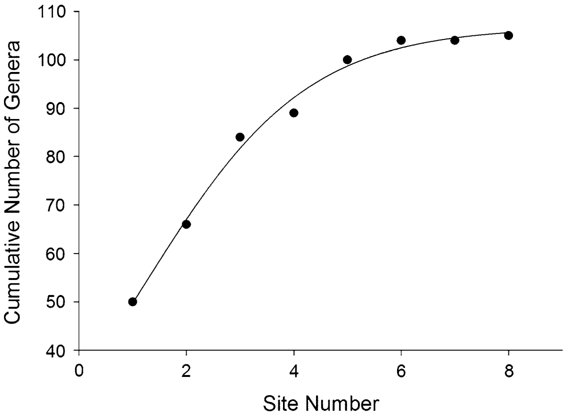

Fig. 3 Cumulative algae genera collected during the study going from upstream to downstream in the Kiamichi River during this time period

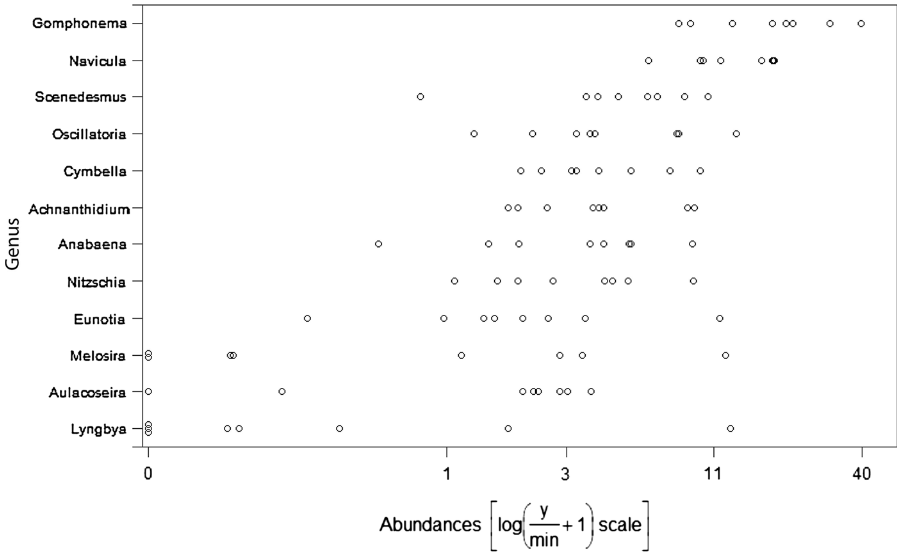

Fig. 4 Figure depicting the most common genera across all sites. The two most common groups, *Gomphonema* and *Navicula*, are both diatoms

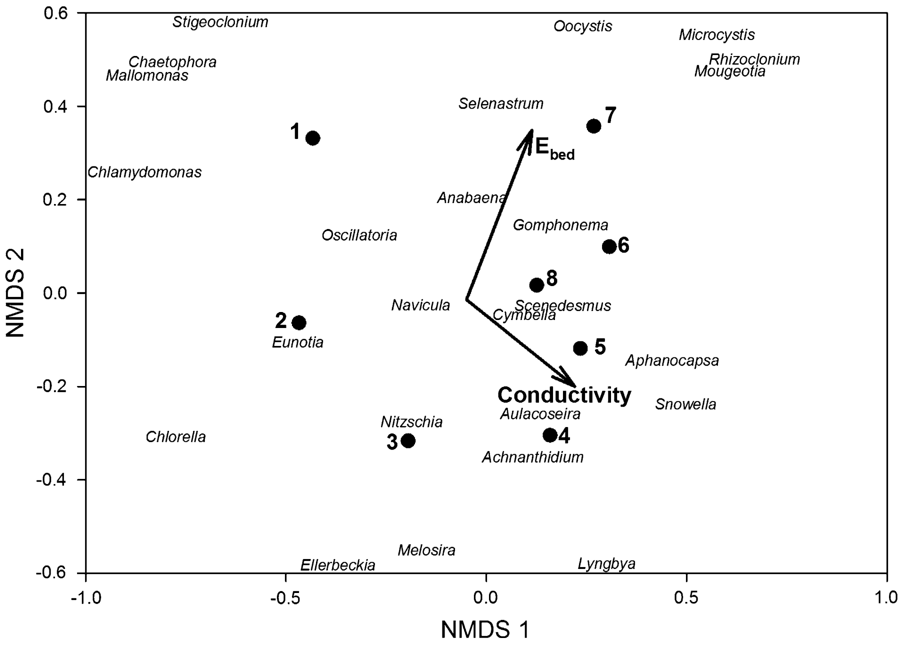

Fig. 5 Non-metric dimensional scaling plot indicating the algal community composition of the sites (points with corresponding site id) with the significant joint plot predictors shown. Conductivity and the light reaching the channel bed (E_{bed}) are the strongest predictors of algae community composition

Pseudostaurastrum) and positively related to *Mougentia*, *Selenastrum*, and *Stigeoclonium*. Joint plot analysis indicated that algae genera composition was most strongly regulated by light reaching the bottom of the stream (E_{bed}) and conductivity (Fig. 5), while pH, nutrient concentrations and temperature were not significant predictors.

Abiotic data, land cover data and hierarchy

There was a strong correlation structure within the data. Conductivity was positively correlated with both watershed area and percent agriculture in the basin (Fig. 6; $\rho = 0.83$, $p = 0.02$; $\rho = 0.90$, $p = 0.004$, respectively). Total phosphorus was negatively

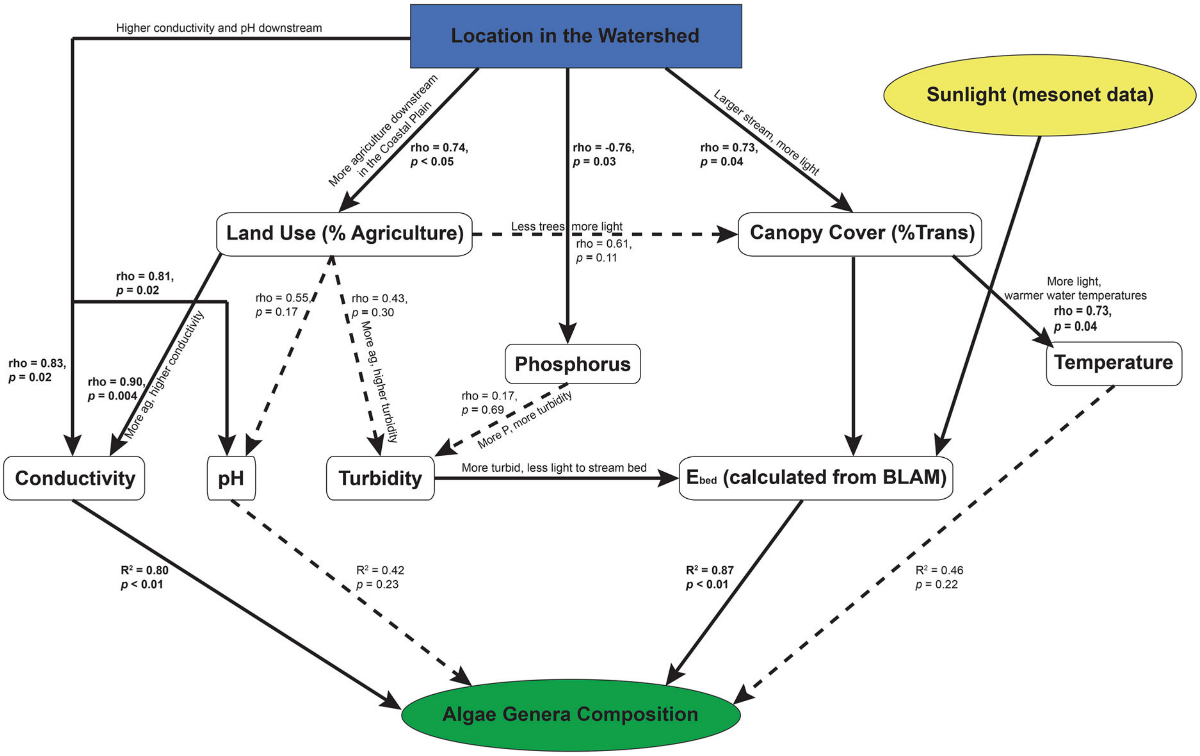

Fig. 6 Conceptual diagram showing the controls on algal community assemblage. Significant predictors are shown with a *dark solid line*, while nonsignificant predictors are shown with a *dotted line*

correlated with watershed area, but not agricultural land cover ($\rho = -0.76$, $p = 0.03$; $\rho = -0.51$, $p = 0.19$, respectively). Total nitrogen (N) was not significantly correlated with watershed area or percent agriculture ($\rho = 0.47$, $p = 0.24$; $\rho = 0.29$, $p = 0.50$, respectively). The pH at the site was significantly correlated with watershed area (Fig. 6; $\rho = 0.81$, $p = 0.02$), but was not significantly correlated with agricultural land cover ($p = 0.17$). Turbidity was lowest at the most upstream site and was highest at site 3 (12.2 NTU) and remained relatively constant until declining downstream of site 5 and was not correlated with the amount of agriculture in the upstream basin ($\rho = 0.43$, $p = 0.30$). The amount of light coming though the canopy (% trans) was also significantly positively correlated with the watershed area ($\rho = 0.73$, $p = 0.04$), and the stream temperature was significantly positively correlated with the amount of light coming through the canopy ($\rho = 0.73$, $p = 0.04$). This suggests that the overall position in the watershed affects the two factors (i.e., conductivity and light reaching the benthic habitat) that most strongly regulated algae community composition in this watershed.

Discussion

Our results indicate that landscape factors influence in-stream physiochemical parameters that play a role in controlling algal community composition in streams, supporting Stevenson's (1997) framework. Both light reaching the stream bed and conductivity were direct regulating factors impacting the broader algal assemblage structure. However, in order to understand how these factors operated over an entire watershed and the landscape features that lended to these patterns, we had to examine watershed-scale factors that influence light and conductivity. By viewing streams as hierarchically organized systems, we were able to focus on a small set of variables at each level that most determine system behaviors and capacities within the relevant spatiotemporal frame. Our hierarchical approach successfully linked land cover to biotic responses through a series of intermediate abiotic links. Unlike bivariate comparisons, between land cover and species composition, our framework allowed for some mechanistic understanding of how landscape features are propagated to ultimately influence organisms. Previous results have shown that diatom assemblages are distributed continuously along gradients of conductivity (Potapova and Charles 2003), but did not investigate higher-order factors. By viewing our stream community as a system organized and developed around spatially defined habitats (Frissell et al. 1986; Poff 1997), we increased our understanding of the spatial structure and levels of organization. Stream communities can be viewed as systems organized within this hierarchical habitat template.

The qualitative expectation of light availability proposed in the RCC (Vannote et al. 1980) is a parabolic distribution in which light is low in the upper and lower reaches and high in the middle reaches, reflecting a transition from shading by riparian vegetation giving way to aquatic light attenuation by increasing turbidity in larger river reaches. While we observed decreased riparian shading as we moved downstream, turbidity did not necessarily get higher as we moved downstream, but was highest in the middle reaches which lead to a negative unimodal pattern in benthic light availability in our study system. Higher turbidity in downstream reaches has been noted in agricultural systems (Julian et al. 2008c), while an asymptotic pattern in turbidity was seen in a larger investigation of several unaltered streams (Julian et al. 2008a), suggesting that these varying patterns may be common and related to watershed condition. Water clarity is primarily dictated by the particulates in the water column rather than by dissolved constituents (Julian et al. 2008a, b, c). While we did not note any correlation between agricultural land cover and water turbidity in our study, there is some logging in the Kiamichi basin (C. Atkinson, personal observation) that could drive some of the patterns in turbidity.

At larger (multiple regions or continental) spatial scales, factors such as geology, ecoregion classification, disturbance and watershed land cover may have a greater impact and perform better in predicting species composition (Allan 2004; Cardinale et al. 2006; Pyne et al. 2007). However, our approach was important in determining the landscape-scale factors that influenced local abiotic conditions that lead to variability in algae genera composition within a watershed. Whether or not algal genera are structured in a similar fashion across broad geographic regions is not fully known. However, Potapova and Charles (2002) found in a national-level study that diatoms were structured by three major ecologic gradients, a gradient associated with the RCC, mineral content and pH and a temperature gradient-related latitude/altitude of sites, but did not investigate light and its association with the RCC. They found that temperature measured at the site at time of sampling had no direct relationship community composition, yet only at a national scale did variation in temperature correlate with species abundance.

Benthic light availability was most strongly correlated with benthic algal assemblages in our study. Our study shows that the BLAM model is effective to understand light availability and was a significant factor in determining algae genera community assemblage. More work across larger scales needs to be done to fully appreciate the importance of light on algal assemblages. This model may be used in future studies to predict the available energy for primary consumers and trade-offs between gross primary productivity and community assemblage. The importance of forest canopy cover can influence light levels received by the stream benthos, reducing incoming energy and nutrients, shifting the balance between algal groups (e.g., those that tolerate low light, such as diatoms, and those tolerate high light such cyanobacteria and green algae). Studies of timber harvest show distinct changes in algae flora with timber harvest (Hansmann and Phinney 1973). The influence of basin-scale disturbances such as timber harvest in previous studies correlates with diatom species community changes in part explained by higher total nitrogen, phosphorus, turbidity and conductivity versus unharvested watersheds (Naymik et al. 2005). We observed timber harvesting occurring in this basin, but it was difficult to map the extent and time period of harvests, and thus, direct data on timber effects could not be incorporated into this study. Yet, using the BLAM allowed us to incorporate both shading and turbidity into a single variable, which was successful in describing community composition.

An interplay between disturbance (flood frequency) and nutrients in flowing waters often results in higher species richness at intermediate levels (Biggs and Smith 2002; Cardinale et al. 2006). While we did not investigate temporal variability in benthic algal assemblages, our study investigated “stable” algae communities during summer flow periods, the time period of the highest biological activity in temperate streams. We observed little variability in overall genera richness across the sites (49–66 genera), there were not differences in the assemblage within the habitat types sampled at a site, and there was not a longitudinal pattern. Overall, this is a low-nutrient system (Atkinson et al. 2013), and we found that many of the genera detected in this system are often associated with nutrient-poor waters (Dillard 1999; Pan et al. 1996; Winter and Duthie 2000). Because it is a relatively nutrient-poor system, nutrients may be taken up at a high rate due to biological demand, potentially preventing us from detecting a nutrient affect. Furthermore, nutrients can be highly temporally variable; in-stream nitrogen concentrations based on a limited sampling frequency in agricultural streams are often poorly correlated with diatom metrics (Porter et al. 2008). Conductivity increased significantly with the percentage of the catchment in agricultural land cover as found in Biggs (1995); however, the correlation between location within the watershed and conductivity was relatively strong as well, making it difficult to determine whether it was a land cover effect.

Our study showed that a set of hierarchical factors affected the benthic genera composition, suggesting that better predictions can arise from the knowledge of the higher-scale factors that constrain lower- and local-scale factors. Many of these higher-scale factors may also have a strong influence on assemblage structure across systems; however, varying disturbance regimes and climate lead to different communities (Power and Stewart 1987). The influence of light, nutrients and consumer density can affect periphyton production through both bottom-up and top-down control (Mallory and Richardson 2005). Freshwater mussels have been found to be important in influencing algal assemblage structure within rivers in this region and can lead to variation in algal communities where they dominate (Atkinson et al. 2013). A multitude of factors operating various spatial and temporal scales that we did not incorporate can influence algal assemblages. Thus, incorporating a hierarchical framework with other models including the temporal framework and spatial heterogeneity across broad geographic areas will increase understanding of complex ecosystems and ability to deal with large-scale environmental changes.

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References

Allan JD (2004) Landscapes and riverscapes: the influence of land use on stream ecosystems. Annu Rev Ecol Evol Syst 35:257–284. doi:10.1146/annurev.ecolsys.35.120202.110122

Atkinson CL, Vaughn CC, Forshay KJ, Cooper JT (2013) Aggregated filter-feeding consumers alter nutrient limitation: consequences for ecosystem and community dynamics. Ecology 94:1359–1369

Bergey EA, Weaver JE (2004) The influence of crevice size on the protection of epilithic algae from grazers. Freshw Biol 49:1014–1025

Biggs BJF (1995) The contribution of flood distrubance, catchment geology and land-use to the habitat template of periphyton in stream ecosystems. Freshw Biol 33:419–438

Biggs BJF, Smith RA (2002) Taxonomic richness of stream benthic algae: effects of flood disturbance and nutrients. Limnol Oceanogr 47:1175–1186

Burcher C, Valett H, Benfield E (2007) The land-cover cascade: relationships coupling land and water. Ecology 88:228–242

Cardinale BJ, Hillebrand H, Charles DF (2006) Geographic patterns of diversity in streams are predicted by a multivariate model of disturbance and productivity. J Ecol 94:609–618. doi:10.1111/j.1365-2745.2006.01107.x

Chazdon RL, Pearcy RW (1991) The importance of sunflecks for forest understory plants—photosynthetic machinery appears to be adapted to brief, unpredictable periods of radiation. Bioscience 41:760–766. doi:10.2307/1311725

Clarke KR (1993) Nonparametric multivariate analyses of changes in community structure. Aust J Ecol 18:117–143. doi:10.1111/j.1442-9993.1993.tb00438.x

Dillard GE (1999) Common freshwater algae of the United States: an illustrated key to the genera (excluding the diatoms). Gebrüder Borntraeger, Berlin

Dixit SS, Smol JP, Kingston JC, Charles DF (1992) Diatoms: powerful indicators of environmental change. Environ Sci Technol 26:23–33

Frazer GW, Canham CD, Lertzman KP (1999) Gap light analyzer (GLA), version 2.0: imaging software to extract canopy structure and gap light transmission indices from true-colour fisheye photographs, users manual and program documentation. Simon Fraser University, Burnaby, British Columbia and the Institute of Ecosystem Studies, Millbrook New York

Frissell CA, Liss WJ, Warren CE, Hurley MD (1986) A hierarchical framework for stream habitat classification—

viewing streams in a watershed context. Environ Manag 10:199–214

Greenwood J, Lowe R (2006) The effects of ph on a periphyton community in an acidic wetland, USA. Hydrobiologia 561:71–82

Hansmann EW, Phinney HK (1973) Effects of logging on periphyton in coastal streams of oregon. Ecology 54:194–199. doi:10.2307/1934390

Hill BH, Herlihy AT, Kaufmannc PR, DeCelles SJ, Vander Borgh MA (2003) Assessment of streams of the eastern united states using a periphyton index of biotic integrity. Ecol Indic 2:325–338

Homer C, Huang C, Yang L, Wylie B, Coan M (2004) Development of a 2001 national land cover database for the United States. Photogramm Eng Remote Sens 70:829–840

Hynes HBN (1975) The stream and its valley. Verh Int Ver Limnol 19:1–15

Julian JP, Doyle MW, Powers SM, Stanley EH, Riggsbee JA (2008a) Optical water quality in rivers. Water Resour Res. doi:10.1029/2007wr006457

Julian JP, Doyle MW, Stanley EH (2008b) Empirical modeling of light availability in rivers. J Geophys Res Biogeosci. doi:10.1029/2007jg000601

Julian JP, Stanley EH, Doyle MW (2008c) Basin-scale consequences of agricultural land use on benthic light availability and primary production along a sixth-order temperate river. Ecosystems 11:1091–1105. doi:10.1007/s10021-008-9181-9

Kirk JTO (1994) Light and photosynthesis in aquatic ecosystems. Cambridge University Press, New York

Lawson LL (1999) Epilithic diatoms as indicators of stream condition in arid lotic ecosystems of the American southwest. Dissertation, University of Arizona

Likens GE, Bormann FH, Pierce RS, Reiners WA (1978) Recovery of a deforested ecosystem. Science 199:492–496. doi:10.1126/science.199.4328.492

Mallory MA, Richardson JS (2005) Complex interactions of light, nutrients and consumer density in a stream periphyton-grazer (tailed frog tadpoles) system. J Anim Ecol 74:1020–1028. doi:10.2307/3505251

Matthews WJ, Vaughn CC, Gido KB, Marsh-Matthews E (2005) Southern plains rivers. In: Benke AC, Cushing CE (eds) Rivers of North America. Academic Press, Burlington

Naymik J, Pan Y, Ford J (2005) Diatom assemblages as indicators of timber harvest effects in coastal oregon streams. J N Am Benthol Soc 24:569–584. doi:10.1899/03-054.1

Oksanen J, Blanchet FG, Kindt R, Legendre P, Minchin PR, O'hara RB, Simpson GL, Solymos P, Henry M, Stevens H, Wagner H (2011) Vegan: community ecology package. R package version 2.0-2. https://cran.r-project.org/web/packages/vegan/index.html

Pan Y, Stevenson RJ, Hill BH, Herlihy AT, Collins GB (1996) Using diatoms as indicators of ecological conditions in lotic systems: a regional assessment. J N Am Benthol Soc 15:481–495

Poff NL (1997) Landscape filters and species traits: towards mechanistic understanding and prediction in stream ecology. J N Am Benthol Soc 16:391–409. doi:10.2307/1468026

Porter SD, Mueller DK, Spahr NE, Munn MD, Dubrovsky NM (2008) Efficacy of algal metrics for assessing nutrient and organic enrichment in flowing waters. Freshw Biol 53:1036–1054

Potapova MG, Charles DF (2002) Benthic diatoms in USA rivers: distributions along spatial and environmental gradients. J Biogeogr 29:167–187

Potapova MG, Charles DF (2003) Distribution of benthic diatoms in us rivers in relation to conductivity and ionic composition. Freshw Biol 48:1311–1328. doi:10.1046/j.1365-2427.2003.01080.x

Potapova MG, Charles DF (2005) Choice of substrate in algae-based water-quality assessment. J N Am Benthol Soc 24:415–427. doi:10.1899/03-111.1

Potapova MG, Charles DF (2007) Diatom metrics for monitoring eutrophication in rivers of the United States. Ecol Indic 7:48–70. doi:10.1016/j.ecolind.2005.10.001

Power ME, Stewart AJ (1987) Disturbance and recovery of an algal assemblage following flooding in an Oklahoma stream. Am Midl Nat 117:333–345. doi:10.2307/2425975

Pyne MI, Rader RB, Christensen WF (2007) Predicting local biological characteristics in streams: a comparison of landscape classifications. Freshw Biol 52:1302–1321. doi:10.1111/j.1365-2427.2007.01767.x

R Development Core Team (2012) R: a language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria

Reavie ED, Jicha TM, Angradi TR, Bolgrien DW, Hill BH (2010) Algal assemblages for large river monitoring: comparison among biovolume, absolute and relative abundance metrics. Ecol Indic 10:167–177. doi:10.1016/j.ecolind.2009.04.009

Smucker NJ, Vis ML (2011) Diatom biomonitoring of streams: reliability of reference sites and the response of metrics to environmental variations across temporal scales. Ecol Indic 11:1647–1657. doi:10.1016/j.ecolind.2011.04.011

Snelder TH, Biggs BJF (2002) Multiscale river environment classification for water resources management. J Am Water Resour Assoc 38:1225–1239. doi:10.1111/j.1752-1688.2002.tb04344.x

Soininen J, Eloranta P (2004) Seasonal persistence and stability of diatom communities in rivers: are there habitat specific differences? Eur J Phycol 39:153–160. doi:10.1080/0967026042000201858

Stelzer RS, Lamberti GA (2001) Effects of N:P ratio and total nutrient concentration on stream periphyton community structure, biomass, and elemental composition. Limnol Oceanogr 46:356–367

Stevenson RJ (1997) Scale-dependent determinants and consequences of benthic algal heterogeneity. J N Am Benthol Soc 16:248–262. doi:10.2307/1468255

Stevenson RJ, Pan Y, Manoylov KM, Parker CA, Larsen DP, Herlihy AT (2008) Development of diatom indicators of ecological conditions for streams of the western us. J N Am Benthol Soc 27:1000–1016. doi:10.1899/08-040.1

Tabachnick BG, Fidell LS (2007) Using multivariate statistics. Pearson, Boston, MA

Taylor SL, Roberts SC, Walsh CJ, Hatt BE (2004) Catchment urbanisation and increased benthic algal biomass in streams: linking mechanisms to management. Freshw Biol 49:835–851. doi:10.1111/j.1365-2427.2004.01225.x

Tuchman M, Stevenson RJ (1980) Comparison of clay tile, sterilized rock, and natural substrate diatom communities in a small stream in southeastern Michigan, USA. Hydrobiologia 75:73–79. doi:10.1007/bf00006564

Vannote RL, Minshall GW, Cummins KW, Sedell JR, Cushing CE (1980) The river continuum concept. Can J Fish Aquat Sci 37:130–137

Wang YK, Stevenson RJ, Metzmeier L (2005) Development and evaluation of a diatom-based Index of Biotic Integrity for the Interior Plateau Ecoregion, USA. J N Am Benthol Soc 24:990–1008

Weilhoefer CL, Pan Y (2006) Diatom assemblages and their associations with environmental variables in Oregon coast range streams, USA. Hydrobiologia 561:207–219. doi:10.1007/s10750-005-1615-1

Winemiller KO, Flecker AS, Hoeinghaus DJ (2010) Patch dynamics and environmental heterogeneity in lotic ecosystems. J N Am Benthol Soc 29:84–99. doi:10.1899/08-048.1

Winter JG, Duthie HC (2000) Stream biomonitoring at an agricultural test site using benthic algae. Can J Bot 78:1319–1325

Zampella RA, Laidig KJ, Lowe RL (2007) Distribution of diatoms in relation to land use and ph in blackwater coastal plain streams. Environ Manage 39:369–384