

LOCAL AND WATERSHED INFLUENCES ON THE SPECIES COMPOSITION AND
FUNCTIONAL ORGANIZATION OF STREAM DIATOM COMMUNITIES IN THE
ACID-IMPACTED ADIRONDACK REGION OF NEW YORK

by

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Dear Amos,

You were with me the entire time I was writing my dissertation. No one knew more intimately what I was going through than you. I only wish I was given the opportunity to know you. How you brought me so much joy and so much sorrow. You will always be my first born.

Love,

Momma



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Abstract

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The University of Texas at Arlington, 2013

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For over 40 years, acid deposition has been recognized as a serious international environmental problem, but efforts to restore acidified streams and biota have had limited success. The need to better understand the effects of different sources of acidity on streams has become more pressing with the recent increases in surface water organic acids, or 'brownification', associated with climate change and decreased acid deposition. This dissertation is a large scale multi-seasonal investigation of stream diatom communities in the Adirondack region of New York, one of the most acid-impacted regions in the United States. My first objective is to explore the pathways of wetland control on stream organic matter concentrations, aluminum chemistry, and diatom taxonomic and functional composition. I demonstrate that streams with larger watershed wetlands have higher organic content, lower concentrations of acidic anions, and lower ratios of inorganic to organic aluminum, all beneficial for diatom biodiversity and guilds producing high biomass. For my second objective, I examine species turnover, or beta diversity, of the overall diatom community and individual functional guilds during periods of low acidity, high organic acidity, and high inorganic acidity in streams. My results indicate that while both sources of acidity reduce beta diversity, the reduction in

beta diversity is more severe when the source of acidity is inorganic. I also find significant differences in species turnover across guilds, with small-bodied, tolerant species exhibiting lower beta diversity than larger-bodied, less tolerant species. For my third objective, I examine the roles of deterministic versus stochastic processes in shaping stream diatom communities across periods varying in source and extent of acidity. I find that the role of stochastic processes is reduced during periods of high relative to low acidity. Overall, my results indicate that diatom communities in this region are more structured by environmental rather than spatial factors.

Table of Contents

Acknowledgements	iv
Abstract	v
List of Illustrations	ix
List of Tables	xi
Chapter 1 General Introduction.....	1
Chapter 2 Wetlands serve as natural sources for improvement of stream ecosystem health in regions affected by acid deposition.....	3
Introduction	3
Methods	7
Study Region, Sampling, and Laboratory Protocols.	7
Statistical Analyses and Acid Stream Selection.....	9
Results.....	12
Discussion	16
Chapter 3 Greater beta diversity in organically versus inorganically acidified streams in a region impacted by acid deposition	21
Introduction	21
Methods	26
Study Region, Sampling and Laboratory Protocols.	26
Statistical Analysis.....	27
Results.....	29
Discussion	35
Chapter 4 The importance of stochastic processes is diminished in acid stressed streams.....	40
Introduction	40

Methods	45
Sampling and Laboratory Protocols	45
Statistical Analysis	45
Results	47
Discussion	53
Chapter 5 Conclusion.....	59
Appendix A Guild classifications for all 171 diatom taxa found in Adirondack streams in this study.	61
Literature Cited.....	69
Biographical Information	81

List of Illustrations

Figure 2.1 Suggested pathways of wetland and organic matter control of diatom richness in acid streams through reductions of SO_4^{2-} and NO_3^- concentrations and $\text{Al}_{\text{im}}:\text{Al}_{\text{om}}$ ratio. 6

Figure 2.2 Map of the study area showing the 192 stream sites and mean water color over the sampling period. PtCo stands for Platinum-cobalt color scale. Green dots represent sites within the 0-50th percentile for stream color, the yellow dots represent sites within the 51st-75th percentile, and the red dots represent sites within the 76th-100th percentile..... 9

Figure 2.3 A structural equation model of wetland and water chemistry effects on diatom richness (RMSEA < 0.000001). 13

Figure 2.4 Redundancy analysis (RDA) of 471 stream samples showing the influence of stream chemistry and wetlands on diatom richness and relative abundance of ecological guilds..... 14

Figure 2.5 Redundancy analysis (RDA) of **a)** 513 stream samples showing the influence of season on stream chemistry and **b)** 514 stream samples showing the influence of season on diatom richness and relative abundance of ecological guilds. 15

Figure 3.1 Conceptual model showing my predictions for SAC during periods of low acidity, high inorganic acidity, and high organic acidity. I predict the steepest SAC slope during periods of low acidity, least steep slope when streams are exposed to high inorganic acidity, and a slope somewhere in between the two when streams are exposed to high organic acidity. 26

Figure 3.2 SAC for overall diatom communities across sampling periods. 30

Figure 3.3 Slopes of SAC for overall diatom communities across sampling periods. Error bars are 95% confidence intervals..... 31

Figure 3.4 Intercepts of SAC for overall diatom communities across sampling periods. Error bars are 95% confidence intervals.....	31
Figure 3.5 a) Slopes of SAC for diatom ecological guilds across sampling periods. b) Intercepts of SAC curves for diatom ecological guilds across sampling periods. The intercepts for the high profile guild overlapped completely in March 2004 and August 2004; therefore, the mean and error bars of March 2004 cannot be seen. Error bars are 95% confidence intervals in both graphs.	33
Figure 3.6 Mean chemistry plots across sampling periods. Error bars are ± 1 standard error. Significantly different means, as detected by Tukey's post hoc comparisons, are denoted by different letters. a) pH, b) ln-transformed color c) ln-transformed NO_3^-	34
Figure 4.1 Variance in diatom communities explained by pure environmental and pure spatial factors and their covariance across all four sampling periods. Residual = nonexplained variance.	50
Figure 4.2 The first two axes of the RDAs for environmental predictors and selected species for each sampling period. Variance explained by environmental predictors is indicated for each axis.	51

List of Tables

Table 2.1 Mean \pm 1 SE, minimum (Min), and maximum (Max) values of water chemistry parameters, proportion wetlands in the watershed, diatom richness, and proportion high profile, low profile, and motile guilds across all 514 stream samples. Aluminum measurements were missing from one sample in August 2004, therefore $n = 513$ for $Al_{im}:Al_{om}$ ratio. Wetland data were available for 156 streams. PtCo stands for platinum-cobalt color scale.	11
Table 4.1 Mantel and partial Mantel test results showing the correlation of species dissimilarity with environmental and geographic distance across sampling periods. Pure environment indicates the relationship between species dissimilarity and environmental distance after the effects of geographic distance are controlled for. Likewise, pure distance indicates the relationship between species dissimilarity and geographic distance after the effects of the environment are controlled for. The first number in each column indicates the Mantel r statistic and the number in parentheses indicates the p -value.	48
Table 4.2 List of species and acronyms.....	52
Table 4.3 RDA axis 1 and 2 scores for spatial predictors. Predictors that were not included in an RDA model are marked by NA.	53

Chapter 1

General Introduction

Acid deposition has been recognized as a serious environmental problem in Europe, the northeastern United States, and Canada since the late 1960s and early 1970s (Likens *et al.* 1972; Likens and Bormann, 1974). Atmospheric acids are released as NO_x and SO_4^{2-} from anthropogenic emissions and may be deposited as dry matter or as “acid rain”. Acid deposition can alter the structure and functioning of ecosystems through acidification of lakes and streams (Baker *et al.* 1990; Wigington *et al.* 1996), elimination of acid sensitive aquatic species (Schofield, 1976; Baker *et al.* 1996), and changes in leaching rates of nutrients from plants and watershed soils (Overrein, 1972; Lawrence, 2002). In addition, acid rain results in the mobilization of toxic aluminum from terrestrial soils as acidic runoff flows through the watershed. Aluminum is toxic to all aquatic organisms and is known to cause mortality in fishes and decreased species richness and changes in the community composition of macroinvertebrates and algae (Rosemond *et al.* 1992; Stokes, 1986; Smock and Gazzera, 1996; van Sickle *et al.* 1996).

My study region is located in the Adirondack region of New York, which is one of the most severely acidified regions due to acid deposition in the United States (NADP, 2006). In addition to acid deposition, Adirondack streams are acidified by natural, organic acidity originating from the soils and wetlands in watersheds (Lawrence *et al.* 2007). While organic matter contributes to further acidification of streams, it also mitigates some of the harmful effects of acidification by forming biologically unavailable complexes with aluminum (Gensemer and Playle, 1999), referred to as organic aluminum (Al_{om}). Conversely, inorganic aluminum (Al_{im}), including free aluminum ions and aluminum hydroxides, sulfates, and fluorides, remains highly toxic to all aquatic biota (Gensemer

and Playle, 1999). Streams rich in organic matter are often referred to as “brown-water” streams, due to the effect of organic acids on water color (Findlay and Sinsabaugh, 2003), while humic-poor streams are referred to as “clear-water” streams.

This study examines the taxonomic and functional structure of stream diatom communities in the acid-impacted Adirondack region of New York. Diatoms are the most speciose group in the periphyton community, which influences higher trophic levels and ecosystem processes (Mulholland *et al.* 1994; Steinman, 1996; Power and Cardinale, 2009). Furthermore, diatoms are sensitive to chemical conditions and are well established indicators of stream acidity and overall water quality (Van Dam *et al.* 1994; Planas 1996; Battarbee *et al.* 2010). Therefore, diatom communities will prove useful in monitoring progress in stream recovery with the recent reductions in SO_4^{2-} and NO_x emissions. In addition, the need for understanding the effects of different sources of acidity on streams and their biota has become more pressing with the recent increases in surface water organic acids, known as ‘brownification’, associated with climate change and decreased inorganic acid deposition (Evans *et al.* 2012).

In chapter 2 I explore the pathways of wetland control on stream organic matter, aluminum chemistry, and diatom species richness and functional composition. In chapter 3 I examine diatom species turnover, or beta diversity, across periods of low acidity, high organic acidity, and high inorganic acidity in streams. I further assess whether beta diversity or species turnover differs among diatom functional guilds and whether guild beta diversity varies in response to acidification and different sources of acidity. In chapter 4, I examine the relative importance of stochastic versus deterministic processes in shaping diatom communities in streams across periods differing in source and extent of acidity and determine the contribution of unique environmental variables and spatial factors to explained variance in species composition and distribution.

Chapter 2

Wetlands serve as natural sources for improvement of stream ecosystem health in regions affected by acid deposition

Introduction

Acidification of streams, lakes, and soils from acid deposition is one of the most serious environmental problems in the northeast US and northern Europe (Curtis et al. 2009; Omerod & Durance 2009) associated with loss of taxonomic and functional biodiversity, elevated mortality, and simplified food web structure (Rosemond et al. 1992; Havens 1993; Baldigo & Lawrence 2000; Kowalik et al. 2007). To address this issue, the US Congress passed amendments to the Clean Air Act in 1990 and the US EPA implemented the Acid Rain Program in 1995, which led to the reduction of SO_4^{2-} and NO_x emissions (Driscoll et al. 2001). Although decreases in SO_4^{2-} and NO_3^- concentrations and increases in pH have been observed as a result of these actions (Driscoll et al. 2007), lakes and streams continue to experience acidification and biological communities have not recovered and returned to their pre-acidification state (Arseneau et al. 2011). To this day, acidification remains widespread in the Adirondacks, NY, one of the most acid-impacted regions in the country (Nierzwicki-Bauer et al. 2010; Waller et al. 2012).

As streams and lakes continue to recover from acid deposition, surface water organic matter concentrations have increased in regions of North America and Europe (Driscoll et al. 2003; Evans et al. 2005). Initial explanations for this trend included climate-related mechanisms, i.e., higher organic matter decomposition rates due to warming (Freeman et al. 2001; Evans et al. 2002) and rising atmospheric CO_2 (Freeman et al. 2004). However, recent evidence suggests that changes in deposition chemistry over the past two decades, specifically declines in SO_4^{2-} and NO_x , are the main drivers of increased organic matter concentrations in freshwaters (Evans et al. 2006; Evans et al.

2012). Therefore, acid-impacted streams are at the forefront in the study of stream “brownification,” the term used to describe increasing concentrations of dissolved organic carbon (DOC), which change the water color. Concerns over brownification include decreased water clarity and degraded drinking water quality (Evans et al. 2006; Evans et al. 2012), but for many streams and lakes recovering from acid deposition, brownification is actually a return to their natural state (Driscoll et al. 2003; Evans et al. 2005).

While organic matter may be considered a pollutant from the human health perspective, there is recent evidence that organic matter in the form of DOC may benefit biodiversity in stream ecosystems, and consequently, primary production. In a study of hard water streams throughout the continental United States, Passy (2010) found that diatom richness was positively related to iron supply, DOC, proportion of wetlands, and soil organic matter in the watershed and proposed that wetlands increase diatom species richness through export of bioavailable DOC-bound iron. Since species richness controls biomass accumulation (Cardinale et al. 2005; Passy and Legendre, 2006), environmental factors with impact on richness will also influence algal production, which is a major contributor of organic carbon in streams and rivers.

In this investigation of stream producers, which is among the largest in acidified streams worldwide, we examine whether increased diatom species richness (DR) is associated with wetland-derived organic matter in severely to slightly acidified streams in the Adirondack region of New York and whether source of acidity has an influence on diatom ecological guilds. The study of how functional groups respond to environmental variables is valuable in ecology as such knowledge has more general application than specific observations for individual species (McGill et al. 2006). The functional composition of the freshwater biofilm is currently a subject of intensive research. Passy (2007a) proposed three diatom ecological guilds based on a trade-off between spatial

position in the biofilm and stress tolerance, namely low profile, high profile, and motile species. The low profile guild comprises short-statured understory species, tolerant to nutrient stress and disturbance, while the extended high profile guild and the motile guild occupy the overstory and include sensitive species (Passy & Larson 2011). Recently, the guilds were shown to respond to a variety of environmental stimuli and stressors, including nutrient enrichment, physical disturbance, acidification, organic pollution, and pesticide contamination (Berthon et al. 2011; Rimet & Bouchez 2011; Gottschalk & Kahlert; Stenger-Kovács et al. 2013). However, the influence of different sources of acidity has not been examined. Adirondack streams are acidified by both inorganic acid deposition and organic acids, originating from soils and wetlands (Lawrence et al. 2007), which offers an excellent opportunity to examine the influence of these two sources of acidity on diatom richness and guild composition.

I predict that wetland export of organic matter benefits producer communities in acidified streams via two pathways. The first pathway is through complexation and detoxification of aluminum (Gensemer & Playle, 1999), decreasing the ratio of toxic, inorganic monomeric aluminum (Al_{im}) to non-labile organic monomeric aluminum (Al_{om}). The second pathway is through stimulation of microbial assimilation and processing of sulfur and nitrogen. Wetlands and organically enriched soils can be very good sinks for both SO_4^{2-} and NO_3^- because their anoxic environments promote microbial anaerobic respiration, whereby SO_4^{2-} and NO_3^- are removed through sulfate reduction and denitrification, respectively (Whitmire & Hamilton, 2005). Both processes are important in the sediments of acid streams, where DOC is used as an electron donor for SO_4^{2-} and NO_3^- reduction in anaerobic respiration (Baesman et al. 2006; Sanchez-Andrea et al. 2012). In addition, high concentrations of DOC stimulate microbial activity and demand for nitrogen by heterotrophic bacteria (Bernhardt & Likens, 2002; Bernhardt et al. 2002),

which compete with nitrifying bacteria for NH_4^+ . As nitrifying bacteria are considered poor competitors for NH_4^+ relative to heterotrophic bacteria, increased assimilation of NH_4^+ in DOC-rich environments may also lead to decreased nitrification (Strauss & Lamberti 2000; Goodale et al. 2009). This reduction in SO_4^{2-} and NO_3^- , caused by the influence of wetlands and organic matter on microbial processing and/or assimilation, is expected to result in decreased mobilization of inorganic aluminum, a subsequent increase in stream algal biodiversity (Figure 2.1), and a shift toward sensitive guilds. In view of the general tolerance of the low profile guild, we predict it would increase in abundance in streams with high $\text{Al}_{\text{im}}:\text{Al}_{\text{om}}$ ratios and concentrations of inorganic acids. Likewise, we predict that high profile and motile guilds will have higher abundance in wetland-controlled streams with high organic matter content and low $\text{Al}_{\text{im}}:\text{Al}_{\text{om}}$ ratios.

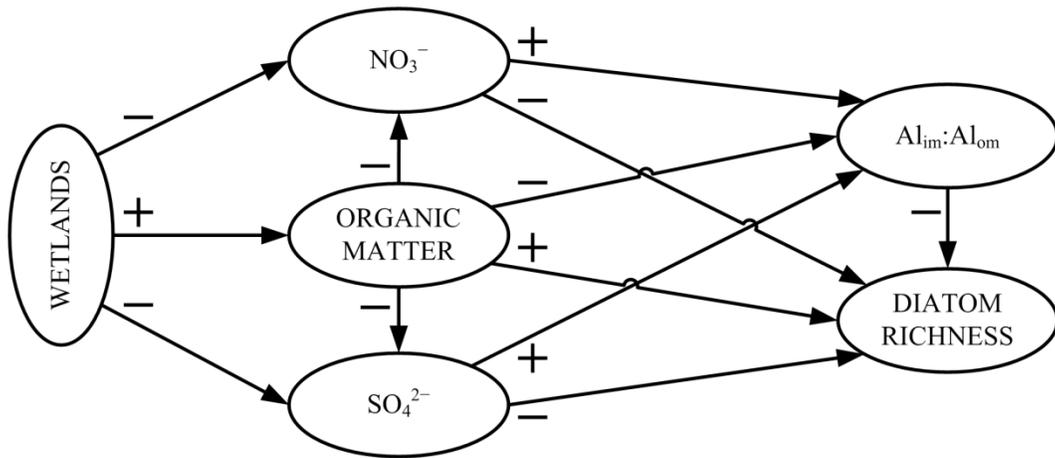


Figure 2.1 Suggested pathways of wetland and organic matter control of diatom richness in acid streams through reductions of SO_4^{2-} and NO_3^- concentrations and $\text{Al}_{\text{im}}:\text{Al}_{\text{om}}$ ratio.

In addition to spatial variability in chemistry due to differences in wetland distribution and soil composition, Adirondack streams also experience seasonal variability

in amounts and sources of acidity. Streams are least acidified during summer base flow when watershed runoff is lowest because of high evapotranspiration rates (Lawrence, 2002). Streams are most acidified following autumn precipitation and spring snowmelt when the runoff is enriched with SO_4^{2-} and NO_3^- from the soil and snowpack, respectively (Lawrence, 2002). Organic acidity is highest in autumn due to leaf loss from trees, and this period coincides with annual lows in stream NO_3^- concentrations (Lawrence et al. 2008a) caused by increased nitrogen assimilation by heterotrophic bacteria and subsequent decreased nitrification by nitrifying bacteria (Bernhardt & Likens, 2002; Goodale et al. 2009). Inorganic acidity is the highest during spring snowmelt due to accumulation of acid anions in the snowpack and a potential rebound in stream nitrification rates (Goodale et al. 2009). This analysis includes samples collected from Adirondack streams during summer base flow, autumn storms, and spring snowmelt, allowing diatom biodiversity and guild composition to be examined along an acidity gradient and across types of acidification. The goals of this paper are to explore the effects of organic matter on producer biodiversity and guild composition and to demonstrate the potential use of wetlands as natural sources for improving stream ecosystem health in acid-impacted regions. Therefore, I 1) examined the pathways of organic matter and wetland control of aluminum chemistry, diatom richness, and guild composition and 2) assessed the seasonal variability in the strength of these pathways.

Methods

Study Region, Sampling, and Laboratory Protocols.

The study region is located in the Black and Oswegatchie River basins that lie within the western portion of the Adirondack Park in upstate New York. Streams in this region vary in organic content, ranging from humic-poor “clear-water” to humic-rich “brown-water” (Figure 2.2). Diatom and water chemistry samples ($n = 637$ total) were

collected from 192 streams, sampled 1 to 4 times over four sampling periods (6 were sampled once, 15 were sampled twice, 83 were sampled 3 times, and 88 were sampled on all 4 dates). Sampling occurred twice during summer base flow (August 25-28, 2003 and August 16-18, 2004), once during fall storms (October 27-29, 2003), and once during spring snowmelt (March 29-31, 2004). Wetlands cover data were available for 172 of the streams, or for 571 of the 637 diatom and chemistry samples. Water samples were analyzed for pH, water color, and concentrations of acidic anions, inorganic monomeric Al, and organic monomeric Al (Lawrence *et al.* 1995). Diatom subsamples were taken from all available substrates in each locality, including rocks, sand, and macrophytes and preserved in 4% formaldehyde. In the lab, all subsamples from each stream were combined, shaken vigorously, and processed via acid digestion or bleaching (Passy, 2006). The clean samples were mounted onto glass slides with Naphrax[®]. From each glass slide, 300 diatom frustules were counted and identified to species level using a 100 × 1.35 numerical aperture oil immersion objective.

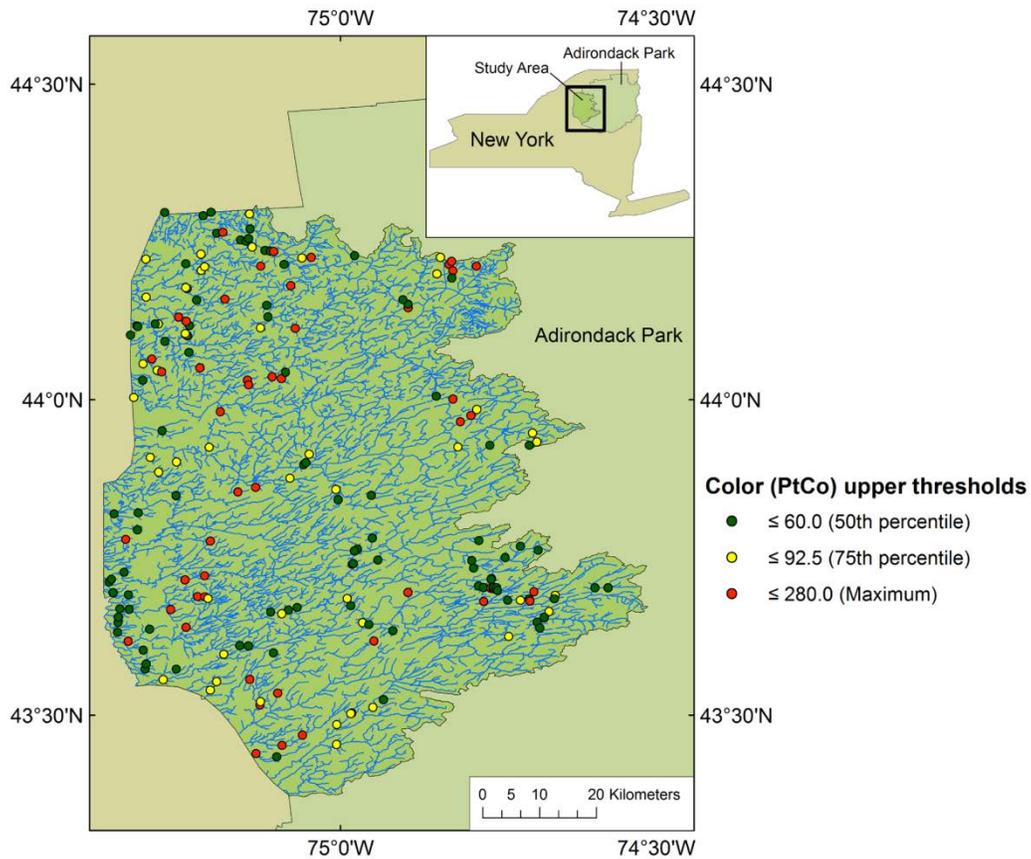


Figure 2.2 Map of the study area showing the 192 stream sites and mean water color over the sampling period. PtCo stands for Platinum-cobalt color scale. Green dots represent sites within the 0-50th percentile for stream color, the yellow dots represent sites within the 51st-75th percentile, and the red dots represent sites within the 76th-100th percentile.

Statistical Analyses and Acid Stream Selection.

All chemical variables except pH were ln-transformed and the proportion of wetlands was arcsine square-root transformed to improve normality. Initial examination indicated significant non-linear relationships between pH and water color. In order to assess the unique effect of organic acidity on diatom richness, I used a regression tree

analysis to determine the region of the pH gradient, where pH was not correlated with color. This procedure estimated a threshold pH value of 6.89 (Proportional reduction in error = 0.11), separating the pH gradient into regions where pH and color were not significantly correlated (at $\text{pH} \leq 6.89$) vs. negatively correlated (at $\text{pH} > 6.89$). There were 514 stream samples with $\text{pH} \leq 6.89$, of which 472 samples from 156 streams had available wetland cover data (Table 2.1).

Table 2.1 Mean \pm 1 SE, minimum (Min), and maximum (Max) values of water chemistry parameters, proportion wetlands in the watershed, diatom richness, and proportion high profile, low profile, and motile guilds across all 514 stream samples. Aluminum measurements were missing from one sample in August 2004, therefore $n = 513$ for $Al_{im}:Al_{om}$ ratio. Wetland data were available for 156 streams. PtCo stands for platinum-cobalt color scale.

Variable	Mean	Min	Max
pH	5.6 \pm 0.03	4.2	6.9
Color (PtCo)	78.1 \pm 2.9	5	440
SO ₄ ²⁻ (μ mol·L ⁻¹)	43.9 \pm 0.54	2.7	79.9
NO ₃ ⁻ (μ mol·L ⁻¹)	16.0 \pm 0.94	0.2	123.2
$Al_{im}:Al_{om}$	0.65 \pm 0.05	0	10.5
Wetlands	0.10 \pm 0.01	0	0.36
Diatom richness	24.0 \pm 0.44	3	60
High profile guild	0.77 \pm 0.01	0.01	1
Low profile guild	0.19 \pm 0.01	0	0.99
Motile guild	0.04 \pm 0.002	0	0.32

Structural equation modeling (SEM) was used to test the pathways of wetland and organic matter control of aluminum chemistry and DR, proposed in Figure 2.1. Non-significant pathways were eliminated in a stepwise manner in order to achieve the most

parsimonious model. The root mean square error of approximation (RMSEA) was used to evaluate the goodness of fit.

Diatom species were assigned to one of three ecological guilds, i.e. low profile, high profile, and motile guilds, based on examination of growth forms in unprocessed samples and classifications of Passy (2007a) and Rimet and Bouchez (2012). The low profile guild comprises species of short stature that make up the understory of the biofilm, such as solitary prostrate, adnate, erect or unattached cells and slow moving species. The high profile guild encompasses species of tall stature that reach into the upper layers of the biofilm such as erect, filamentous, branched, chain-forming, tube-forming, and stalked species. Fast-moving species make up the motile guild (Appendix A). The proportion of species within each guild (relative abundance) was calculated for each sample and arcsine square-root transformed to improve normality.

Redundancy analysis (RDA) in CANOCO 4.5 was used to examine the influence of stream chemistry and wetlands on diatom richness and guild relative abundance and the influence of season on stream chemistry, diatom richness, and guild relative abundance. Variance decomposition was performed with a partial RDA to determine the fractions of biotic variance explained by the environment, season, and their covariance.

Results

The proportion of wetlands in the watershed (referred to as wetlands henceforth) significantly influenced stream color and NO_3^- concentrations, as shown by the SEM (Figure 2.3). Although the correlation between wetlands and NO_3^- concentration was non-significant ($p = 0.06$), this correlation in the SEM was positive due to collinearity; all other relationships in the model were consistent with the respective pair-wise correlations. The pair-wise correlations also indicated that wetlands influenced SO_4^{2-}

(Pearson $r = -0.16$, $p < 0.001$), but in the model, the wetland effect on sulfate was subsumed by color. Both SO_4^{2-} and NO_3^- levels significantly decreased with color, and color and NO_3^- significantly influenced the $\text{Al}_{\text{im}}:\text{Al}_{\text{om}}$ ratio, as predicted in Figure 2.1. The model indicated that DR increased with color but decreased with NO_3^- and $\text{Al}_{\text{im}}:\text{Al}_{\text{om}}$ ratios. While DR also decreased with SO_4^{2-} (Pearson $r = -0.11$, $p = 0.01$), this relationship was not significant in the model because of the overriding influence of NO_3^- and $\text{Al}_{\text{im}}:\text{Al}_{\text{om}}$ ratio on DR.

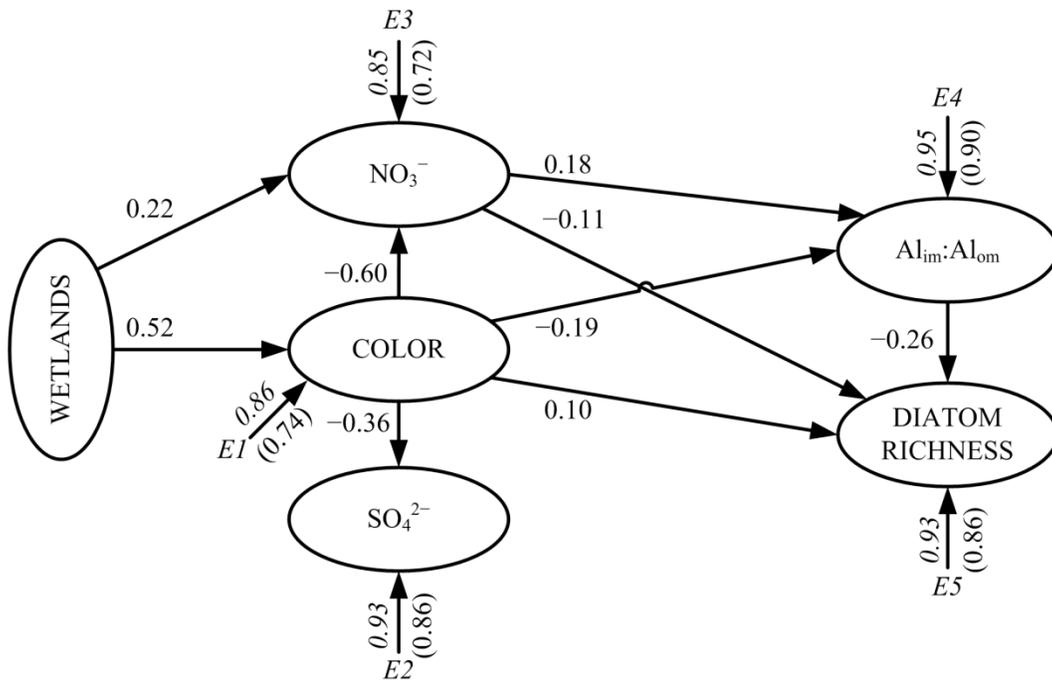


Figure 2.3 A structural equation model of wetland and water chemistry effects on diatom richness (RMSEA < 0.000001).

Redundancy analysis and partial RDA were employed to examine the sources of variability in diatom richness and guild composition (Figure 2.4). The first two RDA axes (RDA1 and RDA2) showed that the environment explained 27.5% of the variance in diatom richness and proportion of the three diatom guilds. Inorganically acidified streams

with high $Al_{im} : Al_{om}$ ratios and impoverished diatom flora, abundant with tolerant low profile species, had high RDA1 scores. Organically acidified streams with large watershed wetlands as well as lower acidity streams both with low RDA1 scores were comparatively species-rich with greater proportions of the sensitive high profile and motile guilds. The second axis revealed that organically acidified streams, with low RDA2 scores, had greater proportion of high profile species, while lower acidity streams, with high RDA2 scores, had the highest diatom richness and proportion of motile species. Therefore, both type and amount of acidity were important sources of biotic variability in this large-scale study.

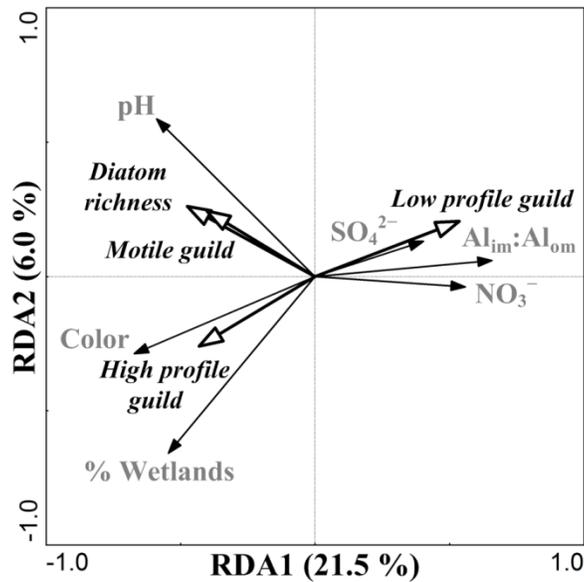


Figure 2.4 Redundancy analysis (RDA) of 471 stream samples showing the influence of stream chemistry and wetlands on diatom richness and relative abundance of ecological guilds.

When sampling months were used as predictors, RDA explained 32.2% of the variance in stream chemistry (Figure 2.5a). The first axis separated the sources of acidity, i.e. streams with high color (negative RDA1 scores) versus streams with high

NO_3^- concentrations (positive RDA1 scores). Color was the highest in October 2003 and August 2004, while NO_3^- concentrations were the greatest in March 2004. The second axis separated streams with high pH, associated with both August sampling periods.

Season explained only 6.4% of the variance in DR and diatom guilds (Figure 2.5b). The first RDA axis segregated the high profile guild with peaks during both August sampling periods from the low profile guild, reaching maximum in March 2004. The second axis was positively correlated with DR and the motile guild, which were the highest in October 2003 and August 2004. Partial RDA indicated that pure environment, pure season, and their covariance explained, respectively, 24.8%, 3.3%, and 2.9 % of the variance in diatom richness and guild composition. All RDA axes were tested with 999 Monte Carlo permutations and were significant ($P = 0.001$).

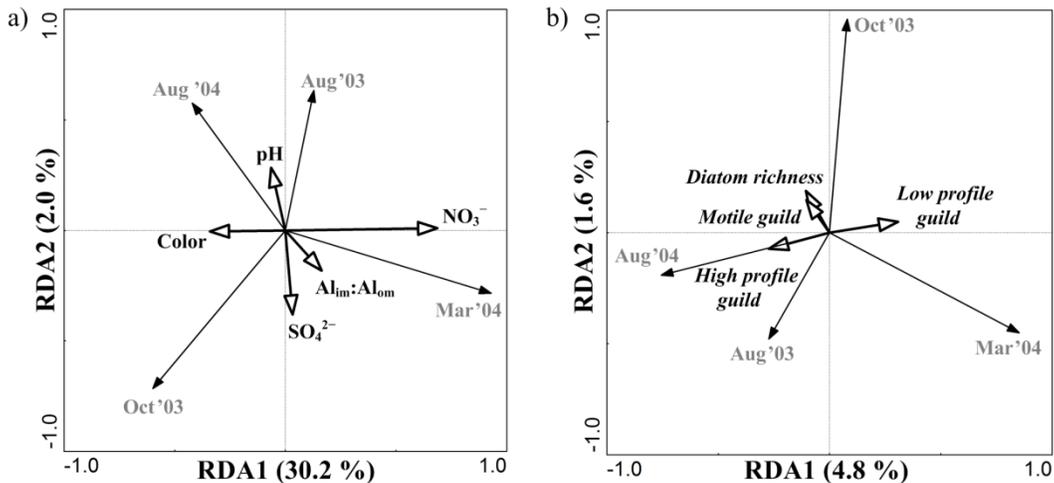


Figure 2.5 Redundancy analysis (RDA) of **a)** 513 stream samples showing the influence of season on stream chemistry and **b)** 514 stream samples showing the influence of season on diatom richness and relative abundance of ecological guilds.

Discussion

The present research makes three important discoveries with far-reaching implications for biodiversity preservation and stream monitoring and restoration. First, at the regional scale, the type of acidity controls diatom biodiversity in acid stressed streams. Earlier studies reported that organic vs. inorganic acidity caused diverging patterns of diatom richness and composition in two Adirondack streams (Passy, 2006; Passy *et al.* 2006). However, the positive relationship between diatom richness and organic acidity in this large scale investigation reveals that there is a general pattern of elevated organic matter inputs leading to greater biodiversity across acid streams. It is also noteworthy that a higher number of species can tolerate a given pH at higher organic matter concentrations, i.e. diatom richness was the highest when organic acidity was the highest in October 2003 and August 2004, despite significantly lower pH in October compared to August. Organic matter forms non-labile complexes with aluminum (Gensemer & Playle, 1999) and can moderate the negative impacts of aluminum and lower the pH threshold for survival of fish (Laudon *et al.* 2005; Serrano *et al.* 2008). As other studies have demonstrated higher biodiversity in naturally versus anthropogenically acidified streams for macroinvertebrates (Collier *et al.* 1990; Dangles *et al.* 2004, Petrin *et al.* 2008a; Petrin *et al.* 2008b) and fish (Collier *et al.* 1990; Greig *et al.* 2010), the influence of type of acidity on biodiversity appears to be important across all major trophic levels in stream ecosystems.

Second, we reveal that the link of wetlands with stream organic matter and diatom biodiversity, suggested for hard streams (Passy, 2010), also exists in acid streams. Therefore, the pathway of watershed control of local stream diversity through wetland export of organic matter is universal in running waters. The mechanism of increased diatom richness through export of DOC-bound Fe from wetlands observed in

Passy (2010), may operate in our streams as well, given the direct positive effect of color on diatom richness in our path model (Figure 2.3) and the strong correlation between color and Fe concentrations in Adirondack lakes (Maranger *et al.* 2006). However, our investigation further demonstrates that wetland-derived organic matter mitigates the impacts of acid deposition through complexation with aluminum and removal of acid anions. Our path analysis indicates that organic matter from wetlands decreased both the $Al_{im}:Al_{om}$ ratio and NO_3^- concentrations, resulting in higher diatom richness. Our finding that humic streams, with a greater proportion of wetlands in the watershed, have lower $Al_{im}:Al_{om}$ ratios, is consistent with the observation of lower Al:DOC ratios in wetland watersheds (Cory *et al.* 2006). Thus, in acid sensitive regions, such as the Adirondacks, wetland drainages may provide less stressful and more suitable habitats for species typically absent from anthropogenically acidified streams.

Acidification and type of acidity displayed distinct seasonal patterns. Although streams had similar pH in October 2003 and March 2004, the sources of acidity were very different across these two months. Consistent with other studies, streams contained the highest organic acidity during leaf fall in October (Lawrence *et al.* 2008a) when NO_3^- concentrations were the lowest, most likely due to increased activity of heterotrophic bacteria, as already discussed (Bernhardt & Likens, 2002; Goodale *et al.* 2009). The highest levels of inorganic acidity in the form of NO_3^- were observed in March together with the lowest values of color. The high NO_3^- concentrations in March could be due to accumulation in the snowpack, accumulation in the forest floor as a result of reduced uptake during the dormant season, or a rebound in stream nitrification rates as organic substrate becomes less available to heterotrophic bacteria (Goodale *et al.* 2009).

A decrease in organic matter during snowmelt has been observed in other streams that, similarly to many streams in this investigation, are controlled by wetlands in

the watersheds (Agren *et al.* 2008; Laudon *et al.* 2011). If wetlands comprise > 10% of the watershed, stream organic matter is predominantly of wetland origin during base flow (Agren *et al.* 2008, Laudon *et al.* 2011). Elevated flow paths have a flushing effect on wetlands, and organic matter concentrations in associated streams decline due to dilution (Gergel *et al.* 1999, Laudon *et al.* 2004, Eimers *et al.* 2008). In addition, the surface of wetlands may be frozen during snowmelt, so that melt water runoff has little contact with wetland organic matter (Laudon *et al.* 2004, Laudon *et al.* 2007). Wetlands compose > 14% of the land cover in the Adirondacks (Roy *et al.* 1996), and approximately 40% of the streams in our study belong to watersheds with $\geq 10\%$ wetland coverage. Therefore, concentrations of organic matter in many streams in this study should have patterns similar to streams in other wetland dominated watersheds during snowmelt.

Diatom ecological guilds are now broadly recognized as a powerful biomonitoring tool (Berthon *et al.* 2011; Rimet & Bouchez 2011; Stenger-Kovács *et al.* 2013); however, we have no knowledge of their response to brownification. The third finding of this paper is that acidification and type of acidity influence producer functional structure in addition to diatom richness, whereby the sensitive motile guild increases in abundance with pH and color, the sensitive high profile guild is stimulated by organic acidity and wetland cover, while the tolerant low profile guild proliferates in the most unfavorable conditions of high inorganic acidity and high $Al_{im}:Al_{om}$ ratios. This suggests that diatom guilds may be good indicators of source of acidity, providing a simpler approach to stream monitoring that would not require species level identification.

Seasonal patterns in abundance of low profile and motile species reflected guild adaption to chemistry fluctuations. The low profile guild was most abundant in March 2004 when inorganic acidity and $Al_{im}:Al_{om}$ ratio were the highest. The motile guild was least abundant in March when streams had low pH and the lowest organic matter. The

high profile guild was most abundant during both August sampling periods and since it had no correlation with pH, its August peak can be attributed to lower flow disturbance during the summer base flow months. The high profile guild is the most sensitive to physical disturbance (Passy 2007a) and its lower abundance in October 2003, despite a positive correlation with organic acidity, may be due to the physical stress of high flow during fall storms.

Shorter statured species reached greater abundance at higher inorganic acidity, similarly to the findings of another study, reporting a transition toward smaller sized diatoms in a lake that became more acidified over time due to acid deposition (Cattaneo et al. 1998). However, our results further demonstrate that the nature of acidification controls not only species' cell size but also the functional composition and, with this, the spatial complexity of the biofilm, which in turn determines species coexistence and primary production (Passy & Legendre 2006, Passy 2008). Thus, dominance of understory forms in inorganically acidified freshwaters translates into less complex periphyton communities with shorter internal resource gradients and fewer opportunities for coexistence, resulting in low biodiversity and production. Conversely, preponderance of overstory high profile and motile species under organic acidification is associated with greater biofilm complexity, richness, and biomass.

There has been concern over the effects of brownification as streams recover from acid deposition. Our results suggest that as streams transition from inorganically acidified clear-water to organically acidified brown-water, biofilm biodiversity will likely increase. Furthermore, the abundance of sensitive, high profile and motile diatoms will also increase, resulting in more complex biofilm communities and higher primary production. Therefore, brownification may be beneficial from the ecosystem perspective. |

further propose that wetlands, being the source of organic matter in humic streams, should be incorporated in restoration of streams impacted by acid deposition.

Currently, direct liming of streams is used to reduce acidity and restore acidified streams, often for the specific purpose of increasing fish populations (Menendez *et al.* 1996). While in-stream liming is shown to significantly elevate pH and lower aluminum concentrations, its long-term success in increasing biodiversity and persistence of acid sensitive species is very limited (Rundle *et al.* 1995; Bradley & Ormerod 2002). Furthermore, liming may not be appropriate in streams acidified naturally by organic acids (Bishop *et al.* 2001). Although generally less diverse, naturally acidic streams can be as functional as circumneutral streams and possess unique taxonomic assemblages (Petrin *et al.* 2007a). Thus, liming humic streams is likely to disturb their natural community structure and functioning (Mickie *et al.* 2006).

As demonstrated here, wetlands promote stream biodiversity in acid-sensitive regions, such as the Adirondacks, where many native species are adapted to naturally acidic conditions (Petrin *et al.* 2007b; Petrin *et al.* 2008b) and would be harmed by stream liming. Therefore, further research is needed to develop the best combination of approaches for reversing chemical acidification in ways that will restore the diversity of species sensitive to acid deposition, while protecting species adapted to natural acidity. This research needs to recognize the importance of wetlands for stream ecosystem health in acid-impacted regions and consider their direct use in remediation of stream acidification, e.g. through stream rechanneling or wetland construction in appropriate hydrologic settings.

Chapter 3

Greater beta diversity in organically versus inorganically acidified streams in a region impacted by acid deposition

Introduction

The species-area relationship (SAR), or the increase in species richness with sampled area, is one of the oldest, most studied patterns in biogeography (Arrhenius, 1921; Connor and McCoy, 1979; He and Legendre, 2002; Drakare *et al.* 2006). The SAR slope is an indicator of spatial turnover in species composition, or beta diversity, and SAR curves have been used to assess how species turnover varies across spatial gradients (Drakare *et al.* 2006; Qian *et al.* 2007; Wang *et al.* 2009; Qiao *et al.* 2012), taxonomic groups (Azovsky, 2002; Horner-Devine *et al.* 2004; Drakare *et al.* 2006), and habitats (Kallimanis *et al.* 2008; Ranjard *et al.* 2013). Species accumulation curves (SAC), a counterpart of SAR, have been used to evaluate species turnover across sites or samples when area is not explicitly measured (Dahl *et al.* 2009; Azovsky *et al.* 2012).

A variety of hypotheses have been proposed to explain why species richness increases with area and by extension, what factors influence the slope of species accumulation curves. Some of the main hypotheses are derived from the equilibrium theory of island biogeography, which predicts that species richness increases with area, as larger habitats are expected to support more species (MacArthur and Wilson, 1967). In addition, this theory predicts that species richness will decrease with isolation because fewer species are able to disperse to remote habitats. Based on the premise that islands have steeper SAR slopes than mainlands (Rosenzweig, 1995), factors such as habitat isolation and dispersal limitation are expected to increase SAR slope. Alternatively, SAR may be determined by niche-based factors, as species traits and environmental

tolerances may shape their distributions (Chase and Leibold, 2003). More specifically, anthropogenic disturbance has been shown to have a homogenizing effect on species composition, reducing the steepness of SAR slope (Passy and Blanchet, 2007). This finding is consistent with the prediction that harsh environmental conditions serve as environmental filters that select only for the most tolerant species, causing spatially separated communities to become more similar to each other (Chase, 2007) .

Examining SAR and SAC in relation to species traits may provide further insight into how different factors influence species distributions (Franzén *et al.* 2012). More specifically, species traits are related to both the ability to disperse to isolated habitats and persist under different environmental conditions. Therefore, species distributions should be determined by both dispersal limitations and niched-based factors. Studies that have examined SAR in relation to species traits found that the steepness of the SAR slope increases with body size (Azovsky, 2002; Drakare *et al.* 2006), niche-specialization (Steffan-Dewenter and Tschardt, 2000; Krauss *et al.* 2003; Cagnolo *et al.* 2009; Franzén *et al.* 2012), and low dispersal ability (Öckinger *et al.* 2010). Traits-based approaches have gained popularity in ecology due to their utility in bio-monitoring (Berthon *et al.* 2011; Rimet and Bouchez, 2011; Stenger-Kovács *et al.* 2013) and ability to detect general patterns that lead to higher predictability about communities than more specific, nomenclature approaches (McGill *et al.* 2006). Therefore, studying SAR and SAC across guilds may help develop general principles on how species traits influence species distributions.

Passy (2007a) proposed three ecological guilds, namely low profile, high profile, and motile species, which exhibit trade-offs between spatial position in the biofilm and stress tolerance. The low profile guilds consists of species of short stature that make up the understory of the biofilm and are shown to be tolerant of environmental stressors

such as nutrient limitation and physical disturbance (Passy, 2007a; Passy and Larson, 2011). The high profile and motile guilds comprise the overstory of the biofilm and are considered sensitive to nutrient limitation (Passy and Larson, 2011), with high profile species being the most susceptible to physical disturbance (Passy, 2007a; Stenger-Kovács *et al.* 2013). Several studies have examined the response of guild abundance to different stressors and stimuli, including nutrient enrichment, physical disturbance, acidification, organic pollution, and pesticide contamination (Berthon *et al.* 2011; Rimet and Bouchez, 2011; Gottschalk and Kahlert, 2012; Stenger-Kovács *et al.* 2013), but no studies have examined the response of within guild diversity and turnover to different environmental conditions.

The Adirondack region of New York is one of the most severely acidified regions due to acid deposition in the United States (NADP, 2006). In addition to acid deposition, Adirondack streams are acidified by natural, organic acidity originating from soil organic matter and wetlands (Lawrence *et al.* 2007). Organically-rich streams are often referred to as “brown-water” streams due to the influence of organic acids on water color (Findlay and Sinsabaugh, 2003), which is a surrogate measure of organic matter. Pulses of acidity in the Adirondacks are mainly driven by organic acids and the inorganic anion NO_3^- (Wigington *et al.* 1996; Lawrence *et al.* 2008a), and streams in the Adirondacks exhibit seasonal variability in both levels and sources of acidity. Streams are least acidified and have the highest pH during summer base flow when watershed runoff is lowest due to high rates of evapotranspiration (Lawrence, 2002). During this time many streams are sustained by groundwater, which is well neutralized compared to soil runoff (Lawrence, 2002). Streams are most acidified following high flow rain events and snowmelt when runoff is enriched with acid anions from the soil or snowpack, respectively (Lawrence, 2002). Organic acidity is highest in autumn due to leaf loss from trees, and inorganic

acidity is highest during spring snowmelt when streams reach annual peaks in NO_3^- concentrations (Lawrence *et al.* 2008a). Acidic runoff due to both inorganic and organic acids mobilizes toxic aluminum into streams (Lawrence *et al.* 2007), but organic matter mitigates this toxicity by forming biologically unavailable complexes with the metal (Gensemer and Playle, 1999). Natural, organically acidified streams have been shown to have higher alpha diversity than anthropogenically acidified streams (Collier *et al.* 1990; Dangles *et al.* 2004; Passy *et al.* 2006; Petrin *et al.* 2008a; Petrin *et al.* 2008b; Greig *et al.* 2010), however; it is unknown how these two sources of acidity affect species turnover across streams. The dynamic nature of Adirondack stream chemistry provides an excellent opportunity to examine this question of whether acidification and source of acidity affect beta diversity.

In this chapter, I first test whether stressful environmental conditions reduce species turnover, or beta diversity, across streams. I do this by examining the response of SAC across streams during periods of low acidity in August 2003 and 2004, high organic acidity in October 2003, and high inorganic acidity in March 2004. I predict that acidification in general will decrease species turnover across streams as acidity is shown to reduce diversity regardless of the source (Petrin *et al.* 2007; Petrin *et al.* 2008a; Petrin *et al.* 2008b). However, as organic acidity is demonstrated to be less stressful to biota than inorganic acidity (Collier *et al.* 1990; Dangles *et al.* 2004; Passy *et al.* 2006; Petrin *et al.* 2008a; Petrin *et al.* 2008b; Greig *et al.* 2010), I predict that diatom communities will be more homogenized, or similar to one another, when the source of acidity is inorganic versus organic. I propose a conceptual model showing my predictions for SAC across streams during periods of low acidity, high inorganic acidity, and high organic acidity (Figure 3.1). Secondly, I examine SAC within diatom ecological guilds (Passy, 2007a). I predict that, of the three ecological guilds (low profile, high profile, and

motile), low profile species will have the least steep SAC slope. I make this prediction for two reasons: 1) species within this guild are shown to be tolerant to stressful conditions (Passy and Larson, 2011), which may allow them to persist in a variety of habitats and 2) this guild typically consists of species with small body size, which is associated with greater distribution in passive dispersers such as diatoms (Passy, 2012). Conversely, I predict that the larger-bodied, more sensitive high profile and motile guilds will exhibit a much steeper SAC slope compared to low profile species, due to lower dispersal ability and more narrow tolerance of environmental conditions. I predict that SAC of diatom ecological guilds will follow the same general response to acidification and source of acidity as curves of the overall species composition, i.e. be less steep in conditions of high inorganic compared to high organic acidity and the most steep during conditions of low acidity.

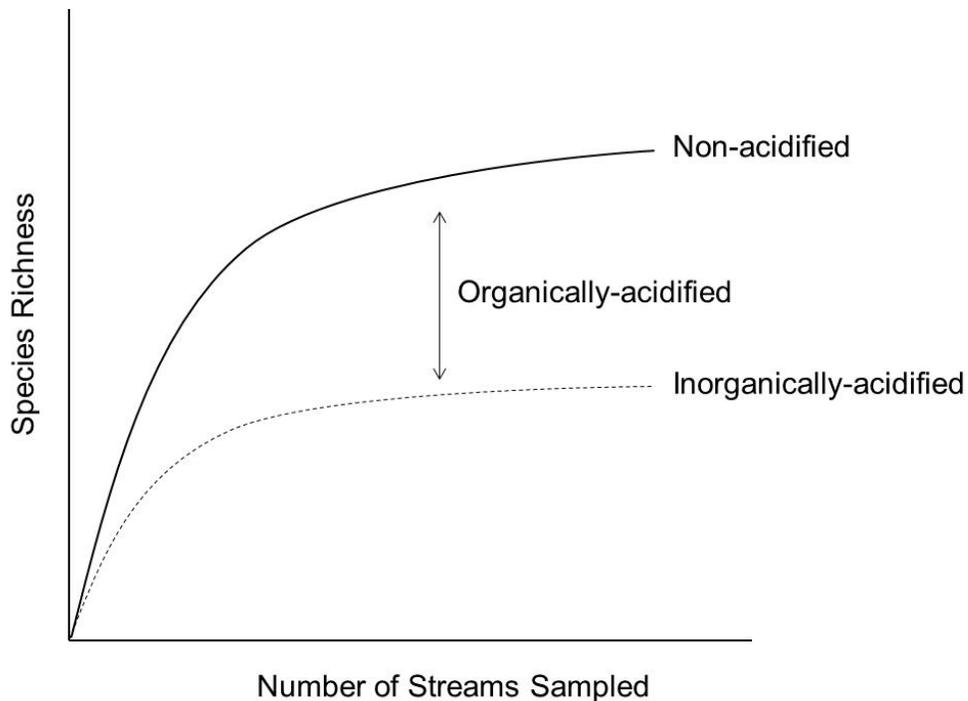


Figure 3.1 Conceptual model showing my predictions for SAC during periods of low acidity, high inorganic acidity, and high organic acidity. I predict the steepest SAC slope during periods of low acidity, least steep slope when streams are exposed to high inorganic acidity, and a slope somewhere in between the two when streams are exposed to high organic acidity.

Methods

Study Region, Sampling and Laboratory Protocols.

This analysis includes 88 streams sampled for water chemistry and diatoms over all four sampling periods (August 2003, October 2003, March 2004, and August 2004) during the Western Adirondack Stream Survey (Lawrence *et al.* 2008b). The geographic span of the study area was 4,585 km². Most of the study streams were first order, headwater streams, and none of the streams were nested (i.e., flowing into one another).

Water samples were analyzed for pH, water color, and concentrations of acidic anions, inorganic monomeric Al, and organic monomeric Al (Lawrence *et al.* 1995). Diatom subsamples were taken from all available substrates in each locality, including rocks, sand, and macrophytes and preserved in 4% formaldehyde. In the lab, all subsamples from each stream were combined, shaken vigorously, and processed via acid digestion or bleaching (Passy, 2006). The clean samples were mounted onto glass slides with Naphrax[®]. From each glass slide, 300 diatom frustules were counted and identified to species level using a 100 × 1.35 numerical aperture oil immersion objective.

Statistical Analysis

SAC for each sampling period were produced in PRIMER 6 as the increase in species richness with the number of streams sampled. The curves were calculated with 999 permutations so that each point on the curve showed an average number of species found in a given number of streams. In cases where 999 permutations were not possible, all permutations were averaged. Within each sampling period, SACs were produced for the overall diatom community and for species within each diatom ecological guild (low profile, high profile, and motile). Diatom species were assigned to ecological guilds based on examination of growth forms in unprocessed samples and the criteria of Passy (2007a) and Rimet and Bouchez (2012). The low profile guild consists of species of short stature that make up the understory of the biofilm, such as solitary prostrate, adnate, erect or unattached cells and slow moving species. The high profile guild comprises species of tall stature that reach into the upper layers of the biofilm such as erect, filamentous, branched, chain-forming, tube-forming, and stalked species. The motile guild is composed of fast-moving species (Appendix A).

All SAC fits were generated by a semi-log regression: $y = b_0 + b_1 \ln x$, where x is the number of sampled streams, y is the average species richness, and b_0 and b_1 are

intercept and slope, respectively. The semi-log function was shown to be a reasonably good fit across all curves for the overall diatom community ($r^2 \geq 0.98$) and for curves within guilds (r-squared values ≥ 0.87). The slope of the curves was used as an estimate of beta diversity or species turnover. As the intercept of the curves represents the average number of species found in a single stream, the intercept was used as an estimate of alpha diversity (Scheiner, 2003). Gamma diversity was estimated as the total number of species found across all 88 streams within a sampling period.

Model II regression was used to test for significant differences in slope and intercept among SACs. Differences in SACs across sampling periods for the overall diatom community were tested with the following model:

$$y_{ij} = b_{01} + b_{02} + b_{03} + b_{04} + b_{11}\ln x_{i1} + b_{12}\ln x_{i2} + b_{13}\ln x_{i3} + b_{14}\ln x_{i4} + \epsilon_{ij}$$

where y_{ij} = average species richness in $i = 1, 2, \dots, 88$ streams during sampling periods $j = (1, 2, 3, 4) = (\text{August 2003, October 2003, March 2004, and August 2004})$, $x_{i1} - x_{i4}$ = the number of streams within the corresponding sampling period, the slopes are represented by $b_{11} - b_{14}$, $b_{01} - b_{04}$ are the intercepts, and ϵ_{ij} is the error term. Differences in SAC across sampling periods within diatom ecological guilds were tested by this model:

$$y_{ijk} = b_{011} + b_{012} + b_{013} + \dots + b_{041} + b_{042} + b_{043} + b_{111}\ln x_{i11} + b_{112}\ln x_{i12} + b_{113}\ln x_{i13} + \dots + b_{141}\ln x_{i41} + b_{142}\ln x_{i42} + b_{143}\ln x_{i43} + \epsilon_{ijk}$$

where $i = 1, 2, \dots, 88$ streams sampled during periods $j = (1, 2, 3, 4)$ and $k = (1, 2, 3) = (\text{low profile, high profile, and motile guilds})$. Slopes and intercepts were considered significantly different if their 95% confidence intervals did not overlap.

SAC slope estimates of beta diversity for the overall diatom community were validated by calculating Sørensen dissimilarity across each pair of streams within each sampling period. Repeated measures analysis of variance (ANOVA), followed by Tukey's post-hoc comparisons, was used to test for differences in mean dissimilarity across

sampling periods. The same procedure was also used to examine differences in key chemical variables across sampling periods, namely pH, color (a surrogate measure of organic matter), and NO_3^- . These variables were chosen to examine how diatom beta diversity corresponded to periods of low acidity, high organic acidity, and high inorganic acidity in streams.

Due to the seasonal variation in Adirondack stream chemistry, it is difficult to separate the influence of stream chemistry versus other seasonal factors, such as temperature, on species turnover in diatom communities. Therefore, Mantel tests were performed across all stream samples combined, in order to examine the correlation of Sørensen dissimilarity with Euclidean distance in temperature versus the correlation with Euclidean distance in the chemical variables pH and color.

Results

The Model II regressions for overall diatom communities and guilds were both highly significant ($p < 0.000001$) with $r^2 > 0.99$. All regression coefficients (slope and intercept) were significant, except for the intercept for motile species in March 2004 ($p = 0.42$).

Figure 3.2 shows the SAC for overall diatom communities across sampling periods. Streams had the highest gamma diversity (γ) during August 2003 and August 2004 ($\gamma = 136$ and 139 , respectively), slightly lower gamma diversity in October 2003 ($\gamma = 131$), and considerably lower gamma diversity in March 2004 ($\gamma = 112$). None of the 95% confidence intervals across SAC slopes overlapped (Figure 3.3), indicating that all slopes were significantly different from one another. As indicated by the SAC slopes, streams had the highest beta diversity during August 2003, followed by August 2004 and October 2003, and lowest beta diversity in March 2004. Figure 2.4 shows the SAC intercepts for the diatom communities across sampling periods. The intercepts indicated the highest

alpha diversity in October 2003 and August 2004 and the lowest in August 2003 and March 2004.

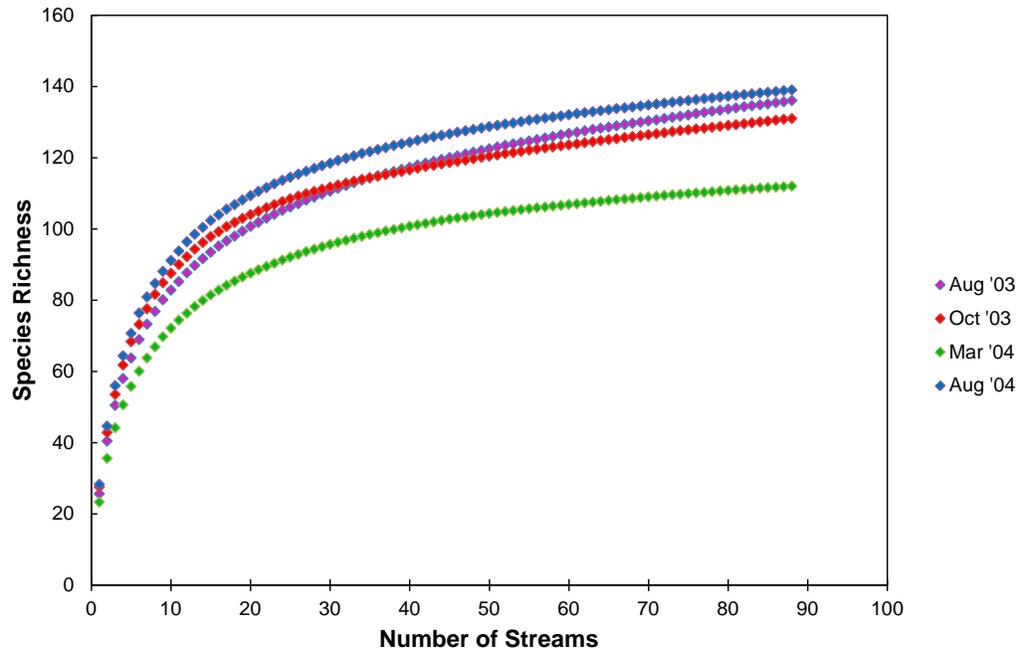


Figure 3.2 SAC for overall diatom communities across sampling periods.

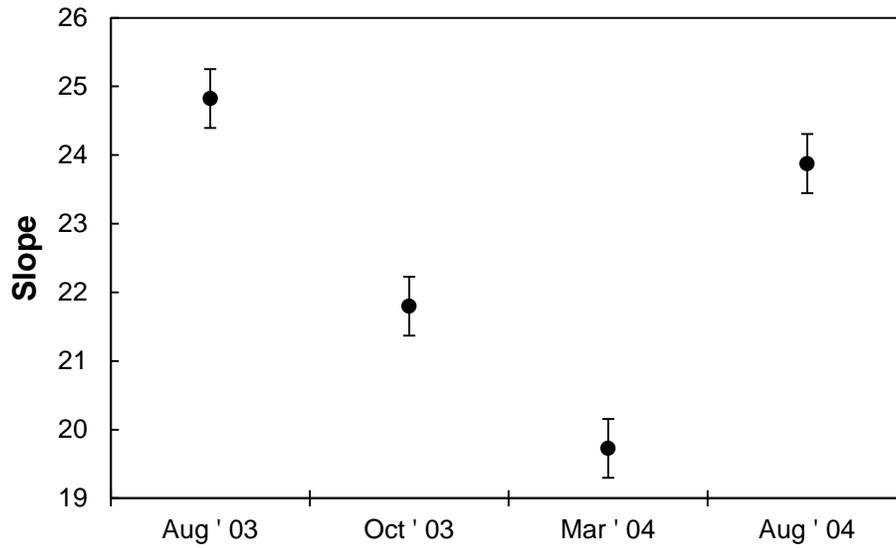


Figure 3.3 Slopes of SAC for overall diatom communities across sampling periods. Error bars are 95% confidence intervals.

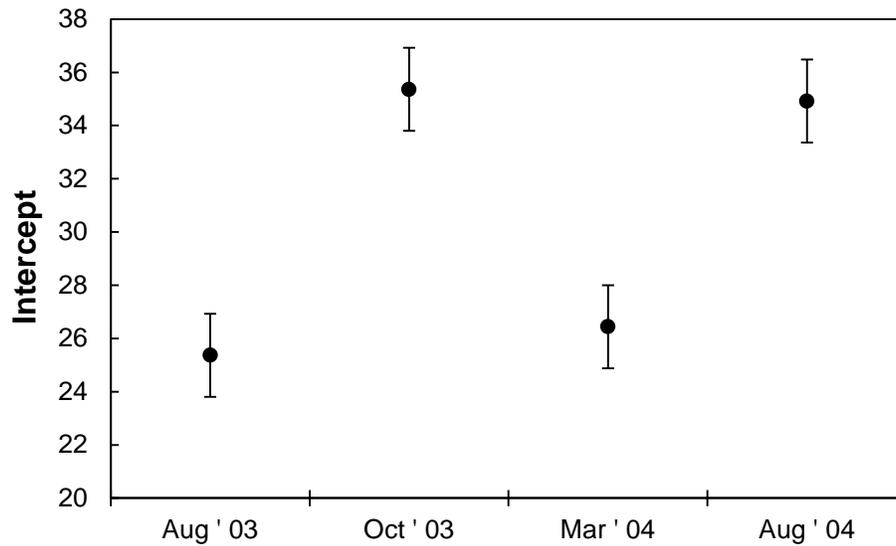


Figure 3.4 Intercepts of SAC for overall diatom communities across sampling periods. Error bars are 95% confidence intervals.

Repeated measures ANOVA and a Tukey post-hoc test of Sørensen dissimilarity for the diatom communities across sampling periods verified patterns in beta diversity

detected by the SAC slopes (F-ratio = 222.6, $p < 0.000001$). Sørensen dissimilarity was highest in August 2003 and lowest in March 2004.

Figure 3.5a shows the SAC slopes for diatom ecological guilds indicating differences in beta diversity across guilds and sampling periods. The low profile species exhibit a much lower beta diversity compared to the high profile and motile species. In each sampling period, the motile guild had significantly higher beta diversity than the high profile guild. Beta diversity for the low profile and high profile guilds was lowest in March 2004 and highest during August 2003. Motile species had the highest beta diversity in August 2004, followed by August 2003. There were no differences in slopes for motile species between October 2003 and March 2004.

The intercepts of SAC for diatom ecological guilds indicate differences in alpha diversity among guilds and across seasons (Figure 3.5b). The high profile guild had the highest alpha diversity while the motile guild had the lowest alpha diversity across all sampling periods. Alpha diversity for the high profile guild did not differ between October 2003, March 2004, and August 2004 but was significantly lower in August 2003. Both the low profile and motile guilds had the highest alpha diversity in October 2003 and August 2004, and lowest alpha diversity in August 2003 and March 2004.

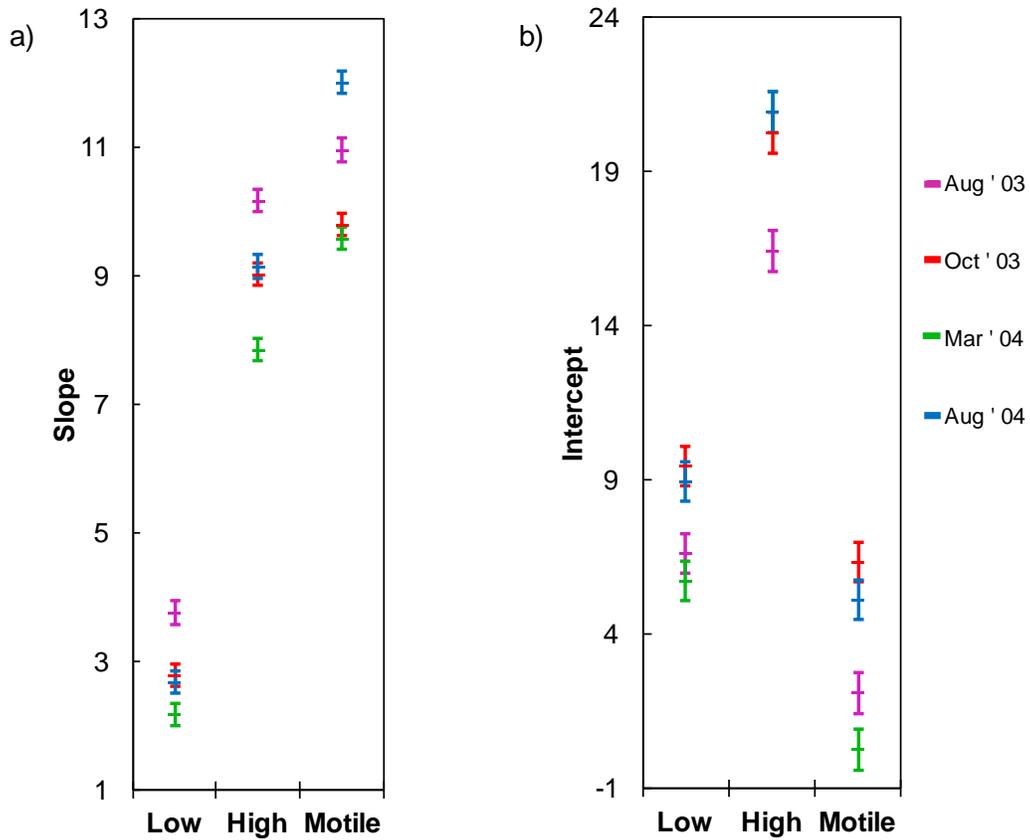


Figure 3.5 a) Slopes of SAC for diatom ecological guilds across sampling periods. b) Intercepts of SAC curves for diatom ecological guilds across sampling periods. The intercepts for the high profile guild overlapped completely in March 2004 and August 2004; therefore, the mean and error bars of March 2004 cannot be seen. Error bars are 95% confidence intervals in both graphs.

There were significant seasonal patterns in pH, color, and NO_3^- detected by repeated measures ANOVA, followed by Tukey's post-hoc comparisons (Figure 3.6). Streams had the highest pH in August 2003, followed by August 2004 (F-ratio = 201.1, $p < 0.000001$). Streams did not differ in pH in October 2003 and March 2004. Organic matter, as indicated by color, was highest in October 2003 and August 2004 and lowest in

August 2003 and March 2004 (F-ratio = 30.6, $p < 0.000001$). Streams had the highest NO_3^- in March 2004 and lowest NO_3^- in October 2003 and August 2004 (F = 153.1, $p < 0.000001$).

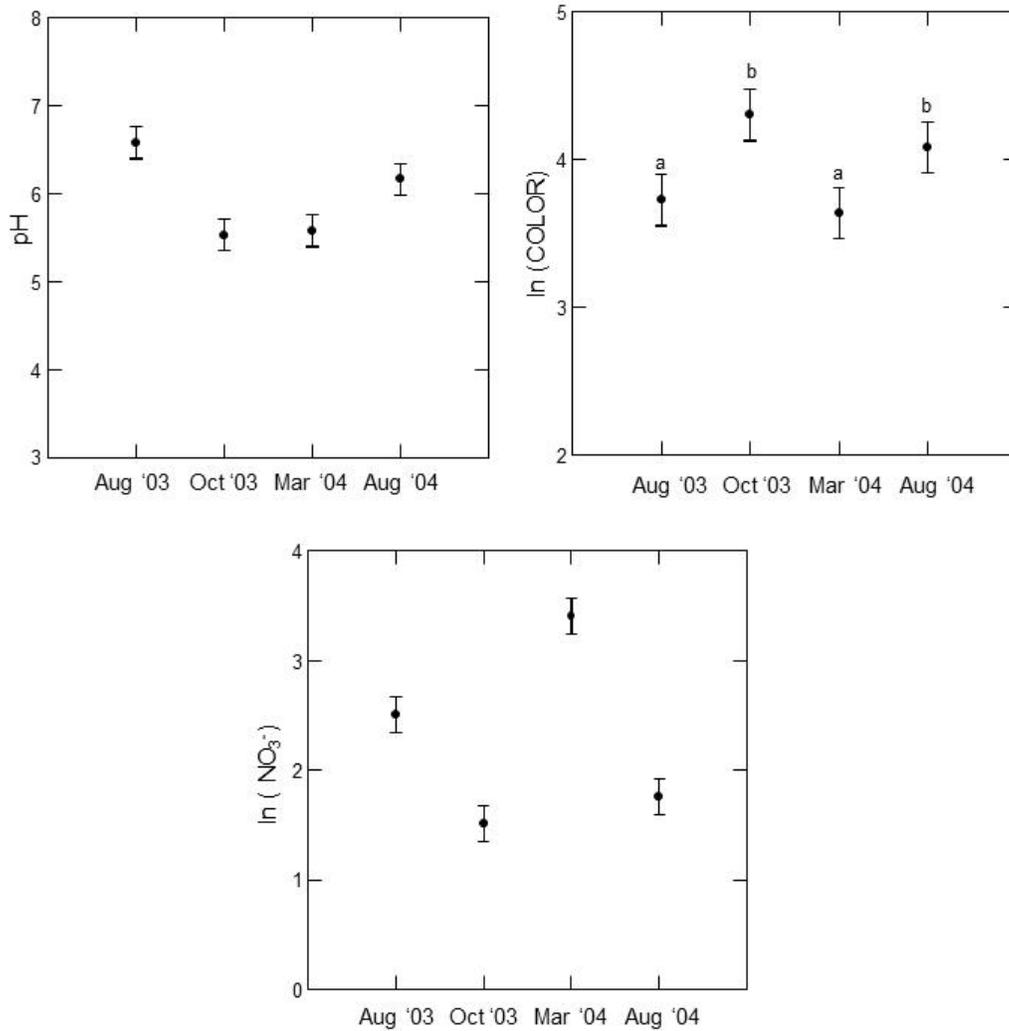


Figure 3.6 Mean chemistry plots across sampling periods. Error bars are ± 1 standard error. Significantly different means, as detected by Tukey's post hoc comparisons, are denoted by different letters. a) pH, b) ln-transformed color c) ln-transformed NO_3^- .

Mantel tests across all stream samples revealed that Sørensen dissimilarity was not correlated with ln-transformed temperature but was highly significantly correlated with pH ($r = 0.43$, $p = 0.001$) and ln-transformed color ($r = 0.14$, $p = 0.001$).

Discussion

Most studies of anthropogenic impacts on biodiversity only focus on one component of diversity (i.e., alpha diversity). Studies examining the impacts of acid deposition on biota are no exception. While the negative impacts of acid deposition on local diversity are well known (Hall *et al.* 1980; Havens, 1993; Guerold *et al.* 2000; Driscoll *et al.* 2003; Baldigo *et al.* 2009; Nierzwicki-Bauer *et al.* 2010), the impacts of acidification and source of acidity on beta diversity are virtually unknown. In this chapter, my first objective was to examine the response of diatom species turnover to acidification and different sources of acidity. The results confirmed my prediction that acidification in general would serve as an environmental filter, reducing species turnover across streams. Streams had the highest beta diversity when least acidified in August but the lowest when most acidified by inorganic acids in March. Although pH did not differ between organically acidified streams in October 2003 versus inorganically acidified streams in March 2004, beta diversity was significantly higher in October, indicating that species turnover is influenced by source of acidity in addition to pH. A previous study found more similar species composition in 10 inorganically versus six organically acidified ponds (Van Dam *et al.* 1981), but my results demonstrate this pattern of beta diversity response to source of acidity on a much larger scale and in streams.

In addition to variation in beta diversity, low acidity and inorganically versus organically acidified streams also differed in alpha and gamma diversity. These three measures of diversity are related, as the regional species pool is determined by how diversity is partitioned among the alpha and beta components (Loreau, 2000). Despite

low alpha diversity in August 2003, high species turnover across streams resulted in high gamma diversity. Alpha diversity was comparatively high in organically acidified streams in October, whereas beta diversity was reduced compared to streams with low acidity, and gamma diversity was slightly lower. In contrast, inorganically acidified streams in March had low alpha and beta diversity, which was reflected in a much less diverse regional species pool compared to both low acidity and organically acidified streams. The overall low diversity of inorganically acidified streams may be indicative of stronger environmental filtering on species composition (Chase, 2007). Similarly, Heino *et al.* (2003) suggested that adverse water chemistry conditions across a region (i.e., low pH) may result in low local richness, low species turnover, and an impoverished regional species pool. However, my study further shows that these patterns are temporally dynamic, especially in regions such as the Adirondacks where local habitats are subject to strong disturbance and environmental fluctuations. Multi-seasonal studies examining impacts of acid deposition on biota have typically included a small number of streams (Baker *et al.* 1996; Passy, 2006; Passy *et al.* 2006; MacDougall *et al.* 2008), but even larger multi-seasonal studies (including ≥ 20 streams) have focused on impacts of acidification to local species richness or taxonomic composition and abundance (Guerold *et al.* 2000; Lepori *et al.* 2003; Lepori and Ormerod, 2005). To my knowledge this study is the largest multi-seasonal investigation of biota in an acidified region and the first to demonstrate that acidification and source of acidity impact all three components of diversity (alpha, beta, and gamma).

The low alpha diversity despite high gamma diversity in August 2003 may indicate environmental constraints on the local species pool. While alpha diversity generally increases with the size of the regional species pool (Heino *et al.* 2003; Soininen *et al.* 2009), local environmental factors can be equally or more important in

determining local species richness (Passy, 2009; Gronroos and Heino, 2012). For instance, low alpha despite high gamma diversity may be attributed to resource limitation in the local environment (Viljanen *et al.* 2010). Streams had significantly lower organic content in August 2003, relative to periods with higher alpha diversity. Wetlands and associated organic matter are important sources of micronutrients to streams (Dillon and Molot, 1997; Gorham *et al.* 1998; Goulet and Pick, 2001; Björkvald *et al.* 2008), and local micronutrient concentrations, followed by regional species richness, were found to be major predictors of local diatom richness in a continental wide study (Passy, 2009). Another continental-wide study by Passy (2010) found that diatom richness was positively correlated with proportion wetlands in the watershed and stream concentrations of dissolved organic carbon and iron. Based on these findings, Passy (2010) proposed that wetland-derived organic matter increases diatom diversity through complexation and increased export of the micronutrient iron into streams. The direct link between diatom richness and color demonstrated in Chapter 2 combined with the strong correlation between iron and water color in Adirondack lakes (Maranger *et al.* 2006), indicate that the same mechanism of increased diatom richness due to organically-bound iron may be operating in the acid streams in this study (Passy, 2010). Therefore, iron enrichment from organic matter may explain the higher diatom alpha diversity in October, despite significantly lower pH relative to August 2003.

The second objective of this chapter was to examine alpha and beta diversity across diatom ecological guilds. The results are consistent with my prediction that the small-bodied, tolerant, low profile guild would have lower beta diversity compared to the large-bodied, sensitive high profile and motile guilds. Previous studies have reported less steep SAR slopes for small-bodied organisms (Azovsky, 2002; Drakare *et al.* 2006) and species with higher dispersal ability (Öckinger *et al.* 2010). In contrast, more sensitive

species with narrow niche breadth are shown to have steeper slopes (Steffan-Dewenter and Tschardtke, 2000; Krauss *et al.* 2003; Cagnolo *et al.* 2009; Franzén *et al.* 2012). However, it should be noted that the low profile guild had considerably lower total regional species richness summed across all four sampling periods ($\gamma = 25$) when compared to the high profile and motile guilds ($\gamma = 70$ and 72 , respectively). Therefore, I cannot rule out the possibility that low profile species accumulated at a much slower rate because this group had much lower regional diversity.

When comparing within sampling periods, the motile guild had the highest beta diversity across all guilds and considerably lower alpha diversity than the high profile guild, even though both had similar regional species pools summed across all sampling periods (motile and high profile $\gamma = 72$ and 70 , respectively). In addition to low alpha diversity, the motile guild occurred at considerably lower relative abundance in streams compared to the high profile guild (average relative abundance = 4.7% and 73.3%, respectively), indicating that motile species were relatively rare. A previous study reported steeper SAR slopes for species with low abundance and attributed it to rare species being more prone to local extinction with lower probability of recolonization (Franzén *et al.* 2012). On account of being rare, motile species in this study may be less well distributed compared to the more common high profile species, resulting in higher turnover across streams. The much lower alpha diversity of motile species could be due to the high number of eutrophic and pollution tolerant species in this guild (Passy, 2007a) which may not reach high abundance in the oligotrophic, pristine mountain streams found in this study. In contrast, high profile species had much higher richness than either of the two guilds. The prominence of high profile species in the study may be attributed to abundance of acid-tolerant *Eunotia* species occurring in these streams, which are generally high profile. Furthermore, high profile species in this study may have benefited

from reduced grazing pressure due to the absence of acid sensitive grazers (Planas, 1996). Species within the high profile guild make up the over-story of periphyton and are most vulnerable to grazing (Steinman, 1996). Likewise, Gottschalk and Kalhert (2012) attributed the shift toward high profile species in acid lakes to decreased grazing pressure.

Within guild alpha and beta diversity responded to acidification and different sources of acidity in a similar way to the overall diatom community, with some differences. Alpha diversity across all guilds was high during the humic-rich periods of October 2003 and August 2004 and was lower in low profile and motile guilds when streams were inorganically acidified in March. For the high and low profile guilds, beta diversity was significantly reduced when streams were inorganically acidified in March but was the highest when streams were least acidified in August 2003. Beta diversity of motile species did not differ between periods of inorganic versus organic acidification and was higher in August 2004 relative to August 2003. These results indicate that within guild diversity and turnover also respond to environmental stressors and stimuli and may reflect patterns of diversity and turnover across the entire diatom community.

In conclusion, this study is the first to examine the effects of acidification and source of acidity on all three components of diversity (i.e., alpha, beta, and gamma) and is also the largest to examine the response of beta diversity to inorganic versus organic acidification. The results provide evidence that inorganic acidity functions as a much harsher environmental filter than organic acidity. In addition, this is the first study to demonstrate that diatom ecological guilds exhibit differences in species turnover and local diversity across streams. These results provide insight into how ecological differences between these guilds influence species distributions

Chapter 4

The importance of stochastic processes is diminished in acid stressed streams

Introduction

A central question in the study of organismal communities is whether they are shaped deterministically - by their local environment, stochastically - by random but spatially constrained dispersal, or some combination of the two. Niche theory emphasizes the importance of species traits and environmental conditions in limiting species distributions (Chase and Leibold, 2003), whereas neutral theory attributes assemblage variation to dispersal limitation and stochastic processes such as random colonization, extinction, birth, and death (Hubbell, 2001). Deterministic communities that are shaped by the environment should exhibit high species turnover along environmental gradients. Stochastic communities that are not controlled by environmental factors should primarily be limited by dispersal and become more dissimilar from one another with geographic distance (Tuomisto *et al.* 2003).

It is likely that a combination of niche-based versus stochastic processes operate on communities, as many studies examining the roles of these two processes have found a significant contribution of both (Tuomisto *et al.* 2003; Thompson and Townsend, 2006; Dumbrell *et al.* 2010; Stegen *et al.* 2012; Chust *et al.* 2013; Myers *et al.* 2013). However, the relevance of stochastic versus deterministic factors in shaping communities may be altered by environmental stress. Harsh environmental conditions are shown to act as “environmental filters” that reduce the importance of stochastic factors in community assembly, causing communities to become more deterministic (Chase, 2007). Under such conditions, geographically-constrained dispersal should be less important, as less tolerant species may be unable to survive and reproduce in stressful environments, even if those environments are within range of dispersion. Similarly, Jabot *et al.* (2008)

found that the immigration rate into local communities declines with increased intensity of environmental filtering.

To what extent community composition varies spatially as a result of spatial variability in the environment or dispersal limitation is a subject of intensive research. Although microorganisms are traditionally considered excellent dispersers primarily structured by their environment, i.e. “everything is everywhere but the environment selects” (Baas Becking, 1935), a number of studies have demonstrated that spatial predictors account for a large amount of unexplained variance in diatom distributions (Potapova and Charles, 2002; Soininen *et al.* 2004; Passy, 2007b; Heino *et al.* 2010; Smucker and Vis, 2011). The significance of pure space as a predictor of diatom composition in these studies indicates a role for stochastic mechanisms, after ruling out the potential influence of spatially-constrained unmeasured environmental variability. A study of global patterns in diatom diversity further suggested that large-scale historical processes related to dispersal and habitat connectivity and isolation play a dominate role in shaping diatom distributions across regions (Vyverman *et al.* 2007). Such findings have led to the recommendation that factors such as dispersal limitation should be considered in biomonitoring in order to improve predictions of species-environmental relationships (Heino, 2013).

Biomonitoring relies on the assumption that species are controlled by their environment and focuses on how taxonomic composition responds to individual environmental variables. This question is of particular importance in the Adirondacks, where streams are acidified by both inorganic acid deposition and natural organic acidity originating from soil organic matter and wetlands (Lawrence *et al.* 2007). Acidic runoff due to inorganic acid deposition mobilizes toxic aluminum into streams, but organic matter mitigates this toxicity by forming biologically unavailable complexes with the metal

(Gensemer and Playle, 1999). Thus, organic acidity is expected to be less stressful to biota. Only two studies have examined diatom species composition across one brown-water stream that was organically acidified by a *Sphagnum* wetland and one clear-water stream that was predominately acidified due to inorganic acid deposition (Passy, 2006; Passy *et al.* 2006). In these studies, the inorganically acidified stream was dominated year-round by the small and acid tolerant species *Eunotia exigua* while the organically acidified stream supported a more diverse flora of diatom species. In Chapter 2, I examined the influence of acidification and different sources of acidity on diatom functional composition. I demonstrated that high ratios of inorganic to organic aluminum ($Al_{im}:Al_{om}$) associated with inorganic acidity resulted in increased dominance of shorter statured low profile diatom species. This finding is consistent with another study that reported a shift toward smaller sized diatom species in a lake that became more acidified due to acid deposition over time (Cattaneo *et al.* 1998). In Chapter 2 I also found that the abundance of high profile species increased along a gradient of water color that was positively associated with wetlands. However, it is still uncertain which species are driving these changes in functional composition. Furthermore, the influence of inorganic versus organic acidification on the composition of diatom species has not been examined on a large regional scale, where both spatial and environmental factors may play a role in shaping species distributions.

The first objective of this chapter is to examine the relative importance of stochastic dispersal versus deterministic/environmental factors in shaping diatom communities across streams during periods of low acidity in August 2003 and August 2004, high organic acidity in October 2003, and high inorganic acidity in March 2004. Mantel tests were used to examine this first objective. Mantel is a distance-based technique recommended for testing Hubbell's neutral theory (Tuomisto and Ruokolainen,

2006). This technique examines the correlations between two dissimilarity or distance matrices (i.e., species dissimilarity versus environmental or geographic distance). Distance-based approaches are more appropriate than “raw data” approaches such as Canonical Correspondence Analysis (CCA) and Redundancy Analysis (RDA) for testing neutral theory, as the predictions of neutral theory are stated in terms of distance, i.e., communities will become more dissimilar with increased geographic distance (Tuomisto and Ruokolainen, 2006). Whereas canonical analysis is concerned with explaining changes in species abundances across directional gradients (both environmental and spatial), neutral theory disregards species identities or abundances, as under this theory species are considered ecologically equivalent and abundances are expected to fluctuate at random (Tuomisto and Ruokolainen, 2006). However, these fluctuations are spatially autocorrelated due to dispersal limitation, so species composition between sites is expected to become more dissimilar with distance (Tuomisto and Ruokolainen, 2006).

In the previous chapters I found that inorganically acidified streams are associated with higher ratios of $Al_{im}:Al_{om}$, lower species richness, and lower diatom beta diversity relative to streams with natural, organic acidity. Other studies have reported higher diversity in organically acidified streams when compared to streams that are inorganically acidified due to anthropogenic causes (Collier *et al.* 1990; Dangles *et al.* 2004; Passy *et al.* 2006; Petrin *et al.* 2008a; Petrin *et al.* 2008b; Greig *et al.* 2010). These findings provide evidence that inorganic acidity is more stressful to biota than organic acidity and may serve as a stronger environmental filter. As the roles of stochastic processes and dispersal assembly may be reduced under stressful environmental conditions (Chase, 2007), I predict that diatom communities will be the most controlled by deterministic factors and that stochastic processes, measured as species turnover with geographic distance, will be least important during the period of

high inorganic acidity in March. Conversely, periods of low acidity should be the least stressful for biota as low acidity streams were demonstrated to have the highest beta diversity in Chapter 3, and species are shown to be sensitive to acidification regardless of the source (Van Dam *et al.* 1994; Petrin *et al.* 2007; Petrin *et al.* 2008a; Petrin *et al.* 2008b). Therefore, I predict that stochastic processes will be the most important during periods of low acidity in August. Finally, I predict that stochastic processes will be of intermediate importance during the period of high organic acidity in October.

While Mantel tests are ideal for testing neutral theory and examining the relative importance of niche versus neutral processes in communities, a weakness of this approach is that it does not address questions of how individual species vary in presence or abundance across sites nor can it indicate which environmental factors or spatial gradients are important drivers of changes in species composition. All information on species identity, specific environmental variables, and geographic coordinates is lost when dissimilarity or distance matrices are calculated (Tuomisto and Ruokolainen, 2006). Mantel tests merely examine the extent in change of species composition with extent in change of environment or distance. Questions about how species composition changes along environmental gradients and whether species exhibit unique spatial patterns can only be answered with raw data approaches such as Redundancy Analysis (RDA).

For my second objective I will use RDA to examine diatom species composition along environmental and spatial gradients in order to determine the relative contribution of unique environmental variables and spatial factors to species' abundances and distributions. This objective addresses the questions of how diatom species composition changes along gradients of acidification and source of acidity on a regional scale and whether spatial factors play a role in shaping diatom species abundances and distributions in this region.

Methods

Sampling and Laboratory Protocols.

This analysis included 636 diatom and chemistry samples collected from 192 streams during the Western Adirondack Stream Survey (112 streams sampled in August 2003, 175 streams sampled in October 2003, 172 streams sampled in March 2004, and 177 streams sampled in August 2004). Chemistry analyzed by USGS collaborators included: inorganic aluminum (Al_{im}), organic aluminum (Al_{om}), Ca^{2+} , color, conductivity, Cl^- , dissolved organic carbon (DOC), F^- , K^+ , Mg^{2+} , Na^+ , NH_4^+ , NO_3^- , pH, SiO_2 , and SO_4^{2-} (Lawrence *et al.* 1995). All chemical variables were ln-transformed except pH to improve normality. Diatom subsamples were taken from all available substrates in each locality, including rocks, sand, and macrophytes and preserved in 4% formaldehyde. In the lab, all subsamples from each stream were combined, shaken vigorously, and processed via acid digestion or bleaching (Passy, 2006). The clean samples were mounted onto glass slides with Naphrax[®]. From each glass slide, 300 diatom frustules were counted and identified to species level using a 100×1.35 numerical aperture oil immersion objective.

Statistical Analysis

Mantel tests were used to address my first objective which was to examine the relative importance of stochastic versus deterministic processes across periods of low acidity, high organic acidity, and high inorganic acidity. Within each sampling period, species abundance data were transformed into Sørensen dissimilarity matrices. Likewise, within each sampling period, Euclidean distance matrices for geographic distance were calculated from UTM geographic coordinates between streams, and Euclidean distance matrices for environmental distance were calculated from differences in the 16 measured chemical variables among streams. Mantel tests were used to calculate the correlation between species dissimilarity and geographic and environmental distance matrices. In

addition, partial Mantel tests were used to test whether the relationship between species dissimilarity and geographic distance remained significant after their correlations with the environment were accounted for, and vice versa. Partial Mantel tests examine the correlation between two dissimilarity matrices while controlling for the effects of a third matrix (Legendre and Legendre, 1998). The significance of correlations was tested with 999 permutations. Mantel and partial Mantel tests were performed in the R-package *Vegan* (Oksanen *et al.* 2008).

RDA was used to examine my second objective concerning how diatom species composition changes along environmental and spatial gradients within each sampling period. Prior to RDA, species with < 1.0% abundance across all streams within a sampling period were removed and proportional abundance of species was arcsine square root-transformed to improve normality.

Each RDA included three different matrices: species abundance, environmental, and spatial data. The spatial matrix consisted of the third order polynomial terms of the standardized latitude (x) and longitude (y) coordinates: x, y, x^2 , xy, y^2 , x^2y , y^2x , x^3 , and y^3 , as examining third order polynomials captures more spatial complexity in species distributions than the linear coordinates x and y alone (Borcard *et al.* 1992). Within each month, two RDAs were first run separately to select the best environmental and spatial predictors of species abundance. The RDAs were run using forward selection and 999 Monte Carlo permutations in order to select significant predictors in each group ($p < 0.05$). If two variables were found to be highly correlated, the better of the two predictors was included in the model in order to keep variance inflation factors below 10. As color and dissolved organic carbon (DOC) were highly correlated throughout samples (Pearson $r = 0.88$), and color was found to be the stronger predictor of species composition across all sampling periods, DOC was excluded from all RDAs. Likewise,

bivalent cations Ca and Mg were highly correlated (Pearson $r = 0.92$). Therefore, the raw concentrations of these cations were summed, ln-transformed, and examined as a single predictor. Once both environmental and spatial predictors were selected, combined RDAs were run to obtain the combined variance explained by both sets of predictors. Variance partitioning was used to determine the pure and covariance effects of environmental and spatial predictors on species composition.

Results

Mantel tests indicated that species dissimilarity was highly correlated with environmental distance across all sampling periods (Table 4.1). Controlling for the effects of geographic distance had little effect on this relationship as the correlation between species dissimilarity and pure environmental distance was either the same or similar. The correlations between species dissimilarity and geographic distance were also significant. However, after controlling for the effects of environmental distance, this relationship was only significant during low acidity periods in August 2003 and 2004, marginally non-significant during the period of high organic acidity in October 2003, and non-significant during the period of high inorganic acidity in March 2004.

Table 4.1 Mantel and partial Mantel test results showing the correlation of species dissimilarity with environmental and geographic distance across sampling periods. Pure environment indicates the relationship between species dissimilarity and environmental distance after the effects of geographic distance are controlled for. Likewise, pure distance indicates the relationship between species dissimilarity and geographic distance after the effects of the environment are controlled for. The first number in each column indicates the Mantel r statistic and the number in parentheses indicates the p-value.

	Aug '03 n = 112	Oct '03 n = 175	Mar '04 n = 172	Aug '04 n = 177
Environment	0.39 (0.001)	0.51 (0.001)	0.57 (0.001)	0.55 (0.001)
Pure Environment	0.39 (0.001)	0.50 (0.001)	0.57 (0.001)	0.55 (0.001)
Distance	0.11 (0.001)	0.10 (0.001)	0.05 (0.007)	0.13 (0.001)
Pure Distance	0.10 (0.001)	0.03 (0.07)	NS	0.09 (0.001)

Overall, RDA indicated that diatoms, across all sampling periods, were better predicted by pure environmental than pure spatial factors, but there was a high amount of species variance explained by the covariance of the two groups of factors (Figure 4.1). Figure 4.2 (a – d) shows the first two axes of the RDAs for environmental predictors and selected species for each sampling period. Species names and their abbreviations can be found in Table 4.2. Spatial predictors and their scores on RDA axes 1 and 2 may be found in Table 4.3. Only environmental predictors with absolute correlation of > 0.20 with at least one of the first two axes are shown on the RDA plots. RDA across all sampling periods indicated that diatom community composition was best explained by gradients of acidity and second best by color. The first axes of all RDAs were positively correlated with pH and/or basic cations and were negatively correlated with Al_{im} , color, and during

some periods, Al_{om} . Some of the more common diatom species found in high pH streams included *Achnantheidium minutissimum*, *Cocconeis placentula*, *Eunotia cisalpina*, *Gomphonema angustatum*, *Meridion circulare*, and *Synedra ulna*. Color was positively correlated with Al_{im} during August 2003 when streams were least acidified (Figure 3.5a), but these two variables were not correlated in any of the other sampling periods. The second axis of the RDA in August 2003 separated streams with high Al_{im} concentrations and color from streams with high NO_3^- and SiO_2 concentrations. The species *Eunotia trinacria*, *Eunotia bilunaris*, *Eunotia tautoniensis*, *Frustulia rhomboides*, and *Tabellaria flocculosa* were most highly correlated with Al_{im} and color during this month, but these species showed separate distributions along axis 2 in subsequent months when Al_{im} and color were not correlated.

In October 2003, the first RDA axis was highly positively correlated with pH and conductivity (which was highly positively correlated with base cations) and most negatively correlated with Al_{im} . The variables SiO_2 , Na, and anions F^- and SO_4^{2-} were also positively correlated with pH. The positive correlation between SO_4^{2-} and pH and negative correlation between pH and color indicated that the most acidified streams were organically acidified while streams that were less acidified had high concentrations of SO_4^{2-} . The second axis separated diatom communities correlated with high Al_{im} and color. *Eunotia trinacria* was most strongly correlated with Al_{im} , while the species *Tabellaria quadrisepta*, *Eunotia tautoniensis*, *Eunotia bilunaris*, and *Eunotia serra* showed more moderate correlations. The species *Eunotia rhomboidea*, *Frustulia rhomboides*, *Fragilariforma virescens*, and *Tabellaria flocculosa* were associated with high color streams.

In March 2004, the first axis of the RDA was highly positively correlated with pH and negatively correlated with Al_{im} and Al_{om} and the second axis was negatively

correlated with color. Similar to October 2003, the species *E. trinacria* was most highly correlated with Al_{im} , while species *Eunotia bigibba* and *Eunotia exigua* showed more moderate correlations. The species *T. quadrisepta*, *E. tautoniensis*, and *E. bilunaris* were more correlated with Al_{om} . The species correlated with color were the same as those correlated with color in October 2003.

In August 2004, the first axis was highly positively correlated with bivalent cations (Ca + Mg) and Na and most negatively correlated with Al_{im} and Al_{om} . The first axis was weakly positively correlated with F^- and negatively correlated with color. The species *F. rhomboides*, *E. rhomboidea*, and *E. serra* were associated with high color and concentrations of Al_{om} . Similar to other months, *E. trinacria* was highly correlated with Al_{im} while *E. tautoniensis*, *E. bilunaris*, *E. bigibba*, and *T. quadrosepta* showed more moderate correlations.

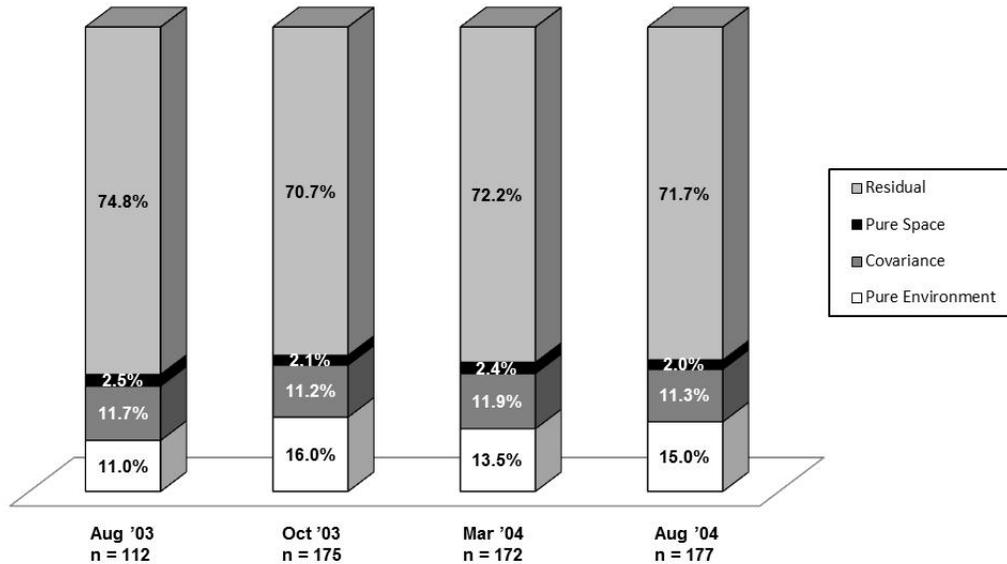


Figure 4.1 Variance in diatom communities explained by pure environmental and pure spatial factors and their covariance across all four sampling periods. Residual = nonexplained variance.

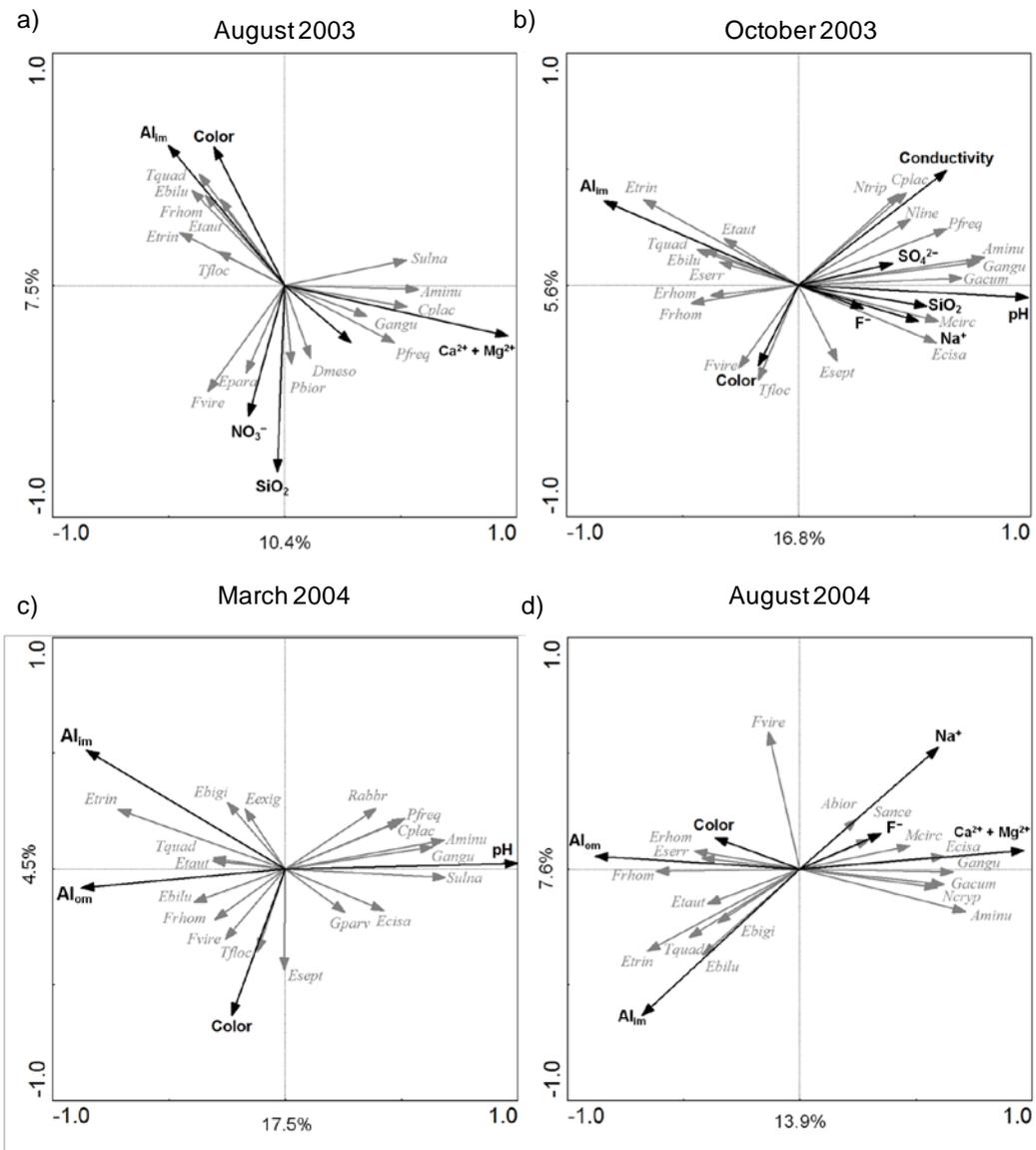


Figure 4.2 The first two axes of the RDAs for environmental predictors and selected species for each sampling period. Variance explained by environmental predictors is indicated for each axis.

Table 4.2 List of species and acronyms.

Taxon	Acronym
<i>Achnantheidium minutissimum</i> (Kützing) Czarnecki	Amin
<i>Cocconeis placentula</i> Ehrenberg	Cplac
<i>Diatoma mesodon</i> Kützing	Dmeso
<i>Eunotia bigibba</i> Kützing	Ebigi
<i>Eunotia bilunaris</i> (Ehrenberg) Schaarschmidt	Ebilu
<i>Eunotia cisalpina</i> Lange-Bertalot & Cantonati	Ecisa
<i>Eunotia exigua</i> (Brébisson ex Kützing) Rabenhorst	Eexig
<i>Eunotia paratridentula</i> Lange-Bertalot & Kulikovskiy	Epara
<i>Eunotia rhombiodes</i> Hustedt	Erhom
<i>Eunotia septentrionalis</i> Østrup	Esept
<i>Eunotia serra</i> Ehrenberg	Eserr
<i>Eunotia tautoniensis</i> Hustedt	Etaut
<i>Eunotia trinacria</i> Krasske	Etrin
<i>Fragilariforma virescens</i> (Ralfs) Williams & Round	Fvire
<i>Frustulia rhomboides</i> (Ehrenberg) De Toni	Frhom
<i>Gomphonema acuminatum</i> Ehrenberg	Gacum
<i>Gomphonema angustatum</i> (Kützing) Rabenhorst	Gangu
<i>Gomphonema parvulum</i> (Kützing) Kützing	Gparv
<i>Meridion circulare</i> (Greville) Agardh	Mcirc
<i>Navicula cryptocephalla</i> Kützing	Ncryp
<i>Navicula tripunctata</i> (Müller) Bory de Saint-Vincent	Ntrip
<i>Nitzschia linearis</i> (Agardh) Smith	Nline
<i>Planothidium frequentissima</i> (Lange-Bertalot) Round & L. Bukhtiyarova	Pfreq
<i>Psammothidium bioretii</i> Germain	Pbior
<i>Rhoicosphenia abbreviata</i> (C. Agardh) Lange-Bertalot	Rabbr
<i>Stauroneis anceps</i> Ehrenberg	Sance
<i>Synedra ulna</i> (Nitzsch) Ehrenberg	Sulna
<i>Tabellaria flocculosa</i> (Roth) Kützing	Tfloc
<i>Tabellaria quadrisepata</i> Knudson	Tquad

Table 4.3 RDA axis 1 and 2 scores for spatial predictors. Predictors that were not included in an RDA model are marked by NA.

	Aug '03		Oct '03		Mar '04		Aug '04	
	Axis 1	Axis 2						
x	0.0223	0.206	NA	NA	NA	NA	0.0737	-0.0035
x ²	0.2755	-0.1754	0.1662	-0.2233	0.2277	-0.2095	0.1669	0.1913
x ³	NA	NA	0.2465	0.1153	0.1681	-0.0217	NA	NA
y	NA	NA	-0.3993	0.1881	-0.4437	0.1884	-0.4925	-0.1371
y ²	0.1173	0.217	0.1287	0.2692	0.111	0.3819	0.0884	-0.2794
y ³	-0.3507	0.1642	-0.3123	0.1649	NA	NA	NA	NA
xy	NA	NA	NA	NA	0.2129	-0.1232	0.2566	0.2206
x ² y	-0.5294	-0.2726	NA	NA	-0.4508	0.1885	-0.4931	0.0175
y ² x	-0.1343	-0.1234	-0.0366	-0.3848	-0.0545	-0.4821	-0.0344	0.328

Discussion

The results from both Mantel tests and RDA indicated that diatom communities are overwhelmingly deterministic in this region. Mantel tests showed that diatom dissimilarity was more highly correlated with the environmental distance across all sampling periods, but the relative influence of geographically-constrained stochastic factors differed among periods of low and high acidity. Consistent with my hypothesis, partial Mantel test revealed that species dissimilarity was only significantly correlated with pure geographic distance during periods of low acidity in August 2003 and August 2004. This correlation was marginally non-significant in organically-acidified streams in October and non-significant in inorganically acidified streams in March. Therefore, the importance of stochastic processes did vary across periods of high and low stress but the environment always played a stronger role than geographic distance in influencing diatom species composition across streams. Similarly, RDA showed that the environment

was a far better predictor than pure spatial factors of diatom species composition and abundance in this study.

The low correlation of species turnover with geographic distance and low variance explained in species composition by spatial factors in this study contrasts with other studies that have found that diatom communities are strongly spatially structured. Virtanen and Soininen (2012) found that diatom dissimilarity was almost equally correlated with environmental and geographic distance across four river basins in Finland and concluded that diatoms are structured by large-scale processes such as history and dispersal (Vyverman *et al.* 2007), in addition to local stream chemistry. Heino *et al.* (2010) reported that pure spatial factors explained more than twice the variance of environmental factors in a study of streams throughout Finland, providing little evidence for the traditional view that diatoms, as microorganisms, are solely structured by their environment (Baas Becking, 1935). Other large scale investigations across the United States and Finland found that pure spatial factors accounted for 20 – 30% of the total explainable variance in diatom composition (Potapova and Charles, 2002; Soininen *et al.* 2004). Part of this difference in importance of geographic distance and spatial factors in my study compared to others may be attributed to differences in spatial extent of the study regions, as my study encompassed a smaller area than the above studies. However, it is unlikely that this is the only factor contributing to the difference, as spatial factors have been shown to be important even at relatively small spatial scales. In a study of the roles of environmental versus spatial factors along a single river, Passy (2007b) found that pure spatial factors accounted for more variance explained in diatom community composition than pure environmental factors. Likewise, pure spatial factors explained over a third of the explainable variance in diatom species composition within two watersheds (both < 600 km²) examined by Smucker and Vis (2011). Even at the riffle

scale, pure spatial factors, after controlling for the effects of current velocity and depth, explained 10% of the variance in species composition across a 16 m² stretch of river (Passy, 2001), which is four times more than the variance explained by space in this large regional study. Therefore, pure spatial factors attributed to dispersal limitation and biotic interactions have been shown to be important in studies far less extensive than my study. An alternative explanation for the weak correlations of diatom communities with geographic distance and spatial factors in my study could be a diminished role of dispersal-related assembly in acid stressed streams. It is possible that diatom communities in Adirondack streams never fully recover from acid episodes and remain deterministic year-round, even during periods of low acidity.

Recently, Heino (2013) proposed that spatial factors be considered in bio-assessment, as metacommunity theory has shown that community structure is influenced by biotic interactions and dispersal, in addition to local environmental conditions. He also specified that the importance of spatial factors would be dependent on the spatial extent of the study and dispersal ability of the organism. He recommended restricting biomonitoring to a single basin as opposed to multiple basins, so that the effects of dispersal limitation do not confound the species-environmental relationships. However, metacommunity research also predicts that species sorting by the environment should increase (Helmus *et al.* 2010; Myers and Harms, 2011; Pellisier *et al.* 2013) and the importance of stochastic processes and assembly history may decrease (Chase, 2007; Jiang and Patel, 2008) in stressed or disturbed environments, which are often the focus of bio-monitoring. My study region spans a geographic range of 4,585 km² and covers two river basins, slightly larger than the extent recommended by Heino (2013). My results suggest that at this spatial scale, in acid-stressed systems, the roles of dispersal and

other spatially-constrained processes (i.e., biotic interactions) are very minimal for diatoms, which are generally considered excellent dispersers (Finlay, 2002).

In this study, diatom species showed distinct distributions along gradients of pH and Al_{im} . Most of the species correlated with high pH and bivalent cation concentrations are classified as circumneutral (associated with neutral pH) or alkaliphilous (associated with alkaline pH) species (Van Dam *et al.* 1994). The abundance of *Eunotia* species generally increased with acidity, as species within this genus are typically classified as acid tolerant (Van Dam *et al.* 1994). However, two *Eunotia* species showed pH distributions contrary to others. The species *E. cisalpina* was more abundant in low acidity streams, while *E. septentrionalis* showed indifference to pH during periods of highest acidity.

Although diatoms have a long history as indicators of acidity (Van Dam *et al.* 1994; Battarbee *et al.* 2010), very little is known about how diatom species respond to different sources of acidity. Color emerged as an important predictor of diatom composition in all sampling periods, and diatom species showed distinct separation between streams with high Al_{im} and high color in three of the four sampling periods, when Al_{im} and acidity were higher. The species *Eunotia rhomboidea*, *Fragilariforma virescens*, *Frustulia rhomboides*, and *Tabellaria flocculosa* were most common in streams with high color. These species are all filamentous or tube-forming species classified in the high profile guild (Appendix A), which was shown in Chapter 2 to be stimulated by high color associated with wetlands. Across all RDAs, color entered the models as a better predictor than DOC, which was subsequently excluded due to collinearity. Although color is a surrogate measurement of DOC, water color is also determined by both the quality of organic matter and iron concentrations, in addition to the amount of organic matter (Kritzberg and Ekstrom, 2012). Furthermore, color was shown to be a better predictor of

stream iron concentrations than DOC in Adirondack lakes (Maranger *et al.* 2006). Iron was found to be an important predictor of local and regional diatom diversity in a continental scale (Passy, 2009; Passy, 2010), and is exported into streams via complexation with organic matter from wetlands (Dillon and Molot, 1997; Gorham *et al.* 1998; Goulet and Pick, 2001; Björkvald *et al.* 2008). Given the importance of iron to stream diatom diversity, iron may also be an important determinant of diatom composition. Thus, color may be a better predictor of diatom composition than DOC because it better accounts for stream iron concentrations.

Consistent with the findings of Passy (2006), the species *Eunotia trinacria* showed a strong, positive relationship with Al_{im} , and this relationship was strongest during periods of high acidity. *E. trinacria* is a relatively small species, that typically occurs as a solitary form and, unlike most *Eunotia* species, does not form long chains. Thus, this species is classified as low profile (Appendix A) and is probably the main reason for the shift toward low profile species in streams with high $Al_{im}:Al_{om}$ ratios found in Chapter 2. Species showing more moderate correlations with Al_{im} include *Eunotia bigiba*, *Eunotia bilunaris*, *Eunotia exigua*, *Eunotia tautoniensis*, and *Tabellaria quadrisepata*. *E. exigua* is another low profile, unicellular species that is often reported in acidified streams (Kwandrans, 1993; Verb and Vis, 2000; Hirst *et al.* 2004; Luis *et al.* 2009). This species may thrive under moderate concentrations of aluminum as Macdougall *et al.* (2008) reported a unimodal response of *E. exigua* to aluminum and Passy (2006) found that this species declined under really high $Al_{im}:Al_{om}$ ratios. The other species showing moderate correlations with Al_{im} are high profile, filamentous. However, these species were likely sub-dominate to *E. trinacria* during periods of high Al_{im} , as their relationship with Al_{im} were relatively weak in comparison during the periods of highest acidity in October and March.

Other environmental variables emerging as predictors of diatom composition across different sampling periods included SiO₂, conductivity, and concentrations of ions (Na⁺, F⁻, SO₄²⁻, and NO₃⁻). The importance of silica as a predictor may be attributed to the high requirements of diatoms for this nutrient to build their siliceous shells. Likewise, diatom distributions are shown to be sensitive to conductivity and individual ion concentrations, with among species variability in optima (Potapova and Charles, 2003; Soininen, 2007).

In this chapter, I examine the relative importance of deterministic versus stochastic processes in shaping diatom communities in acid stressed streams. My results confirm that the relative importance of these factors do differ across periods of low and high acidity, but the correlation of species turnover with geographic distance was always weak compared to the correlation with environmental distance. Likewise, pure spatial factors explained very little variance in diatom composition, which was most strongly correlated with level of acidification followed by source of acidity (i.e., color). Although Heino (2013) recommended considering dispersal-related processes in bio-assessment, my results indicate that at the regional scale of two river basins, stochastic dispersal plays a negligible role for diatom communities in acid-stressed streams. The fact that diatom communities are primarily determined by their environment at this spatial scale makes them reliable indicators of acidification and source of acidity, as species-environment relationships are not confounded by dispersal-related factors.

Chapter 5

Conclusion

For over 40 years, acid deposition has been recognized as a serious international environmental problem, but efforts to restore acidified streams and biota have had limited success. Furthermore, the need to better understand the effects of different sources of acidity on streams has become more pressing with the recent increases in surface water organic acids, or “brownification,” associated with climate change and decreased inorganic acid deposition. In chapter 2, I carried out a large-scale multi-seasonal investigation in the Adirondacks, one of the most acid-impacted regions in the United States, to assess how producer composition in acid streams responds to watershed influences and whether these influences can be used in acidification remediation. I explored the pathways of wetland control on aluminum chemistry and diatom taxonomic and functional composition. The results demonstrate that streams with larger watershed wetlands have higher organic content, lower concentrations of acidic anions, and lower ratios of inorganic to organic monomeric aluminum, all beneficial for diatom biodiversity and high-biomass producing guilds. Although brownification has been viewed as a form of pollution, these results indicate that it may be a stimulating force for primary producers. This research also reveals that the mechanism of watershed control of local stream diatom biodiversity through wetland export of organic matter is universal in running waters, operating not only in hard streams, as previously reported, but also in acid streams. These findings that the negative impacts of acid deposition on Adirondack stream chemistry and biota can be mitigated by wetlands have important implications for biodiversity conservation and stream ecosystem management. Future acidification research should focus on the potential for wetlands to improve stream ecosystem health

in acid-impacted regions and their direct use in stream restoration, e.g. through stream rechanneling or wetland construction in appropriate hydrologic settings.

Chapter 3 focused more on the impacts of acidification and source of acidity on diatom diversity but examined three components of diversity, including alpha, beta, and gamma diversity. Alpha diversity refers to the diversity within a single stream, beta diversity refers to the variation in species composition among streams, and gamma diversity refers to the diversity of an entire region. Other studies have shown that stressful environmental conditions and anthropogenic disturbance have a homogenizing effect on species composition, reducing beta diversity (Chase 2007; Passy and Blanchet 2007). Because of these findings, beta diversity has become more of an important measurement in applied environmental research. The results of chapter 3 are the first to demonstrate that acidification and source of acidity influence all three components of diversity, with organically acidified streams showing higher alpha, beta, and gamma diversity compared to inorganically acidified streams.

In chapter 4, I assessed whether diatom communities are more structured by deterministic processes (i.e., species traits and environmental tolerances) or stochastic processes such as random dispersal, colonization, birth, and death. This question is relevant to both theoretical and applied ecology, as stressful environmental conditions may reduce the importance of stochastic processes in community assembly (Chase 2007). Consistent with these findings, my results indicate that diatom communities in Adirondack streams are overwhelmingly deterministic, with geographic distance and pure spatial factors explaining very little variation in community composition. These findings suggest that diatoms are excellent predictors of acidification and source of acidity, as species-environmental relationships are not confounded by dispersal-related processes

Appendix A

Guild classifications for all 171 diatom taxa found in Adirondack streams in this study.

Taxon	Guild
<i>Achnanthes calcar</i> Cleve	low profile
<i>Achnanthes exigua</i> Grunow	low profile
<i>Achnantheidium minutissimum</i> (Kützing) Czarnecki	low profile
<i>Actinella punctata</i> Lewis	high profile
<i>Amphora ovalis</i> Kützing	low profile
<i>Amphora pediculus</i> (Kützing) Grunow	low profile
<i>Aulacoseira distans</i> (Ehrenberg) Simonsen	high profile
<i>Brachysira serians</i> (Brébisson) Round & Mann	motile
<i>Brachysira vitrea</i> (Grunow) Ross	motile
<i>Caloneis bacillum</i> (Grunow) Cleve	motile
<i>Cavinula pseudoscutiformis</i> (Hustedt) Mann & Stickle	motile
<i>Cavinula scutiformis</i> (Grunow ex Schmidt) Mann et Stickle	motile
<i>Cocconeis placentula</i> Ehrenberg	low profile
<i>Craticula halophila</i> (Grunow) Mann	motile
<i>Cymbella affinis</i> Kützing	low profile
<i>Cymbella aspera</i> (Ehrenberg) Cleve	high profile
<i>Cymbella caespitosa</i> (Kützing) Schutt	high profile
<i>Cymbella cistula</i> (Ehrenberg) Kirchner	high profile
<i>Cymbella ehrenbergii</i> Kützing	high profile
<i>Cymbella parva</i> (Smith) Kirchner	low profile
<i>Cymbella tumidula</i> Grunow	low profile
<i>Cymbella turgidula</i> Grunow	high profile
<i>Cymbopleura naviculiformis</i> Auerswald ex Héribaud	low profile

<i>Cymbopleura subrostrata</i> (Cleve) Krammer	high profile
<i>Denticula</i> sp.	motile
<i>Diadesmis contenta</i> (Grunow ex Van Heurck) Mann	motile
<i>Diatoma anceps</i> (Ehrenberg) Kirchner	high profile
<i>Diatoma hyemalis</i> (Roth) Heiberg	high profile
<i>Diatoma mesodon</i> Kützing	high profile
<i>Diatoma vulgaris</i> Bory	high profile
<i>Diploneis elliptica</i> (Kützing) Cleve	motile
<i>Encyonema lunatum</i> (Smith) Van Heurck	high profile
<i>Encyonema minutum</i> (Hilse) Mann	high profile
<i>Encyonema neogracile</i> Krammer	high profile
<i>Encyonema prostratum</i> (Berkeley) Kützing	high profile
<i>Encyonema silesiacum</i> (Bleisch) Mann	high profile
<i>Encyonopsis cesatii</i> (Rabenhorst) Krammer	low profile
<i>Eucocconeis flexella</i> (Kützing) Meister	low profile
<i>Eucocconeis laevis</i> (Østrup) Lange-Bertalot	low profile
<i>Eunotia arcus</i> Ehrenberg	high profile
<i>Eunotia bidentula</i> Smith	high profile
<i>Eunotia bigibba</i> Kützing	high profile
<i>Eunotia bilunaris</i> (Ehrenberg) Schaarschmidt	high profile
<i>Eunotia carolina</i> Patrick	high profile
<i>Eunotia cisalpina</i> Lange-Bertalot & Cantonati	high profile
<i>Eunotia exigua</i> (Brébisson ex Kützing) Rabenhorst	low profile
<i>Eunotia exsecta</i> (Cleve-Euler) Nörpel-Schempp & Lange-Bertalot	high profile
<i>Eunotia faba</i> (Ehrenberg) Grunow	high profile

<i>Eunotia fallax</i> Cleve	high profile
<i>Eunotia flexuosa</i> (Brébisson ex Kützing) Kützing	high profile
<i>Eunotia glacialis</i> Meister	high profile
<i>Eunotia hexaglyphis</i> Ehrenberg	high profile
<i>Eunotia implicata</i> Nörpel, Lange-Bertalot & Alles	high profile
<i>Eunotia incisa</i> Smith ex Gregory	high profile
<i>Eunotia intermedia</i> (Krasske) Nörpel & Lange-Bertalot	high profile
<i>Eunotia meisteri</i> Hustedt	high profile
<i>Eunotia microcephela</i> Krasske	high profile
<i>Eunotia minor</i> (Kützing) Grunow	high profile
<i>Eunotia monodon</i> Ehrenberg	high profile
<i>Eunotia nymanniana</i> Grunow	high profile
<i>Eunotia paludosa</i> Grunow	high profile
<i>Eunotia parallela</i> Ehrenberg	high profile
<i>Eunotia paratridentula</i> Lange-Bertalot & Kulikovskiy	low profile
<i>Eunotia pectinalis</i> (Kützing) Rabenhorst	high profile
<i>Eunotia rhombiodea</i> Hustedt	high profile
<i>Eunotia richbuttensis</i> Furey, Lowe & Johansen	high profile
<i>Eunotia septentrionalis</i> Østrup	high profile
<i>Eunotia serra</i> Ehrenberg	high profile
<i>Eunotia soleirolii</i> (Kützing) Rabenhorst	high profile
<i>Eunotia sudetica</i> Müller	high profile
<i>Eunotia tautoniensis</i> Hustedt	high profile
<i>Eunotia tetraodon</i> Ehrenberg	high profile
<i>Eunotia trinacria</i> Krasske	low profile

<i>Fragilaria capucina</i> Desmazières	high profile
<i>Fragilaria construens</i> (Ehrenberg) Grunow	high profile
<i>Fragilaria crotonensis</i> Kitton	high profile
<i>Fragilaria delicatissima</i> (Smith) Lange-Bertalot	high profile
<i>Fragilaria vaucheriae</i> (Kützing) Petersen	high profile
<i>Fragilariforma virescens</i> (Ralfs) Williams & Round	high profile
<i>Frustulia rhomboides</i> (Ehrenberg) De Toni	high profile
<i>Frustulia vulgaris</i> (Thwaites) De Toni	high profile
<i>Geissleria declivis</i> (Hustedt) Lange-Bertalot	motile
<i>Gomphonema acuminatum</i> Ehrenberg	high profile
<i>Gomphonema angustatum</i> (Kützing) Rabenhorst	high profile
<i>Gomphonema clevei</i> Fricke	high profile
<i>Gomphonema gracile</i> Ehrenberg	high profile
<i>Gomphonema parvulum</i> (Kützing) Kützing	high profile
<i>Gomphonema pumillum</i> (Grunow) Reichardt & Lange-Bertalot	high profile
<i>Gomphonema truncatum</i> Ehrenberg	high profile
<i>Hantzschia amphioxys</i> (Ehrenberg) Grunow	motile
<i>Hippodonta lesmonensis</i> (Hustedt) Lange-Bertalot, Metzeltin & Witkowski	motile
<i>Karayevia clevei</i> (Grunow) Bukhtiyarova	low profile
<i>Luticola goeppertiana</i> (Bleisch) Mann	motile
<i>Mastogloia</i> sp.	motile
<i>Melosira varians</i> Agardh	high profile
<i>Meridion circulare</i> (Greville) Agardh	high profile
<i>Navicula angusta</i> Grunow	motile
<i>Navicula cryptocephalla</i> Kützing	motile

<i>Navicula cryptotenella</i> Lange-Bertalot	motile
<i>Navicula lanceolata</i> Ehrenberg	motile
<i>Navicula meniscus</i> Schumann	motile
<i>Navicula radiosa</i> Kützing	motile
<i>Navicula rhynchocephala</i> Kützing	motile
<i>Navicula tripunctata</i> (Müller) Bory de Saint-Vincent	motile
<i>Navicula viridula</i> (Kützing) Ehrenberg	motile
<i>Naviculadicta vitabunda</i> (Hustedt) Lange-Bertalot	motile
<i>Neidium affine</i> (Ehrenberg) Pfizer	motile
<i>Neidium bisulcatum</i> (Lagerstedt) Cleve	motile
<i>Neidium iridis</i> (Ehrenberg) Cleve	motile
<i>Neidium ladogensis</i> (Cleve) Foged	motile
<i>Nitzschia dissipata</i> (Kützing) Grunow	motile
<i>Nitzschia gracilis</i> Hantzsch	motile
<i>Nitzschia linearis</i> (Agardh) Smith	motile
<i>Nitzschia obtusa</i> Smith	motile
<i>Nitzschia palea</i> (Kützing) W.Smith	motile
<i>Nitzschia recta</i> Hantzsch ex Rabenhorst	motile
<i>Nitzschia sigma</i> (Kützing) Smith	motile
<i>Nupela lapidosa</i> (Krasske) Lange-Bertalot	low profile
<i>Pinnularia acidophila</i> Hofmann & Krammer	motile
<i>Pinnularia acrosphaeria</i> Smith	motile
<i>Pinnularia acuminata</i> Smith	motile
<i>Pinnularia anglica</i> Krammer	motile
<i>Pinnularia angusta</i> (Cleve) Krammer	motile

<i>Pinnularia biceps</i> Gregory	motile
<i>Pinnularia borealis</i> Ehrenberg	motile
<i>Pinnularia braunii</i> (Grunow) Cleve	motile
<i>Pinnularia brebissonii</i> (Kützing) Rabenhorst	motile
<i>Pinnularia conifera</i> (Brun & Heribaud) Krammer	motile
<i>Pinnularia divergens</i> Smith	motile
<i>Pinnularia erratica</i> Krammer	motile
<i>Pinnularia gibbiformis</i> Krammer	motile
<i>Pinnularia mesogongyla</i> Cleve	motile
<i>Pinnularia mesolepta</i> (Ehrenberg) W. Smith	motile
<i>Pinnularia microstauron</i> var. <i>nonfasciata</i> Krammer	motile
<i>Pinnularia nobilis</i> var. <i>regularis</i> Krammer	motile
<i>Pinnularia obscura</i> Krasske	motile
<i>Pinnularia polyonca</i> (Brébisson) W. Smith	motile
<i>Pinnularia pulchra</i> Østrup	motile
<i>Pinnularia rhomboelliptica</i> Krammer	motile
<i>Pinnularia similiformis</i> Krammer	motile
<i>Pinnularia sinistra</i> Krammer	motile
<i>Pinnularia subanglica</i> Krammer	motile
<i>Pinnularia subcapitata</i> Gregory	motile
<i>Pinnularia subcommutata</i> var. <i>nonfasciata</i> Krammer	motile
<i>Pinnularia tabellaria</i> Ehrenberg	motile
<i>Pinnularia viridis</i> (Nitzsch) Ehrenberg	motile
<i>Placoneis elginensis</i> (Gregory) Cox	motile
<i>Placoneis hambergii</i> (Hustedt) Bruder	motile

<i>Placoneis ignorata</i> (Schimanski) Lange-Bertalot	motile
<i>Placoneis placentula</i> (Ehrenberg) Mereschkowsky	motile
<i>Planothidium frequentissima</i> (Lange-Bertalot) Round & L. Bukhtiyarova	low profile
<i>Planothidium peragalli</i> (Brun et Héribaoud) Round et Bukhtiyarova	low profile
<i>Psammothidium bioretii</i> Germain	low profile
<i>Psammothidium marginulatum</i> (Grunow) Bukhtiyarova & Round	low profile
<i>Psammothidium rossii</i> (Hustedt) Bukhtiyarova & Round	low profile
<i>Psammothidium subatomoides</i> (Hustedt) Lange-Bertalot & Archibald	low profile
<i>Pseudostaurosira parasitica</i> (Smith) Morales	high profile
<i>Rhoicosphenia abbreviata</i> (Argardh) Lange-Bertalot	high profile
<i>Rossithidium linearis</i> (Smith) Round & Bukhtiyarova	low profile
<i>Selaphora pupula</i> (Kützing) Mereschkowsky	motile
<i>Sellaphora americana</i> (Ehrenberg) Mann	motile
<i>Stauroneis anceps</i> Ehrenberg	motile
<i>Stauroneis phoenicenteron</i> (Nitzsch) Ehrenberg	motile
<i>Staurosira leptostauron</i> Ehrenberg	high profile
<i>Stenopterobia curvula</i> (Smith) Krammer	motile
<i>Surirella caproni</i> Brébisson ex F.Kitton	motile
<i>Surirella moelleriana</i> Grunow	motile
<i>Surirella linearis</i> Smith	motile
<i>Synedra ulna</i> (Nitzsch) Ehrenberg	high profile
<i>Tabellaria flocculosa</i> (Roth) Kützing	high profile
<i>Tabellaria quadrisepta</i> Knudson	high profile

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Biographical Information

Katrina was born in Houston, Texas. She earned a bachelor's of science in ecology, evolution, and behavior from the University of Texas at Austin and a master's degree in aquatic biology from Texas State University, San Marcos. Her master's project was analyzing the gut content of an invasive, herbivorous fish, which sparked her interest in periphyton communities. She decided to pursue a PhD at the University of Texas at Arlington so that she could study stream algal ecology under her supervising professor Sophia Passy. While working on her PhD, she met and married her husband Richard Pound. Katrina is interested in research related to stream ecology.