Contrast and comparison of aerial algal communities from two distinct regions in the U.S.A., the Great Smoky Mountains National Park (TN) and the Lake Superior region

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Abstract: The Great Smoky Mountains National Park (GSMNP) and the land surrounding Lake Superior (LSR) are rich in aerial habitats and support diverse aerial algal communities. Currently, the ecology of aerial algal communities is not well understood. Furthermore, no research has been published directly comparing aerial algal floras between geographic regions. We analyzed the ecology of the aerial habitats within each region and compared the overall algal flora between these two regions. Physical and chemical factors, including aspect, moisture levels, light levels, and pH were measured at each sampling location. Communities from both regions were dominated by cyanobacteria with average relative abundances >50% in both the GSMNP and LSR. The aerial algal flora of the GSMNP as a whole was not distinct from that of the LSR. Taxa unique to each region were found to be present in low abundances, while many taxa present in higher abundance were found in both the LSR and GSMNP communities. Non–metric multidimensional scaling ordination of the community data from both regions identified two distinct communities within the GSMNP. Moisture availability within sites contributed to this separation with higher mean relative of abundances of cyanobacteria in the drier habitats and higher mean relative abundances of chlorophytes and diatoms in the wetter habitats.

Key words: Aerial habitat, cyanobacteria, diatoms, Great Smoky Mountains National Park, moisture, NMDS

Introduction

The ecology of aerial algal communities has been understudied relative to aquatic communities and is presently not well understood. Most of the research on aerial habitats has been floristic in nature, focusing on the description and identification of species that are present in these areas (Dodd & Stoermer 1962; Lowe & Collins 1973; Mcmillan & Rushforth 1985). The majority of ecological studies that have been performed on aerial algae are on bryophytic diatom communities mainly in the Arctic and Antarctic (Beyens 1989; Van De Vijver & Beyens 1997; Van Kerckvoorde et al. 2000; Van De Vijver et al. 2008). There have been limited ecological studies of aerial communities from the northern temperate zone (Camburn 1982; Camburn 1983; Rindi et al. 1999; Rindi & Guiry 2004; Lowe et al. 2007; Furey et al. 2007), however, there have been many studies focusing on cryptogamic soil crust communities (Johansen et al. 1984; Johansen & Rushforth 1985; Johansen & St. Clair 1986; Johansen et al. 1993). These ecological studies do demonstrate the significant impact of moisture in these habitats. Moisture availability can be quite variable in these habitats due to the often ephemeral water sources. Sources for water in aerial habitats include groundwater seeps, precipitation, humidity, or waterfall spray. In addition to creating moisture variability across aerial habitats, moisture can vary daily or seasonally within a particular habitat. This fluctuation in moisture can influence the species inhabiting these areas. Species diversity can also be affected by moisture and has been shown to increase as moisture availability increases (Camburn 1983; Johansen et al. 1983; Casamatta et al. 2002).

There has been no published research directly comparing aerial algal floras between geographic regions. While moisture may exert the greatest influence on community composition within a geographic area, other factors may become more influential when examining community composition between different regions. Variables such as pH, geology, and climate may play a role in structuring the general flora of the area while moisture may influence local variability. The Great Smoky Mountains National Park (GSMNP) and the land surrounding Lake Superior in the Upper Peninsula (UP) of Michigan and Ontario, Canada, are abundant in aerial algal habitats. Natural habitats created from stream cuts, waterfall spray, and exposed bedrock, in addition to habitats created by road cuts all provide potential areas for aerial algal communities to develop. We examined both the ecology of habitats within each region and compared the overall flora between the two regions.

We anticipated that the overall aerial algal communities would differ between the two study areas. While there may be some cosmopolitan taxa present across the two regions, we believed that the overall flora from the Lake Superior region (LSR) would be distinct from that of the GSMNP. We expected these two areas to support distinct aerial algal flora due to environmental differences such as climate, geology, and pH. Within the study areas, we expected to see community similarities related to available moisture.

Study Areas

The area of the UP is 42,610 km² and it lies between 45° and 47° north latitude. Elevations range from 179 m to 603 m. The UP belongs to the Western Great Lakes forests ecoregion of the temperate hardwood and broadleaf forest biome. The UP is part of the physiographic region known as the Canadian Shield. The Canadian land surrounding Lake Superior also belongs to the Canadian Shield. The Canadian Shield is mainly comprised of igneous rock covered with a thin soil layer resulting in many areas of exposed bedrock. The north shore of Lake Superior lies at 49° north latitude and is within the boreal forest biome. Both of these areas are within the cool temperate zone. These two locations will be collectively referred to as the LSR for the remainder of this manuscript. The Köppen climate classification for the LSR is a humid continental climate characterized by variable weather conditions and a large range in seasonal temperatures (Peel et al. 2007). Precipitation is greatest during the summer months in this climate.

The GSMNP is located across the Tennessee–North Carolina state line and covers approximately 2,000 km². Elevations range from 267 m to 2025 m. The park lies at 35° north latitude. The GSMNP belongs to the Appalachian–Blue Ridge Forest ecoregion of the temperate hardwood and broadleaf forest biome. One of the largest tracts of deciduous, temperate, old–growth forest in North America is found in the park. The GSMNP belongs to the physiographic region known as the Blue Ridge Mountains and is within the warm temperate zone. The Köppen climate classification for the GSMNP is a humid subtropical climate which is distinguished by relatively mild winters and warm summers (Peel et al. 2007). This climate type experiences high levels of humidity and precipitation that is fairly evenly distributed throughout the year. However, the large variability in elevation within the GSMNP results in significantly variable climate with increasing precipitation and decreasing temperatures as elevation increases (Shanks 1954).

Air pollution has been a documented problem in the GSMNP for several decades. The burning of fossil fuels has resulted in acid precipitation from the atmospheric deposition of sulphur dioxide and nitrogen oxides. The annual precipitation in the GSMNP is five to ten times more acidic than natural rain (National Park Service 2005). This acid precipitation results in the buildup of sulfate and nitrate in the soils as well as the release of aluminum and other toxic metals from the soil (Castro & Morgan 2000; Driscoll et al. 2003).

Methods

Aerial algal samples were collected from the LSR in July and August, 2006. Habitats similar to those found in the LSR were targeted in the GSMNP and were collected from in June and July, 2007. Descriptions of the habitat as well as physical and chemical variables, including pH, moisture levels, light levels, aspect, rock type, and substrate type (epilithon or epiphyton) were recorded for each site. The pH was measured using EMD colorpHast pH–indicator strips (range: 2.5 to 10 pH units; sensitivity of 0.2 to 0.3 pH units) in order to provide an estimate of differences in the acidity of sampling locations. Moisture levels were estimated employing a piece of sponge was placed on each rock face for five or ten seconds, depending upon moisture content of the habitat. The difference in weight of the sponge after removal from the substrate was recorded for each site and values were standardized across sites. The light levels for the LSR were measured using a Licor light meter (LI–189). A Quantum light meter (model QMSS) was used in the GSMNP. Samples were preserved in at least 2% glutaraldehyde.

Samples were analyzed with an Olympus BX51 Photomicroscope with high resolution Nomarski DIC optics, and digital images were recorded with a Spot® camera attached to the microscope and a computer. A minimum of 600 algal units were counted from each sample, and the non–diatom algae were identified from this material. Diatoms counted in each sample were identified from cleaned permanent mounts. Permanent mounts were made by boiling an aliquot of each sample in nitric acid, air drying the cleaned material onto cover glasses, and mounting the material in Naphrax. Algae were identified to the lowest taxonomic level possible using standard references. References consisted of: Geitler (1932), Krammer & Lange–Bertalot (1986), Krammer & Lange–Bertalot (1988), Krammer & Lange–Bertalot (1991a), Krammer & Lange–Bertalot (1991b), Komárek & Anagnostidis (1999), Potapova et al. (2003), Wehr & Sheath (2003), Komárek & Anagnostidis (2005), Thomas et al. (2009), and Furey et al. (2011).

Relative abundances of each taxon were calculated for each sample. Rare taxa were removed from the combined data set prior to statistical analysis. Taxa that did not occur in at least one site with a relative abundance of 2% were considered rare and removed from the data set. This reduced the total number of taxa from 365 to 191. Four moisture categories were created from the sponge measurements for the purpose of statistical analysis. The four categories included dry, damp, wet, and very wet. Weight change less than 0.1 g was considered dry, weight change between 0.1–1.0 g was considered damp, weight change between 1.0–5.0 g was considered wet, and weight change greater than 5.0 g was considered very wet. Algal community patterns were explored via non–metric multidimensional scaling (NMDS) of Bray Curtis similarities of log transformed data. An analysis of similarities (ANOSIM) was used to determine significance among the clusters identified in the NMDS ordinations. Taxa contributing to the clusters were identified through similarity percentages analysis (SIMPER).

Results

Twenty samples were randomly selected for analysis from the LSR. In these samples, pH ranged from 5.2 to 8.8 and light levels ranged from 002–1385 µmol. m^{-2}. s^{-1}. Sixty–six algal genera and 238 taxa were identified, of which 170 were unique to the LSR. Of these taxa, the majority were identified from three divisions, the Cyanophyta, Bacillariophyceae and Chlorophyta, with average relative abundances of 56.1%, 33.7%, and 9.5% respectively. Taxa belonging to the Chrysophyta comprised an average relative abundance of less than 0.5%. In the LSR, nineteen taxa were considered common occurring in >20% of the samples (Table S1). Of these, *Achnanthidium minutissimum* (Kützing) Czarnecki, *Aphanocapsa* cf. *fusco–lutea* Hansgirg, *Leptolyngbya* sp. 2, *Limnothrix* sp. 1, *Pseudanabaena* cf. *minima* (G.S.An) Anagnostidis occurred in >40% of the samples. Taxa with the highest average relative abundances included *Leptolyngbya* cf. *subtilissima* (Kützing ex Hansgirg) Komárek (8.0%), *Gloeothece tepidariorum* (A.Braun) Lagerheim (4.4%), *Leptolyngbya* sp. 2 (4.3%), and *Mougeotia* spp. (4.0%) (Table S1).

Twenty random samples were also analyzed from the GSMNP collections. Of the samples analyzed, pH ranged from 3.0 to 7.9 and light levels ranged from 001–780 µmol. m^{-2}. s^{-1}. Fifty–five algal genera and 190 taxa were identified, of which 122 were unique to the GSMNP. These taxa belonged to three divisions, the Cyanophyta, Bacillariophyceae and Chlorophyta, with average relative abundances of 64.5%, 19.0%, and 14.3% respectively. Thirteen taxa were considered common in the GSMNP, occurring in >20% of the samples (Table S2). Of these, *A. minutissimum*, *Leptolyngbya* sp. 2, and *P.* cf. *minima* occurred in >35% of the samples. Taxa with the highest average relative abundances included *Nostoc sphaericum* Vaucher ex Bornet & Flahault (6.6%), *P.* cf. *minima* (5.9%), *Leptolyngbya* sp. 2 (5.4%), and *A. minutissimum* (3.2%) (Table S2).

The algal communities from both the GSMNP and LSR were dominated by cyanobacteria with mean relative abundances over 50%. More than half of the common taxa, eleven of nineteen, in the LSR were cyanobacteria (Table S1), but less than half of the common taxa, five of thirteen, in the GSMNP were cyanobacteria (Table S2). Just over half of the common taxa in the GSMNP were diatoms (Table S2).

Of the common taxa found in each region, seven taxa were found to be common to both regions (Table S1–S2). These taxa consisted of *A. minutissimum*, *A.* cf. *fusco–lutea*, *L.* cf. *subtilissima*, *Leptolyngbya* sp. 2, *N. sphaericum*, *P.* cf. *minima*, and unknown coccoid Chlorophyte sp.1. The majority of these taxa were present with high relative abundances in the samples from each region with the exception of *A.* cf. *fusco–lutea* and *L.* cf. *subtilissima* with mean relative abundances of 0.6% and 1.2% respectively in the GSMNP, and unknown coccoid Chlorophyte sp.1 with a mean relative abundance of 0.3% in the LSR.

In the LSR, there were 22 taxa with a mean relative abundance greater than 1% with five taxa unique to the LSR region (Table S3). There were 26 taxa in the GSMNP with a mean relative abundance greater than 1%, and of these taxa, 11 were unique to the GSMNP (Table S4). In each region, over 50% of the taxa with a mean relative abundance over 1% were cyanophytes.

The NMDS ordination of the community data did not show distinct separation between the two regions (Figure 1) which was confirmed with the ANOSIM analysis (*p*–value 0.114). However, there was separation in the GSMNP samples, forming two distinct groups with the LSR samples bisecting those groups (Fig. 1). The results from the ANOSIM revealed a significant difference between the GSMNP 1 and GSMNP 2 (*p*–value 0.001) groups as well as between the GSMNP 2 and LSR groups (*p*–value 0.001) (Table 1). Eleven taxa contributed to approximately 50% of the dissimilarity between the two GSMNP groups (Table S5), while seventeen taxa contributed to approximately 50% of the dissimilarity between the GSMNP 2 and LSR groups (Table S6). There was some clustering in the NMDS ordination based on moisture availability with separation between the two extreme moisture categories (Fig. 2). The results from the ANOSIM did not show that a significant difference existed among the moisture categories (Table 2). The lack of significance among the moisture categories was possibly due to the relatively loose clustering of sites within each moisture category. There were no patterns detected for any of the remaining physical and chemical data.

The NMDS ordination for each of the regions did demonstrate separation when the data were categorized by moisture (Figs 3–4). For both the LSR and GSMNP community data, separation was seen between the two extreme moisture categories. However, the ANOSIM found no significant difference among the moisture categories for either region (Table 2). The lack of significance among moisture categories was most likely due to the small sample size within each category. For both regions, there were few to no diatoms present in moisture category "Dry", while diatoms comprised over 60% mean relative abundance in moisture category "Very Wet" for the LSR and over 50% for the GSMNP. Species diversity was highly variable across all samples from each region (Table 3). There was no significant difference found among the species diversity of the communities from the different moisture categories for each region (LSR $p>0.38$, GSMNP $p>0.06$).

In order to explore broad scale patterns, data were consolidated from species to division for each sample. The NMDS ordination of the division data showed no clustering based on region (Fig. 5). A

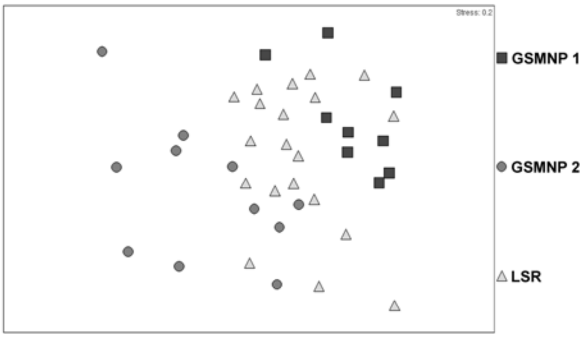

Fig. 1. Non–metric multidimensional scaling plot categorized by region (GSMNP=Great Smoky National Park and LSR=Lake Superior region) of species data for samples of aerial algal communities. Samples from the GSMNP formed two distinct clusters and were coded differently (GSMNP 1, GSMNP 2) to illustrate the separation.

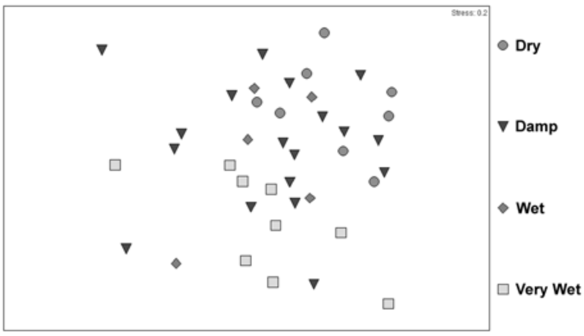

Fig. 2. Non–metric multidimensional scaling plot categorized by moisture categories of species data for samples of aerial algal communities from the Lake Superior region and the Great Smoky Mountains National Park.

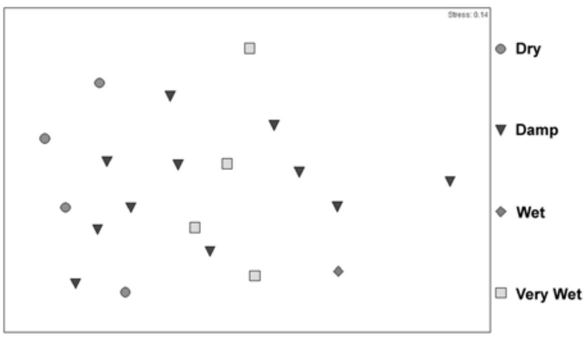

Fig. 3. Non–metric multidimensional scaling plot categorized by moisture of species data for samples of aerial algal communities from the Great Smoky Mountains National Park region.

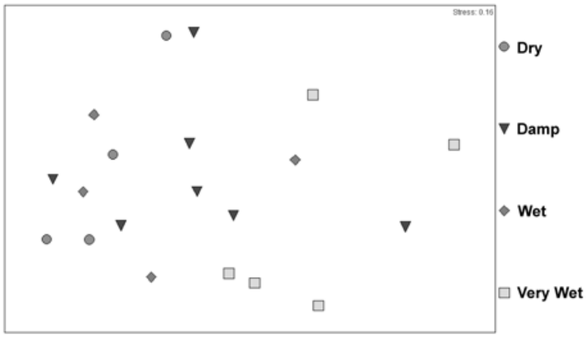

Fig. 4. Non–metric multidimensional scaling plot categorized by moisture categories of species data for samples of aerial algal communities from the Lake Superior region.

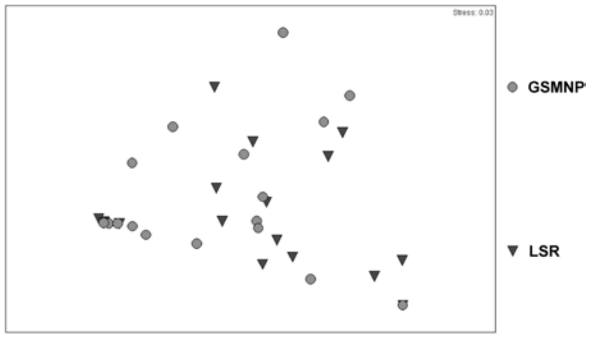

Fig. 5. Non–metric multidimensional scaling plot categorized by region (GSMNP=Great Smoky National Park and LSR=Lake Superior region) of division data for samples of aerial algal communities.

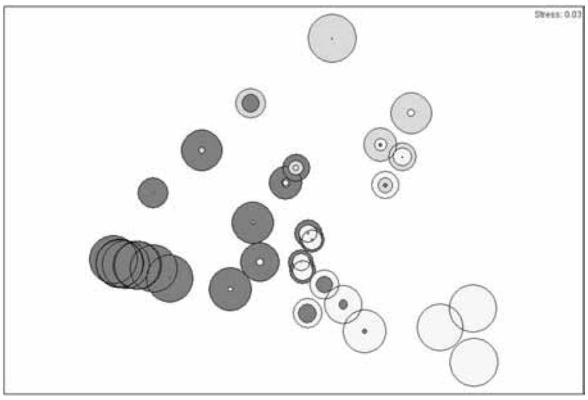

Fig. 6. Bubble plot of samples from NMDS ordination displaying relative abundance of each division in each sample from the Lake Superior region and the Great Smoky Mountains National Park (green =Chlorophyta, yellow=Bacillariophyta, red=Cyanophyta). Each sample is represented by a bubble and corresponds to the abundance of each division within that sample. Samples represented by one bubble were comprised of taxa from only one division, while samples represented by bubbles within bubbles were comprised of taxa from more than one division; abundance corresponds to size of bubble.

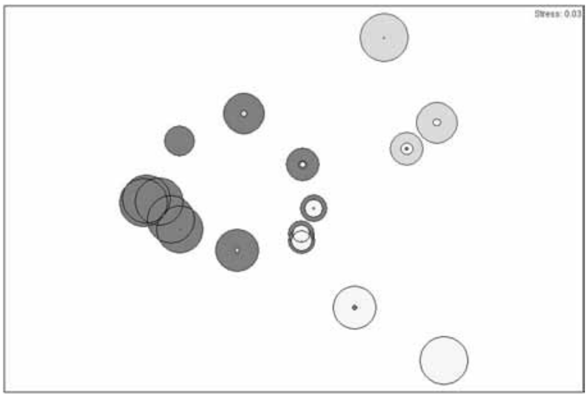

Fig. 7. Bubble plot of samples from NMDS ordination displaying relative abundance of each division in each sample from the Great Smoky Mountains National Park (green =Chlorophyta, yellow=Bacillariophyta, red=Cyanophyta). Each sample is represented by a bubble and corresponds to the abundance of each division within that sample. Samples represented by one bubble were comprised of taxa from only one division, while samples represented by bubbles within bubbles were comprised of taxa from more than one division; abundance corresponds to size of bubble.

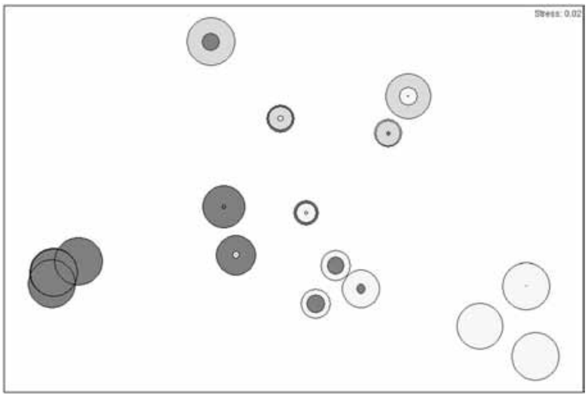

Fig. 8. Bubble plot of samples from NMDS ordination displaying relative abundance of each division in each sample from the Lake Superior region (green =Chlorophyta, yellow=Bacillariophyta, red=Cyanophyta). Each sample is represented by a bubble and corresponds to the abundance of each division within that sample. Samples represented by one bubble were comprised of taxa from only one division, while samples represented by bubbles within bubbles were comprised of taxa from more than one division; abundance corresponds to size of bubble.

bubble plot created from the NMDS ordination did reveal a pattern for the three divisions, Cyanophyta, Chlorophyta, and Bacillariophyta, across all samples (Fig. 6). The samples formed a triangular pattern in the plot, with each tip of the triangle representing high relative abundance for one of the three divisions. Upon examining the uncategorized physical and chemical data, no variable could explain the pattern seen in the plot. Similar patterns were seen in the bubble plots for each region (Figs 7–8), but again, the physical and chemical data could not explain the patterns.

Discussion

Aerial algal communities from both the LSR and GSMNP were dominated by cyanobacteria, with mean relative abundances greater than 50%. Cyanobacteria have typically been found to dominate communities in aerial habitats (Broady 1989; Alfinito et al. 1998; Matthes–Sears 1999). Cyanobacteria are also often found to be the first algal colonizers in aerial habitats (Diels 1914; Hayren 1940; Johansen et al. 1983). The tolerance of many cyanobacterial taxa to wide ranges of moisture and light may contribute to their dominance (Matthes–Sears 1999; Whitton & Potts 2000; Wynn–Williams 2000). It has been shown that cyanobacteria are able to survive and recover more quickly from desiccation than other algae (De Winder et al. 1989). Moisture availability can vary greatly in aerial habitats with algal communities experiencing either sporadic or frequent periods of desiccation. The unpredictability of moisture availability in many aerial habitats creates a major stress upon algae that colonize these areas. The ability of cyanobacteria to begin colonizing new aerial habitats before other algal groups combined with their tolerance to desiccation give them a competitive advantage in these habitats.

The aerial algal flora of the GSMNP as a whole was not distinct from that of the LSR. However, the NMDS ordination did identify two distinct communities within the GSMNP when analyzing the entire data set of both regions (Fig. 1). The GSMNP 1 group had higher mean relative of abundances of cyanobacterial taxa while the GSMNP 2 group had higher mean relative abundances of chlorophytes and diatoms (Table 2). Cyanobacteria are commonly found to dominate extremely dry habitats while the numbers of diatom taxa increase with increasing moisture availability (Pentecost 1992; Casamatta et al. 2002). Moisture availability did contribute to the separation of the two GSMNP groups, with the driest sites within GSMNP 1 and the wettest sites within GSMNP 2 (Figure 2). However, there were sites in both GSMNP groups with intermediate levels of moisture.

Research conducted by Matthes–Sears et al. (1999) found no effects of moisture on algal community composition but attributed this finding to the small range in moisture variability across their study site. Despite the relatively wide range in moisture availabilities in the present study, NMDS ordinations for the LSR–GSMNP combined, the LSR, and the GSMNP community data only revealed separation between the two extreme moisture categories (Figs 2–4). This is possibly due to the fact that algal community composition has a distinct response to extremes of moisture availability while intermediate moisture levels illicit variable responses. Cyanobacteria dominated the "dry" sites while diatoms were almost completely absent (Tables S7–S8). The absence or near absence of diatoms from aerial habitats with low levels moisture is common (Pentecost 1992;

Table 1. Analysis of similarities results for aerial algal community data in each region (LSR=Lake Superior region and GSMNP=Great Smoky Mountains National Park) calculated from the Bray–Curtis Similarity Matrix; * indicates significance (Bonferroni correction factor α = 0.017 used for pairwise comparisons).

		Global R	*p*–value
Region		0.261	0.001*
	Pairwise Comparison	R Statistic	*p*–value
	GSMNP 1, GSMNP 2	0.446	0.001*
	GSMNP 1, LSR	0.12	0.077
	GSMNP 2, LSR	0.287	0.001*

Table 2. Analysis of similarities results of the aerial algal community data categorized by moisture for LSR–GSMNP Combined (LSR=Lake Superior region and GSMNP=Great Smoky Mountains National Park), the LSR, and the GSMNP calculated from the Bray–Curtis Similarity Matrix.

	Global R	*p*–value
LSR–GSMNP Combined	0.075	0.131
LSR	0.038	0.299
GSMNP	0.126	0.114

Casamatta et al. 2002). Species diversity was not found to increase with increasing moisture as has been shown in other studies (Camburn 1983; Johansen et al. 1983; Casamatta et al. 2002).

The physical and chemical characteristics of the LSR and GSMNP were not different enough to lead to distinct algal communities for each region. The range of pH in each region overlapped, and the light levels measured in the GSMNP overlapped the lower range of those measured in the LSR. However, the absence of measured light levels from the higher ranges in the GSMNP could possibly be due to the time of day the measurements were taken. Light exposure at a site depends upon the aspect as well as vegetation cover, and it may have been more revealing to measure maximum light exposure in a 24 hour period for each site. Also, measuring ultraviolet light levels may provide insight into aerial algal community composition and species distribution.

There were taxa that were unique to each region, but these taxa were present in low abundances and their absence from a site may be an artifact of analyzing 600 algal units. Many of the taxa that were present in higher abundance were found in both the LSR and GSMNP communities. Species dispersal may play a role in similarities seen between the community compositions of these regions. Algae have been shown to be easily transported by the wind (Brown et al. 1964). Taxa that can withstand desiccation have the potential to survive aerial transport. Many algal taxa from aerial habitats produce extracellular mucilage which allows them to withstand periods of desiccation (Patrick 1977; Shephard 1987; Potts 1999; Gerrath 2003). UV radiation can also impact the survival of cells in aerial transport. The ability of cyanobacteria to not only withstand desiccation but also to produce photoprotective pigments gives them a competitive advantage for longer distance aerial transport (De Winder et al. 1989; Garcia–Pichel et al. 1992; Ehling–Schulz et al. 1997).

The similarity of microhabitats between the LSR and GSMNP combined with the aerial dispersal of algal cells potentially contributed to the overall similarity of these aerial algal communities. Johansen et al. (1983) found that mucilage producing cyanobacteria and green algae are the first colonizers on moist rock faces, and once established, other species begin to colonize the mucilage. Many of the more abundant taxa from these regions are mucilage producing cyanobacteria which may have a greater potential to survive aerial dispersal and colonize aerial habitats in both regions. Once these establish, more localized species that cannot survive long distance transport can begin to colonize these communities.

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Table 3. Species diversity, represented by the Shannon–Weiner Index (H'), for each moisture category (Dry, Damp, Wet, Very Wet) in both the Lake Superior region (LSR) and the Great Smoky Mountains National Park (GSMNP).

LSR		GSMNP	
Moisture Category	H'	Moisture Category	H'
Dry	1.95	Dry	1.59
Dry	1.59	Dry	0.91
Dry	1.60	Dry	0.26
Dry	1.69	Dry	0.56
Damp	2.55	Damp	0.56
Damp	0.88	Damp	2.57
Damp	1.72	Damp	1.33
Damp	1.74	Damp	1.35
Damp	2.22	Damp	1.50
Damp	0.97	Damp	3.20
Damp	3.09	Damp	1.05
Wet	2.39	Damp	0.85
Wet	2.15	Damp	1.41
Wet	2.67	Damp	2.54
Wet	1.72	Damp	0.69
Very Wet	2.01	Wet	0.26
Very Wet	0.95	Very Wet	2.44
Very Wet	2.11	Very Wet	1.94
Very Wet	0.87	Very Wet	2.66
Very Wet	2.66	Very Wet	1.45

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Supplementary material

the following supplementary material is available for this article:

Table S1. List of common aerial algal taxa encountered across the Lake Superior region samples.

Table S2. List of common aerial algal taxa encountered across the Great Smoky Mountains National Park samples.

Table S3. Aerial algal taxa which occurred at a mean relative abundance (MRA) > 1% in the Lake Superior region (LSR) compared with the mean relative abundance in the Great Smoky Mountains National Park (GSMNP).

Table S4. Aerial algal taxa which occurred at a mean relative abundance (MRA) > 1% in the Great Smoky Mountains National Park (GSMNP) compared with the mean relative abundance in the Lake Superior region (LSR).

Table S5. Similarity percentages analysis displaying taxa contributing to the separation of Great Smoky Mountains National Park samples forming groups GSMNP 1 and GSMNP 2 in the non–metric multidimensional scaling ordination (Figure 1).

Table S6. Similarity percentages analysis displaying taxa contributing to the separation of groups Great Smoky Mountains National Park 2 (GSMNP 2) and Lake Superior region (LSR) in the non–metric multidimensional scaling ordination (Figure 1).

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