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Source: Natural Areas Journal, 30(4):417-424. 2010.
Published By: Natural Areas Association
DOI: http://dx.doi.org/10.3375/043.030.0407
URL: http://www.bioone.org/doi/full/10.3375/043.030.0407

CONSERVATION ISSUES

Potential Impacts of Climate Change on *Sphagnum* Bogs of the Southern Appalachian Mountains

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Natural Areas Journal 30:417–424

ABSTRACT: *Sphagnum b*ogs in the southern Appalachian Mountains of eastern North America are rare and diverse ecosystems; the unique climate range they occupy allows for a mixture of northern and southern species to thrive, creating isolated biodiversity hotspots. Research on northern bogs in Europe and North America has found that climate change and atmospheric nitrogen deposition can shift species composition of bog communities and release carbon; however, research on southern bogs has not begun to answer questions about their fate. We reviewed research conducted in northern bogs and applied this information to southern Appalachian bogs to explore the potential impacts that climate change may have on southern *Sphagnum* bogs. The projected increase in evapotranspiration coupled with nitrogen deposition may lead to the drying up of southern bogs causing: (1) increased decomposition rates, which can lead to the system becoming a carbon source rather than a sink; and (2) local extinction of many bog species, allowing alternative ecosystems to replace the bogs. Because of these threats, we suggest a call to action for scientists and managers to begin investigating the specific impacts that climate change will have on bogs in the southeastern United States so we may better protect and conserve these unique and diverse habitats.

Index terms: Appalachian Mountains, global warming, peatland, southeastern U.S., West Virginia

INTRODUCTION

The southern Appalachian Mountains of eastern North America are home to a diversity of wetland communities, including a series of bogs that run along the central line of the Appalachian Mountains as far south as North Carolina. These bogs are small in size (typically 0.05 to 10 ha) and dominated by the moss genus, *Sphagnum* L. (Cameron 1968, 1970; McDonald 1985; Byers et al. 2007). Southern Appalachians bogs are often species-rich, supporting many threatened and endangered species (e.g., Byers et al. 2007). Cool and moist climatic conditions in certain areas create unique community assemblages consisting of a diverse mix of northern and southern bog species (Warren et al. 2004). High diversity is also partly due to the long-term ecosystem stability of southern bogs, which has allowed for slow adaptation of species to the region's climatic conditions (Gajewski et al. 2001; Byers et al. 2007). Though *Sphagnum* bogs are less common in the southern United States than in the north, they have existed in the southern Appalachian landscape for at least 9500 years (Gajewski et al. 2001; Byers et al. 2007). Studies of northern peatlands (e.g., New England, Canada, and northern Europe) have shown that bogs are susceptible to the impacts of climate change and atmospheric nitrogen deposition (e.g., Malmer et al. 1994; Bragazza et al. 2006; Bubier et al. 2007; Robroek et al. 2007), but little work has been done to assess the potential impacts of climate change on *Sphagnum* bogs in the southern Appalachian Mountains.

The complex topography of the Appalachians has created small pocket bog ecosystems with unique substrate, elevation, slope, and aspect features. Within the southeastern United States, the Appalachians serve as a rare location for *Sphagnum* bogs because of their high elevation (≥ 800 m; Francl et al. 2004), which results in a cool microclimate (Byers et al. 2007). These ecosystems have existed since the last glaciation, and the peat deposits have been developing for the past 9000 to 13,000 years, typically in warmer conditions than bogs found in the north (Wieder et al. 1994).

Within the Appalachians, peat deposits generally decrease with a decrease in latitude, and the deposits become smaller, thinner, and more decomposed (Cameron 1968). Individual bog habitats in the southern Appalachians tend to be more isolated than their northern counterparts due to the scarcity of suitable edaphic and geomorphic sites for bog development (Stewart and Nilsen 1993). However, vegetation physiognomy and biogeochemical processes are comparable between northern and southern Appalachian bogs: both are dominated by small shrubs, are nutrient-poor and acidic, and support *Sphagnum* species that form peat deposits (Wieder et al. 1981; Wieder 1985).

Bog ecosystems evolved in humid cold temperate regions and are generally ombrotrophic: the system is dependent on precipitation for moisture and nutrient inputs. These physical conditions result in acidic and low-nutrient substrates (Byers et al. 2007). *Sphagnum* is well-adapted to these conditions and has the ability to engineer its environment to create conditions favorable for its growth while hampering that of other plants (van Breemen 1995). *Sphagnum* can acidify its surroundings by taking up cations such as calcium and magnesium and releasing hydrogen ions (Sjors and Gunnarsson 2002). In addition, the ability of *Sphagnum* to accumulate nutrients in tissues reduces the availability of nutrients for other bog species (Lee and Woodin 1988). *Sphagnum* is able to use nutrients directly from atmospheric deposition, while vascular plants must rely on nutrients released from the mineralization of organic matter, giving *Sphagnum* a competitive advantage in ombrotrophic bogs (Malmer et al. 1994).

Slow decomposition rates in bogs result from cool temperatures, anoxic conditions, limited decomposer communities, and decomposition-resistant tissues of *Sphagnum* (Moore et al. 2007). Peat formation results from the imbalance of large amounts of plant tissues adding carbon to the system and relatively small amounts of carbon lost from the system (Gorham 1991). *Sphagnum* is slower to decompose than other plant species due to its high C/N ratio and higher lignin content, which is more resistant to microbial decomposition (Verhoeven and Liefveld 1997; Limpens and Berendse 2003; Moore et al. 2007). High water tables found in bogs promote the formation of peat by creating anaerobic conditions, further slowing decomposition rates (Kuhry and Vitt 1996; Davidson and Janssens 2006; Moore et al. 2007). Therefore, *Sphagnum* biomass continues to build up and serves as the substrate in which all other bog plants must grow (Moore 2002; Dorrepaal et al. 2006). To keep up with the continually rising *Sphagnum* surface, vascular plants must continually grow upwards while also developing a stable root system in the accumulating peat (Malmer et al. 1994). Thus, in its ability to dominate and engineer its own environment, *Sphagnum* influences the plant community composition of a bog.

Human activity has dramatically altered the forested landscape of the southern Appalachian Mountains (Yarnell 1998; Pauley 2008); however, activities such as logging and forest fires have generally had minimal effects on the small pockets of high elevation bogs (Gajewski et al. 2001; Byers et al. 2007). Indirect anthropogenic effects such as climate change and atmospheric deposition readily impact these rare and valuable bog ecosystems by increasing temperatures, changing precipitation regimes, and increasing nitrogen deposition (Byers et al. 2007).

Scientists now largely agree that the Earth is experiencing climate change due to anthropogenic additions of greenhouse gases into the atmosphere (EPA 1998; IPCC 2007). The average global surface temperature has increased 0.3 to 0.6 °C during the 20th century, likely the largest increase in the past 1000 years (IPCC 2001). Warming in North America is predicted to be more severe than the global average and will be accompanied by changes in local precipitation patterns (EPA 1998; IPCC 2007). For North America as a whole, precipitation is expected to increase, but whether the added moisture will balance losses by increased evapotranspiration caused by warmer temperatures is uncertain (IPCC 2007).

Understanding how *Sphagnum* may respond to conditions projected by climate models is important for understanding the future of bog ecosystems in the southern Appalachians (Moore et al. 2007). Though climatic impacts on *Sphagnum* growth are well documented from northern bogs, few studies have been conducted in this region. In addition, compounding impacts such as increased nitrogen concentrations may have unexpected effects on southern bog ecosystems (Belyea and Malmer 2004; Gerdol et al. 2007; Wiedermann et al. 2007). Whether elevated nitrogen concentrations result from increased in situ decomposition rates stimulated by climate change or from outside sources such as atmospheric deposition, this added nitrogen may have profound impacts on the primary productivity of *Sphagnum* and other bog plant species. This paper reviews current literature to offer suggestions on how the unique bog ecosystems of the southern Appalachian Mountains may respond to indirect anthropogenic influences including changing climatic conditions and increased nitrogen loading.

RESPONSES TO A WARMER CLIMATE

In the last century, areas with bogs in the southern Appalachians have experienced a temperature increase of 0.6 °C (IPCC 2001). Through an overlay of the potential geographic range of southern Appalachian bogs (defined by elevations of ≥ 800 m, according to Francl et al. 2004) and the region's projected changes in average annual temperature, we found that southern Appalachian *Sphagnum* bogs may experience increases of +3.5 °C during the coming century (Figure 1). After an extensive review of studies focused on global *Sphagnum* productivity, Gunnarsson (2005) found that mean annual temperature was the most important factor explaining *Sphagnum* productivity.

Higher levels of *Sphagnum* growth are predicted in a warmer climate for northern latitudes (Dorrepaal et al. 2006); however, a temperature threshold could be reached for *Sphagnum* in the southern Appalachians. Studies have found that biomass production in northern *Sphagnum* species increased with an increase in temperature, as long as bog water levels remained high (Robroek et al. 2007). Increased *Sphagnum* growth and peat accumulation may result in a higher bog surface, forcing shrubs to grow vertically to keep up with the moss growth. Rapid vertical growth can have a negative impact on bog shrubs as they must allocate more energy and nutrients towards apical stem growth and less towards leaf production. Shrubs that cannot keep up with the increased *Sphagnum* growth rates will decrease in abundance (Dorrepaal et al. 2006).

Conversely, Gerdol et al. (2007) found that increased summer temperatures did not result in higher levels of *Sphagnum* growth in the Southern Alps of Italy. In fact, growth decreased by 30% in the unseasonably warm summer of 2003. Decreased growth was not linked directly to temperature, but

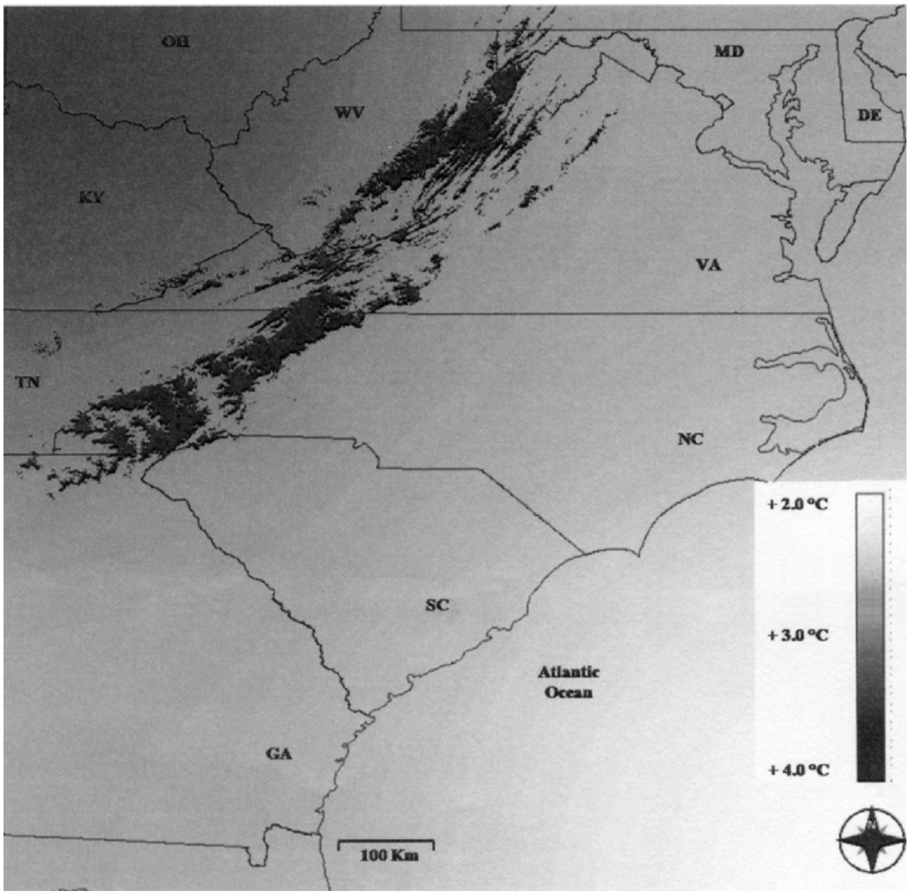

Figure 1. Mean annual temperature change (shown here in grayscale) between 1980 to 1999 and 2080 to 2099 across the southeastern United States. Southern Appalachian bogs occur in the 800 to 1944 m in elevation range (Francl et al. 2004; shown here in black). This figure uses data provided by the Community Climate System Model project (http://www.ccsm.ucar.edu), supported by the Directorate for Geosciences of the National Science Foundation and the Office of Biological and Environmental Research of the U.S. Department of Energy. NCAR GIS Initiative provided CCSM data in a GIS format through the GIS Climate Change Scenarios portal (http://www.gisclimatechange.org).

was linked to warmer summer days that increased evapotranspiration, dessicating the upper layer of *Sphagnum* (Gerdol et al. 2007). *Sphagnum*-dominated bog distribution is determined by the ratio between mean annual total precipitation and rates of evapotranspiration, which is directly related to mean annual temperature (Gignac 2001). Therefore, *Sphagnum* productivity may increase with an increase in temperature, as long as precipitation also increases and a positive moisture balance is maintained. If precipitation does not increase with temperature and temperatures become higher than optimal for moss growth, then *Sphagnum* growth rates may decrease. Indeed, Gunnarsson (2005) found that *Sphagnum* productivity increased with mean annual temperature and precipitation up to a threshold (temperature ≈ 6 °C, precipitation ≈ 1150 mm), beyond which it decreased as the physical variables continued to increase.

Through carbon sequestration, Southern Appalachian bogs serve as sinks in the global carbon cycle (Yavitt et al. 1993). Bogs can sequester carbon as long as the formation of new peat exceeds the amount that undergoes decomposition (Belyea and Malmer 2004). However, an increase in temperature without a subsequent increase in precipitation may result in a negative annual moisture balance, causing *Sphagnum* growth rates and carbon sequestration to decrease. In addition, warmer temperatures speed decomposition rates in bogs, which could result in increased carbon dioxide being lost from the system (Moore et al. 2007; Figure 2). The increased release of carbon dioxide may shift southern Appalachian bog ecosystems from carbon sinks to carbon sources (Yavitt et al. 1993).

RESPONSES TO CHANGES IN PRECIPITATION PATTERNS

Precipitation in bog areas of the southern Appalachians has increased by 10% over the past 100 years, and the Intergovernmental Panel on Climate Change (IPCC) predicts that precipitation will continue to increase here by an additional 5% (IPCC 2007). Though the region may experience increases in precipitation, an increase in evapotranspiration from increases in temperature may negate any effects of additional precipitation. Models of climate change scenarios for the region project drying in lower latitudes (including the study region) because of higher evapotranspiration (IPCC 2001). Temperature and precipitation records from 1971 to 2000 for the bog region of West Virginia (average annual temperature = 8 °C, average annual precipitation =1450 mm; Byers et al. 2007) fall slightly above Gunnarsson's (2005) *Sphagnum* growth threshold (Figure 3). Climate change projections place the physical conditions of the southern Appalachian bogs farther from the *Sphagnum* growth threshold, with a dramatic increase in temperature and only a slight increase in precipitation (Figure 3). Changes in precipitation, temperature, and subsequent evapotranspiration will likely affect net primary productivity in bogs as *Sphagnum* growth is highly dependent on water regimes.

With a relatively drier climate predicted for the southern Appalachians, growth rates of *Sphagnum* are expected to decrease. The height of *Sphagnum* above the water table is the main factor controlling production of these bryophytes (Weltzin et al. 2001). Robroek et al. (2007) found that as water levels decreased, so did *Sphagnum* height and biomass. Though *Sphagnum* species are able to adapt to gradually decreasing water levels (Robroek et al. 2007), they are sensitive to periods of prolonged drought as the tops of the plants dry out (Gerdol et al.

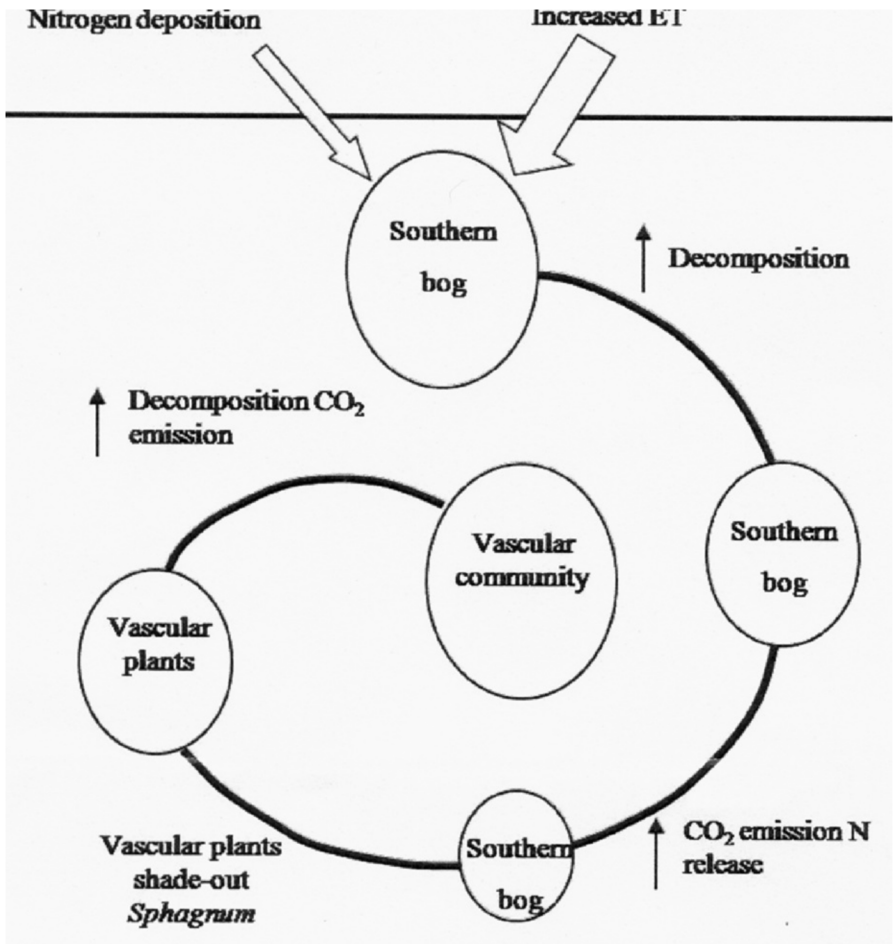

Figure 2. A projected increase in evapotranspiration (ET) and a smaller impact of nitrogen deposition decrease the area of southern Appalachian bog ecosystems through increased decomposition rates, CO2 emissions, and released nitrogen (N). These changes may result in the opportunity for vascular plants to out-compete bog species and facilitate the persistence of a vascular plant community where a southern bog previously existed.

2007). Wieder and Lang (1983), working in Big Run Bog in West Virginia, found that when water table height remained fairly constant, the *Sphagnum* layer desiccated only once during dry conditions in August. Drying of the *Sphagnum*, coupled with decreasing temperatures later in the year, may have caused the drop in productivity seen later in the study. Drought effects are more severe for *Sphagnum* than for vascular plant species in bogs, which are more efficient at conducting water, and this physioloiogcal difference can shift species dominance in the bog ecosystem (Malmer et al. 1994; Figure 2).

Water table position is one of the major factors influencing decomposition rates in *Sphagnum* bogs (Moore et al. 2007). A high water table engulfs lower peat strata and decreases decomposition rates by creating anaerobic conditions; however, a lower water table will expose peat to air, causing increased decomposition rates, which in turn increases carbon lost to the atmosphere (Belyea and Malmer 2004; Davidson and Janssens 2006). In contrast, the anaerobic reduction of carbon to methane (methanogenesis), a more potent greenhouse gas than carbon dioxide (IPCC 2001), occurs when the water table is high. Thus, both carbon sequestration and methane emission by bogs are dependent upon the height of the *Sphagnum* surface above the water table (Bubier et al. 1993; Alm et al. 1997). These processes may counteract one another, in terms of atmospheric flux, as an increased release of carbon dioxide could be offset by a reduction in methane emissions (Whalen et al. 1990).

Decomposition and methanogenesis are processes that are directly related to the hydrology of the bog ecosystem; and, therefore, indirectly depend on the topography of the specific site. Peat cores from old bogs show that within-site spatial variation of carbon loss through decay is dependent on microsite elevation (Belyea and Malmer 2004). Therefore, whether or not a specific bog acts as a carbon sink or emitter depends both on hydrology and topography. More research is necessary to better understand the importance of surface structure and developmental topography of bogs.

RESPONSES TO INCREASED NITROGEN CONCENTRATIONS

Because bogs are ombrotrophic, they naturally have low nutrient inputs and must rely largely on atmospheric deposition to achieve nutrient balance (Byers et al. 2007). *Sphagnum* is efficient in its nutrient use by cycling nutrients within its tissues and absorbing nutrients across the entire surface area of the plant; thus, *Sphagnum* is able to extract nutrients out of the surrounding water, and also from wet and dry deposition (Brown and Bates 1990; Aldous 2002; Gerdol et al. 2007). In addition, *Sphagnum* retains more nutrients as compared to other plant species (Malmer et al. 2003). Therefore, few species are able to out-compete *Sphagnum* under normal nutrient conditions (Ohlson et al. 2001).

Atmospheric deposition of nitrogen is closely linked to fossil fuel use (Wiedermann et al. 2007). West Virginia and other parts of the southern Appalachians receive large amounts of nitrogen deposition due to the high number of coal power plants in the region. Industrial pollution from manufacturing and power plants along the Ohio and Kanawha rivers are an important source of atmospheric nitrogen in portions of the southern Appalachians (EPA 1998). While nitrate deposition in the bog areas of West Virginia has decreased from an average of > 20 kg ha^{-1} in 1985 to 13 kg ha^{-1} in 2007, these areas still rank among the highest for nitrogen deposition in the country (NADP 2009).

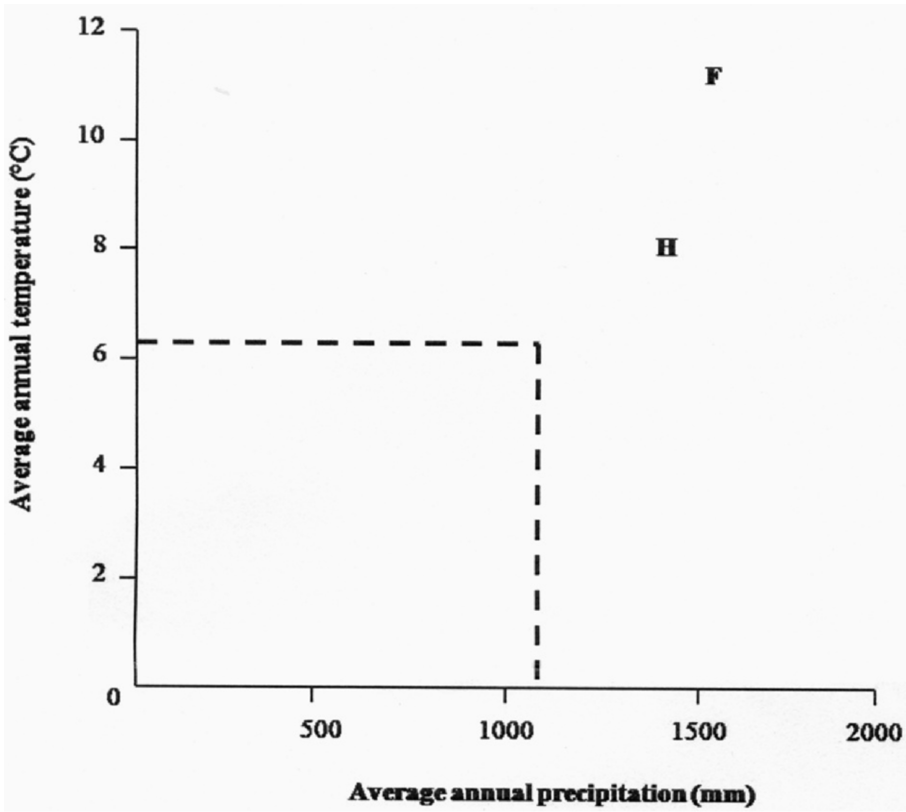

Figure 3. Historical (H) and future (F) temperature and precipitation of southern Appalachian bogs in relation to a *Sphagnum* tolerance threshold (dashed line). Historical temperature and precipitation values were averaged from 1971 to 2000 (Byers et al. 2007) and future values were obtained from the IPCC (2007). The tolerance threshold for *Sphagnum* species is that of Gunnarsson et al. (2005).

Elevated nutrient availability may result in increased biomass production and carbon sequestration abilities of ecosystems by stimulating plant growth (Walker and Steffen 1999; Oerlemans et al. 2007). Vitt et al. (2003) found that nitrogen additions below 14.8 and 15.7 kg ha^{-1} yr^{-1} stimulated the growth of *Sphagnum*, but growth was inhibited at higher nitrogen levels. Though increased nitrogen may increase initial *Sphagnum* growth, eventually *Sphagnum* reaches a threshold where nitrogen concentrations become too great for the moss to retain the nitrogen (Gerdol et al. 2007; Wiedermann et al. 2007). Above this threshold, nutrient additions to a peat bog can shift dominance of the bog ecosystem away from *Sphagnum* and towards vascular plants, thereby creating an entirely different ecosystem (Bragazza et al. 2006; Bubier et al. 2007). When this occurs, *Sphagnum* growth declines and excess nutrients become available to vascular plants, which through increased growth can shade-out the low-stature *Sphagnum* (Limpens et al. 2003; Bubier et al. 2007; Wiedermann et al. 2007). When the vascular plant canopy intercepts > 50% of available light (i.e., PAR), *Sphagnum* growth decreases and woody plants are able to dominate (Limpens et al. 2003).

When a bog ecosystem shifts from dominance by *Sphagnum* to vascular plants, decomposition rates increase and subsequent carbon storage decreases (Bubier et al. 2007; Moore et al. 2007; Wiedermann et al. 2007). For example, Bubier et al. (2007) examined nitrogen additions to *Sphagnum* bogs over a period of five years. Initially, adding nitrogen caused an increase in carbon sequestration because of an increase in vascular plant biomass; however, after the first year, *Sphagnum* photosynthetic capacity and growth decreased over time resulting in decreased carbon sequestration (Bubier et al. 2007). In addition, when decomposition rates increase, more nitrogen will be released into the system and become available for plant uptake, creating a positive feedback loop (Figure 2).

Complex interactions exist between rising temperatures and nutrient additions in bog ecosystems (Heijmans et al. 2008). Wiedermann et al. (2007) found that after nine years, the addition of nitrogen reduced *Sphagnum* cover to 63% of its original cover, but increased temperature along with added nitrogen further reduced *Sphagnum* cover to 20% of its original cover. While increasing temperature alone did not impact *Sphagnum* cover, increasing temperature clearly exacerbated the effects of nutrient loading. Long-term experiments may be needed to understand the influences of temperature and nutrients on *Sphagnum* growth due to a response time lag. For example, Wiedermann et al. (2007) found that within the first four years of their study, *Sphagnum* showed little response to nutrient additions or temperature increase; however, after eight years, *Sphagnum* cover was drastically reduced. More research is also needed to determine interactions between the addition of nitrogen and methane emissions from bog ecosystems. Some studies have found that methane release increased with higher nitrogen levels (Tuittila et al. 2000; Silvola et al. 2003), while others found no correlation between nitrogen addition and methane emissions (Bubier et al. 2007). These conflicting results may be due to the individualistic responses of *Sphagnum* species to nitrogen addition (Bubier et al. 2007).

In summary, given projected increases in evapotranspiration and increased nitrogen concentrations in the southern Appalachians, bogs may shift from *Sphagnum* dominance to a system dominated by woody shrubs (Wiedermann et al. 2007). In addition, increased nutrients could lead to invasions of alien plant species (Tomassen et al. 2004), which would further alter bog structure and function. A change in plant community composition may result in bogs shifting from carbon sinks to carbon sources, thereby interacting with changing climate in a positive feedback relationship (Bubier et al. 2007).

CONCLUSIONS AND RECOMMENDATIONS

Sphagnum bogs are unique and rare communities within the southern Appalachian Mountains that are threatened by changing climate and atmospheric nitrogen deposition. Changes in temperature and precipitation may alter bog community structure and composition differently depending on the identity of dominant *Sphagnum* species present (Robroek et al. 2007). Keyed by differing morphological and physiological traits, *Sphagnum* species replace one another along a hydrologic gradient (Andrus et al. 1983). Climate change may shift the dominance of *Sphagnum* species along this gradient, and scientists are uncertain how species shifts may affect bog ecosystems. For example, if southern bog species shift northward with climate change, it is unclear what species (moss or vascular plants) would dominate the remaining southern bog habitats. A change in dominant species may lead to the local extinction of species dependent on a *Sphagnum*-dominated bog ecosystem, as well as the extinction of the southern *Sphagnum* bog itself. In addition, it is unclear whether southern *Sphagnum* species would have the vagility to colonize northern bog sites. For example, *Sphagnum* spore dispersal patterns tend to be leptokurtic with highest densities of spore deposition closest to the sources (Miles and Longton 1992), and maximum modeled wind-dispersal distances of *Sphagnum* are only around 100 km (Sundberg 2005).

Climate change-induced shifts in community structure are predicted to alter bog ecosystem processes (Robroek et al. 2007). The predicted increase in evapotranspiration of southern Appalachian bogs may lead to lowered water tables and a subsequent increase in decomposition rates. Drying conditions will likely increase decomposition in bogs, creating an imbalance in carbon storage. Southern Appalachian bog ecosystems may then shift from carbon sinks to carbon sources, thereby exacerbating global warming as predicted for boreal peat ecosystems of the north (Bubier et al. 2007; Gerdol et al. 2007; Wiedermann et al. 2007),

While the vast majority of research on climate change and bogs has occurred in northern latitudes, there is a strong need for scientists and land managers to investigate the specific effects of climate change on bogs in the southern Appalachians. Although southern Appalachian bogs share many similarities with northern bogs, the distinctive features of southern bogs (e.g., topography, species composition, nutrient levels, and water table height) suggest potentially unique responses to climate change. An improved understanding of how climate change may affect *Sphagnum* bogs in the southern Appalachians will allow managers to better protect and conserve these unique and diverse habitats.

ACKNOWLEDGMENTS

The authors thank Andrea Berardi, Katia Engelhardt, and anonymous reviewers for their thoughtful and constructive comments on the manuscript. We also thank Colgate University for funding the publication of the manuscript.

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