

# Acidic Deposition and Biodiversity of Forest Understory Plant Communities in the Northern Hardwood Forests of the Adirondack Mountains

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# **Acidic Deposition and Biodiversity of Forest Understory Plant Communities in the Northern Hardwood Forests of the Adirondack Mountains**

*Final Report*

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## Notice

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## Abstract

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This project focuses on relationships between understory vegetation and soil properties as influenced by acidic deposition in Adirondack Mountain forests. Acidic deposition has reduced the acid-buffering capacity of soils by depleting soil reserves of the important nutrients, calcium and magnesium, at many locations. The research reported here determined the associations between acidic deposition and soil base cation supply and understory plant community responses that reflect aspects of biodiversity. During an earlier field study of *Acer saccharum* (sugar maple) trees and soil chemistry, 50 study plots within 20 small Adirondack watersheds were sampled and evaluated for soil acid-base chemistry and *Acer saccharum* growth, canopy condition, and regeneration. For this follow-up study, we characterized how understory plant community composition changed at these same sampling locations across deposition and soil acidification gradients using ordination analysis—nonmetric multidimensional scaling (NMDS). Trees growing on soils with poor acid-base chemistry that received relatively high levels of atmospheric sulfur and nitrogen deposition exhibited minimal to no *Acer saccharum* seedling regeneration, relatively poor canopy condition, and short- to long-term growth declines compared with study plots having better soil condition and lower levels of acidic deposition. Understory species richness was positively related to both exchangeable calcium concentrations and base saturation in both the O<sub>a</sub> and upper B soil horizons. Several plant species were strongly and positively correlated with Axis 1 of the NMDS, suggesting positive responses to increases in pH, base saturation, and availability of plant base cation nutrients. Other plant species were negatively correlated with Axis 1, and richness decreased with acidic deposition and soil acidification. Results of this research suggested that plant understory richness in Adirondack hardwood forests was controlled significantly by acidic deposition and soil acid-base chemistry. Both bivariate and multivariate analyses clearly illustrated an association between the base status of the O<sub>a</sub> and upper B soil horizons and plant understory richness and species composition.

## Keywords

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acidification, forest understory, vegetation, Adirondack Mountains, acidic deposition

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## Summary

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Changes in atmospheric sulfur (S) and nitrogen (N) deposition in the northeastern United States caused pronounced changes in soil condition and habitat suitability for many plant and animal species over the second part of the previous century. The cycling of S, N, and carbon (C) has been significantly altered since preindustrial times in response to human population growth, production and application of N-based fertilizers, prevalence of concentrated livestock operations with associated emissions of ammonia, and fossil-fuel combustion (Galloway et al. 2008, Schlesinger 1997, Vitousek et al. 1997). Atmospheric emissions and deposition of both S and N from the atmosphere to terrestrial ecosystems have altered competitive relationships among plant species and changed the occurrence and/or cover of some species by creating environments that promote or discourage the growth of nitrophilous (prefer high N) or calciphylic (prefer high calcium [Ca]) species (Bobbink et al. 2010, Sullivan et al. 2013a, Sullivan et al. 2013b).

Despite reductions in S and N emissions during recent decades associated with the Clean Air Act Amendments of 1990 and other rules and legislation, S and N deposition values are still elevated in the eastern United States compared with preindustrial conditions (Galloway et al. 2008, Sullivan 2017, Volpe Horii et al. 2005). The pattern of historical (1850 to current) S and N deposition throughout much of the northeastern United States can be generally described as increasing from 1850 until the 1970s, peaking between 1970 and 2000, and then decreasing to a level in 2011 that approximated the early to mid-20th century (Husar et al. 1991; <http://nadp.sws.uiuc.edu>, Likens and Buso 2012).

Historical acidic deposition has acidified soils in Adirondack watersheds having low-base saturation (U.S. EPA 2009). Effects of soil acidification on trees have been studied more extensively than effects on understory plants in the northeastern United States (Driscoll et al. 2003, Sullivan et al. 2013b). Decreased soil Ca availability has been associated with susceptibility of *Picea rubens* trees to freezing damage (DeHayes et al. 1999). Reduced soil exchangeable Ca concentrations and base saturation (BS) in *Acer saccharum* stands in the Adirondack Mountains have been shown to be correlated with decreased crown condition, reduced growth, and low recruitment (Bishop et al. 2015, Sullivan et al. 2013b).

Although it is known that some understory plants that occur in these forests are calciphylic (Horsley et al. 2008), minimal research has been conducted to document the relative sensitivities of these species to soil acidification or to quantify the levels of effects that have occurred to date or that might occur in the

future in response to changes in acidic deposition. In the study reported here, the extent to which the base status of watershed soils is associated with plant community composition affected by acid deposition was determined in this region (species occurrence, relative abundance, cover, and plant community richness).

The team collected new field data at the same 50 plots (distributed among 20 watersheds in the western and central Adirondacks) that were included in the *Acer saccharum* assessment previously conducted for NYSERDA by Sullivan et al. (2013a). Evaluations were made concerning the extent to which the occurrence and cover of forest understory plant species in northern hardwood forests of the Adirondack Mountains are related to soil acid base status, base-cation depletion, and N-enrichment caused by elevated S and N deposition. Estimations were also made on how the species composition of the forest understory plant layer of northern hardwood forests containing canopy *Acer saccharum* may change in the future and where within the Adirondack Mountains these changes are expected to occur. Relationships and linkages among understory plant distribution were assessed, along with levels of acidic deposition, soil BS, Ca and magnesium (Mg) supply in soils, and other soil and watershed variables. While other changes are also occurring in these forests in response to climate, successional dynamics, and forest pests and pathogens (e.g., Wason and Dovciak 2016), team believes the study design maximizes the ability to specifically address the effects of acidic deposition and soil acidification since plots are located across strong gradients in these two variables and not across gradients of the other variables (e.g., climate, land-use, or pathogens) which are likely to vary randomly and to a limited degree across explicit deposition and soil acidity gradients. In addition, recent studies in the Adirondacks suggest that the change in acidic deposition, rather than climate warming, has been the dominant factor causing measurable responses in forest vegetation in this region (Wason et al. 2017).

Plant species richness, or total number of plant species present, in a forest community is a major aspect of forest biodiversity. The ecological significance of the herbaceous layer of temperate forest ecosystems was reviewed by Gilliam (2007). He highlighted contributions of the herbaceous layer to overall biodiversity, competitive interactions that influence canopy tree regeneration, linkages between the understory and the overstory, relationships to ecosystem function, and responses of the herbaceous layer to disturbance. In addition, richness of the forest herbaceous layer plant community can affect the stability of plant species cover and thus variation in community composition and provision of ecosystem services over time (Dovčiak and Halpern 2010). The team documented associations among S and N deposition, soil-base status, and understory plant species richness.

About 125 plant species were documented on the study plots. Some (*Acer saccharum*, *Fagus grandifolia*, *Dryopteris intermedia*) occurred on all 50 plots. Understory layer richness varied on most plots between about 20 and 45 species. The ratio of plant species richness in the herbaceous layer to richness in the tree layer was positively related to BS in the O<sub>a</sub> soil horizon (organic and surface), and to a lesser extent in the upper B horizon (subsoil).

Ordination analysis revealed that community composition varied along two distinct gradients. Axis 1 explained 63.3% of compositional variation and represented a gradient of soil buffering capacity, soil acidification, and atmospheric deposition. Axis 1 was strongly and positively correlated with pH, BS, and plant nutrients and negatively correlated with acidic deposition and soil acidification variables. Axis 2 explained 27.8% of the compositional variation and represented gradients of soil organic matter, canopy cover, and elevation that were negatively correlated with this axis. Interestingly, total soil N was correlated with both axes, likely describing positive effects of soil nutrient status and overstory vegetation on N cycling and total N content in the soil. The ordination described a clear gradient of increasing species richness along the acidification axis 1. Richness was positively correlated with axis 1, increasing with soil pH, BS, and base-cation concentrations (Ca, Mg) and decreasing with acidic deposition and soil acidification.

Species richness across the study watersheds was predicted best by a two-variable model, suggesting statistically significant positive effects of base cations (Ca+Mg) on species richness. In the slightly weaker second-best model, pH replaced Ca+Mg as a significantly positive predictor of richness.

The dramatic and positive effects of bases (Ca, Mg, and BS) on species richness were further highlighted by simple regressions of species richness against BS and individual Ca and Mg concentrations in both the O<sub>a</sub> and upper B horizons. A negative relationship between N and richness appears to be subtler as it is elucidated only by the multivariate models that included stronger predictors related to soil-base status that otherwise masked the effects of N in simple regressions or the non-metric multidimensional scaling (NMDS) ordination. All of these soil variables describe a composite soil gradient (axis 1) in which the individual soil variables co-vary with each other, at least partly in response to a well-defined acidic deposition gradient across the study region. Plot-level percent cover of ferns and club mosses were markedly higher at relatively low-upper B soil horizon BS (< about 20%).

Indicator species analysis revealed that some understory species were indeed associated with high- or low-base saturation. Four species (two species of ferns and two tree species) were associated with base saturation in the upper B horizon  $< 12\%$ . Nine species (six herbaceous and three woody, the latter including *Acer saccharum*) were associated with upper B horizon BS  $> 12\%$ . *Dennstaedtia punctilobula* had the strongest association with the occurrence of low-upper B horizon BS. Conversely, *Arisaema triphyllum*, *Fraxinus americana*, and *Acer saccharum* had the strongest associations with the occurrence of upper B horizon BS  $> 12\%$ .

Indicators of low BS were found in high frequency mainly in the southwestern Adirondacks. In contrast, indicators of high BS were generally rare in the southwestern Adirondacks. An indicator ratio was calculated, by plot, as the number of identified plant species that indicate relatively high BS ( $> 12\%$ ) divided by the number of identified indicator species of relatively low BS ( $< 12\%$ ). This ratio varied according to the measured soil BS in both the O<sub>a</sub> and upper B soil horizons and according to estimated S and N deposition. The ratio generally increased with increasing soil BS in both the upper B and especially the O<sub>a</sub> horizon. Tipping points at which the ratio increased with lower deposition levels for both S and N deposition were near 10–12 kg/ha/yr, for either S or N deposition. The ratio was uniformly low (less than 1) on plots that received deposition more than 12 kg S or N/ha/yr.

# Background

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## 1.1 Introduction

A project was previously conducted by E&S Environmental Chemistry, Inc. in 2009 on behalf of the New York State Energy Research and Development Authority (NYSERDA) to measure and report the health, growth, and regeneration of *Acer saccharum* (sugar maple) trees as affected by S and N deposition and associated soil acidification in northern hardwood forests of the Adirondack Mountains (Sullivan et al. 2013a). *Acer saccharum* was selected for study because it is an important economic and biologic resource in Adirondack regional ecosystems that is sensitive to damage caused by air pollution. The project reported here focused on the responses of the understory plant communities in these same forests to acidic deposition and consequent soil acidification.

The Adirondack Park is an excellent location for investigating the effects of atmospheric S and N deposition on forest understory vegetation. This park is one of the largest protected areas in the eastern United States, has experienced pronounced spatial gradients in acidic deposition, and has been comparatively unaffected by forest fragmentation, land management, or invasions of non-native plants (Sullivan 2015). The Adirondack region hosts a large diversity of plant life. These forests also support wildlife, timber production, and clean water supplies, resources that provide the foundation for tourism and fishing economies and attract millions of visitors who participate in seasonal recreation and enjoy the aesthetics of autumn foliage colors.

The Adirondack Park contains over 1,000 lakes, an extensive network of streams radiating from high-elevation areas, abundant wetlands, and diverse forests. Several environmental factors contribute to high-ecosystem sensitivity of some Adirondack resources to acidification damage, including slow weathering of bedrock and geological glacial deposits, shallow and naturally acidic soils, and steep slopes.

Acidic deposition comprises multiple forms of S and N that are emitted into the atmosphere from such sources as power-generating facilities that burn coal, oil, or natural gas; motor vehicles; agricultural activities; and industry. The term “acid rain” refers to the wet components of the deposition contained in rain and snow. There are also dry components that are composed of gasses and particles that are scavenged from the air, largely by vegetation surfaces. Acidic deposition causes a wide range of environmental impacts, including acidification of soil and drainage water; toxicity to fish and other aquatic biota; depletion of soil nutrient bases, such as Ca and Mg; reduced growth and regeneration of

various plant species; increased susceptibility to winter injury (e.g., *Picea rubens*); and changes in species composition and biodiversity. Such impacts have been especially prevalent, and some have been well-studied in the Adirondack Mountain region of New York (Driscoll et al. 2001, Sullivan et al. 2014, Sullivan et al. 2006a, Sutherland et al. 2015).

Atmospheric deposition of S and N can cause two different kinds of environmental impacts: acidification of soil and drainage water and (2) nutrient enrichment (also called eutrophication). Each type of impact can occur in both aquatic and terrestrial ecosystems. These effects can have both environmental and economic consequences (Beier et al. 2017). Acidification in the Adirondacks has been caused mainly by S, although N has also been involved and is becoming proportionally more important with large reductions in S deposition (Sullivan 2015). Nutrient enrichment can be caused by N deposition, but usually not by S deposition.

Human-caused deposition of S and N from the atmosphere to the earth's surface increased substantially throughout most of the 20th century in the eastern United States in response to pollutant emissions from power plants, motor vehicles, agriculture, industry, and other human-caused and natural sources (Galloway and Cowling 2002, Husar et al. 1991). More than a century of high levels of air pollution has affected these resources and caused substantial damage at some locations. However, federal and state efforts over several decades to reduce air pollutant emissions from power plants, motor vehicles, and industry have decreased pollution levels substantially. Nevertheless, legacy effects on the environment persist because decreases in acidic deposition have not resulted in complete soil recovery to pre-industrial conditions. In particular, acidic deposition has reduced the acid-buffering capacity of soils by depleting soil reserves of the important nutrients calcium (Ca) and magnesium (Mg) at many locations, especially in the southwestern portion of the Adirondack region.

Both S and N acidify base-poor soils and inhibit base nutrient uptake by vegetation. In addition, N is often the limiting nutrient resource for growth of some plant species in temperate forest ecosystems (Vitousek and Howarth 1991). Increased N supply can increase primary production, alter plant species composition, and affect biodiversity (Bobbink et al. 2010). Ecosystem effects of increasing N supply include changes in N and C cycling and plant responses to stress (Neff et al. 2002). The spatial distribution of plant species in the herbaceous layer is well known to be influenced by the spatial heterogeneity of soil nutrients (Gilliam 2006, Small and McCarthy 2003, Whigham 2004). Some plants have reacted to soil acidification and/or N enrichment with changes in occurrence, growth, and abundance

(Gilliam 2007). These changes affect species diversity, threaten rare plants and cause multiple ecological effects as some species are out-competed and eliminated from the plant community (Fenn et al. 2015).

This is important to the Adirondack Park because part of its “forever wild” mission is to maintain natural conditions unaffected by human influence to allow for the enjoyment of nature by future generations ([https://apa.ny.gov/About\\_Park/history.htm](https://apa.ny.gov/About_Park/history.htm)).

This report addresses key findings of the recently completed Adirondack forest understory biodiversity study. This research determined the associations between acidic deposition and soil-base cation supply as compared with understory plant responses that affect overall biodiversity of forest understory plant communities. Plant species that can serve as indicators of high- or low-base supply were identified. Findings were placed in the context of critical loads (CLs) and target loads (TLs) of atmospheric deposition required to protect or restore sensitive resources. Selected aspects of plant understory responses to acidic deposition and soil acidification are discussed here in an effort to inform understanding of the complexities of ecosystem responses to acid and nutrient stress.

Acidic deposition to acid-sensitive soil not only depletes the soil of nutrient-base cations, but also mobilizes aluminum (Al) from soil to soil solution in forms that can be toxic to plant roots. Some plant species, including *Acer saccharum* and red spruce, are known to be highly susceptible to acidification stress (U.S. EPA 2008). Other species may be equally, or more, susceptible, but have not been studied thoroughly. A variety of damage symptoms have been identified in northern hardwood forests that contain *Acer saccharum*, including reduced seedling regeneration (Sullivan et al. 2013b), reduced growth (Bishop et al. 2015), canopy dieback (Horsley et al. 1999), and increased susceptibility to other environmental stressors such as changing climate and forest management practices (Wason and Dovciak 2016).

Mineral acid anions deposited from the atmosphere are more or less mobile in the soil environment, depending on watershed characteristics and are ultimately neutralized largely by the release of base cations (including the nutrients Ca and Mg) to drainage water through the processes of weathering and ion exchange (van Breemen et al. 1983). Sulfate ( $\text{SO}_4^{2-}$ ) and nitrate ( $\text{NO}_3^-$ ) leach to surface waters and are charge balanced by base cations and/or acidic cations (hydrogen  $[\text{H}^+]$  and inorganic Al  $[\text{Al}_i]$ ). Cation loss caused by acidic deposition adds to cation loss caused by the natural leaching of organic and carbonic acids (Hemond 1994). Thus, acidic deposition accelerates the natural base cation loss from the rooting zone of the soil (Cronan et al. 1978). This can damage a variety of plant species,

especially those that require substantial supplies of Ca and/or Mg. Other species might be favored by a more acidic, base nutrient-poor soil environment. Thus, acidic deposition can contribute to changes in plant species composition and loss of biodiversity, including species requiring higher levels of soil exchangeable bases.

Maintenance of biodiversity has been shown to be associated with the preservation of ecosystem productivity, stability, function, and services (Cardinale et al. 2012). The extent to which ecological function is impacted by biodiversity loss is primarily regulated by the functional traits affected (Cardinale et al. 2013, Diaz et al. 2007, Quijas et al. 2010, Srivastava et al. 2009). Richness is an integral part of biodiversity that has been linked to productivity (Isbell et al. 2013), ecosystem and community stability (Tilman et al. 2006), and ecosystem services (Isbell et al. 2011, Sullivan and Jenkins 2014). Terrestrial plant biodiversity has been linked with positive effects on provisioning of plant products, soil fertility, erosion control, resistance to invasion by non-native organisms, and pathogen regulation (Estes et al. 2011, Quijas et al. 2010, Shurin et al. 2002). Plant diversity affects a variety of ecosystem functions, including resilience to disturbance and stability of biomass production or community composition (Dovčiak and Halpern 2010, Tilman et al. 2006).

The herbaceous layer of the forest is likely the vegetative layer most sensitive to changes in nutrient enrichment and acidification (Muller 2014). Gilliam (2007) reviewed the ecological significance of the herbaceous layer of temperate forest ecosystems. He highlighted contributions of the herbaceous layer to overall biodiversity, competitive interactions that influence canopy tree regeneration, linkages between the understory and the overstory, relationships to ecosystem function, and responses to disturbance. On average, for every tree species in a forest in the eastern United States, there can be approximately six species present in the herbaceous layer of the vegetation (Gilliam 2007). Although the above-ground biomass of the herbaceous layer is typically on the order of only 0.2% of the biomass of the overall forest in the northern hemisphere, it commonly provides about 4% of the net primary productivity (NPP), a 20-fold greater contribution to NPP as compared with biomass (Gilliam 2007).

Emissions of S and N into the atmosphere at locations upwind from the Adirondacks increased several-fold during the late 19th and the 20th centuries to levels high enough to impact sensitive terrestrial and aquatic ecosystems. In more recent years, federal and state rules and legislation reduced

S and N emissions and deposition, and some ecosystem recovery has been documented for lakes (Driscoll et al. 2007, Sullivan 2015). Deposition levels have declined substantially since the 1970s in response to emissions controls. Plants have varying life spans and rooting depths and respond to both ambient and cumulative deposition loads.

Aquatic effects of S and N deposition in the Adirondacks have been well studied for the past three decades (cf., Driscoll et al. 2003, Driscoll et al. 2001, Jenkins et al. 2007, Lawrence et al. 2008, Sullivan 2015, Sullivan et al. 2006b). Such studies have included long-term monitoring, process studies, and mathematical modeling of ecosystem responses and TLs. Terrestrial responses in the Adirondacks have been somewhat less studied. However, Sullivan et al. (2006a) reported soil acid-base chemistry at about 200 sites across the region, and Sullivan et al. (2013a) documented effects on *Acer saccharum* health and regeneration. Both of these studies were funded by NYSERDA. Scientists now know a great deal about effects of atmospheric deposition on sensitive natural resources in the Adirondack Mountains. Additional key questions relate to effects on terrestrial resources other than trees, anticipated resource recovery under increasingly lower levels of deposition, and identifying CLs and TLs necessary to affect ecosystem recovery. NYSERDA funds much of the research in this region intended to address these issues. The research reported here is intended to partially satisfy that need.

## **1.2 Objectives**

The goal of the project was to identify relationships among plant understory biodiversity, soil acidification, and nutrient enrichment caused by S and N deposition in Adirondack northern hardwood forests. Major objectives were to identify understory plant indicators of base nutrient-rich and base nutrient-poor forest stands and to describe relationships among acidic deposition, soil chemistry, understory richness, cover, and the presence or absence of indicator plant species. Scientific perspectives presented here will help to inform land managers and decision-makers who are tasked with developing and implementing environmental policy. The work built upon the findings of several recent and ongoing projects (Burns and Sullivan 2015, Lawrence et al. 2017, NYSERDA 2014, Sullivan et al. 2013a, Sullivan et al. 2013b) to make data more relevant to the needs of resource managers and policy makers. It provides substantial leverage of recent research and monitoring in the region. The inventory of the understory vegetation community reported here will facilitate potential modeling efforts to forecast future changes in forest plant community composition in response to changes in atmospheric deposition and climate (cf., McDonnell et al. 2014).

This project is important for the management of the terrestrial ecosystems in New York State that are highly vulnerable to changes in acidic deposition. The study region has received elevated levels of S and N deposition and contains many watersheds that have levels of Ca and Mg in soils that may be insufficient to support healthy growth and regeneration of multiple plant species. This is important because available data suggest that soil-base status in this region appears to have declined since the 1980s (Johnson et al. 2008, Sullivan et al. 2006a, Sullivan et al. 2006b, Warby et al. 2009). The study of Adirondack forest health to date has largely been limited to tree condition, especially *Picea rubens* and *Acer saccharum* (Shortle et al. 1997, Sullivan et al. 2013b). The research on the effects of terrestrial acidification to date has focused mainly on impacts to soil condition, which cause stress to sensitive species through enhanced Al toxicity and reduced nutritional status. Thus, results of the study reported here fill an important knowledge gap by addressing responses of forest understory plant communities to acidic deposition and soil acidification.

## 2 Approach

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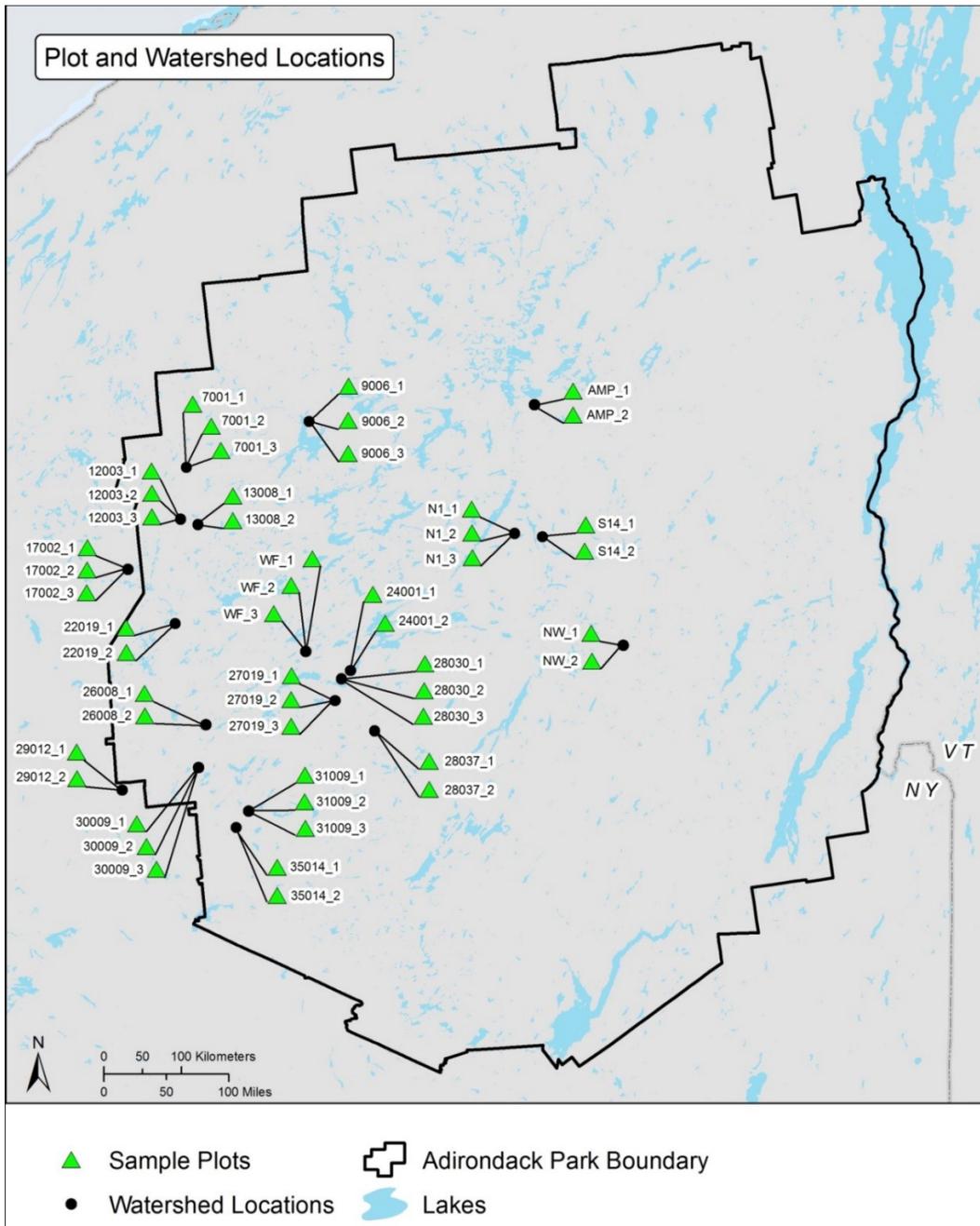
### 2.1 Site Selection

For the previous *Acer saccharum* assessment, 15 watersheds were selected from 200 watersheds in which streams had been sampled in the Western Adirondack Stream Survey (WASS) that were conducted in the Black and Oswegatchie river drainages (Lawrence et al. 2008). Watershed selection was done with a stratified random sampling approach based on WASS stream chemistry so that the 15 watersheds represented a gradient in soil Ca availability. To expand the range in Ca availability to the full extent that occurs in the Adirondack region, an additional five watersheds were added. Each of the 20 watersheds was represented by two or three (50 total) 20 x 50-meter plots. The study design allowed relationships between soils and forest understory plant communities to be developed for the full range of Adirondack Ca availability and enabled the data to be applied to the population of hardwood forests in low-order stream watersheds of the western Adirondacks (Figure 1). Thus, results are broadly representative of low-order stream watersheds, which are mainly present in the southwestern portion of the Adirondack Park.

The study plots and watersheds are covered by northern hardwood forests dominated largely by *Fagus grandifolia*, *Acer saccharum*, and *Betula alleghaniensis*. Watersheds with visible evidence of logging within the past ~40 years were excluded from the study. This forest type is associated with mean winter temperatures between -4.4 and 2.2°C, mean summer temperatures between 23.3 and 26.6°C, annual precipitation between 101.6 and 121.92 cm, mean annual snowfall of 182.88 cm, mean snow cover duration of 87 days, and mean growing (frost-free) season duration of 120 to 150 days per year (McNab et al. 2007).

Within each selected watershed, plots were established to represent the characteristic vegetation and topography of their respective watersheds, while including at least three *Acer saccharum* trees of suitable form for coring in a dominant or co-dominant position in the canopy with a minimum of 35 cm diameter at breast height (DBH). No effort was made to control the occurrence of any other tree species (Sullivan et al. 2013b). Data from individual plots were averaged by watershed.

Figure 1. Plot and Watershed Locations

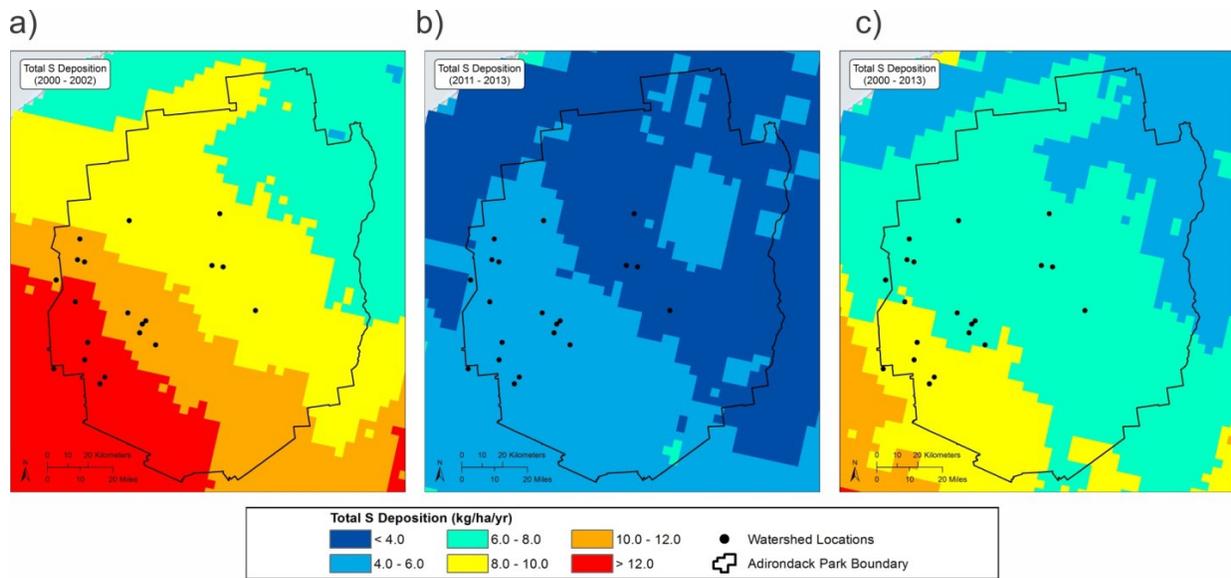


## 2.2 Atmospheric Deposition

Recent levels of S and N deposition in the study region were estimated based on Total Deposition analyses (TDEP; Schwede and Lear 2014) available for the period 2000-2013. Three-year average S deposition zones at the beginning and end of the TDEP period of record for modeled total wet plus dry S deposition are mapped in Figure 2. Also shown is the spatial pattern in the cumulative annual average S deposition for the 14-year full period of TDEP deposition record. The spatial pattern of decreasing S deposition from southwestern to northeastern Adirondacks was most pronounced during the early portion of the record (2000-2002 average), with S deposition above 12 kg S/ha/yr at six of the study watersheds in the southwest, decreasing to less than 10 kg S/ha/yr at five watersheds in the northeast. During the latter portion of the record (2011-2013 average), total S deposition had decreased to less than 6 kg S/ha/yr at all study watersheds. Results for the full period of record were intermediate. Similar results were found for N deposition, with the southwest-to-northeast gradient again being most pronounced for the period 2000-2002 (Figure 3).

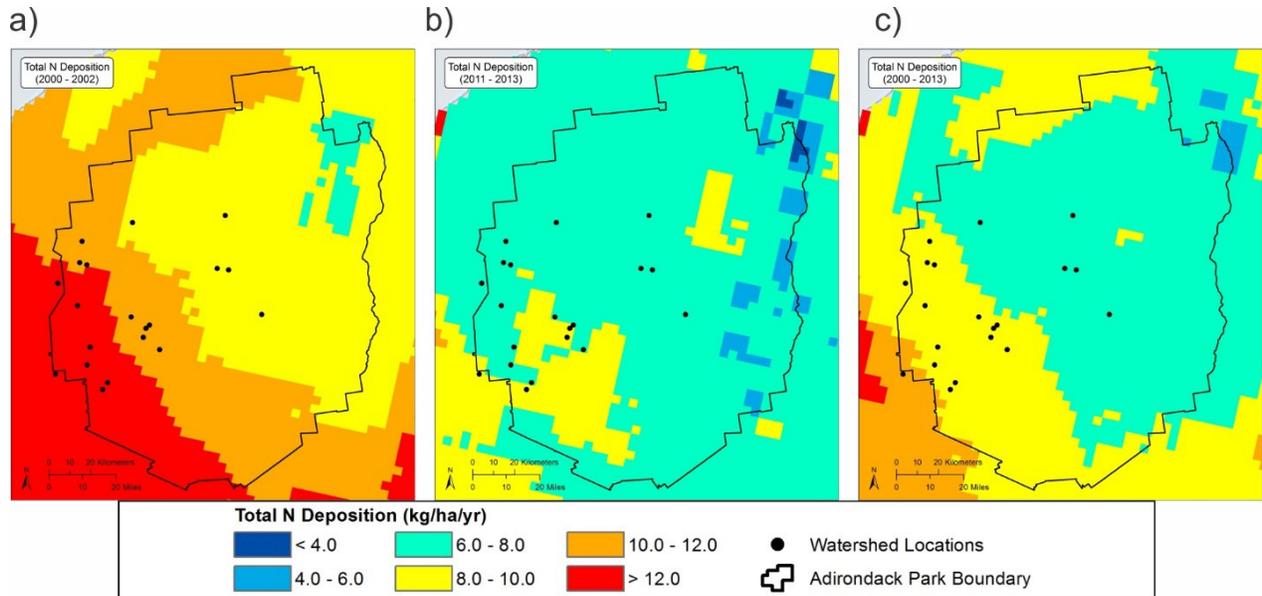
**Figure 2. Map Showing Three-Year Average TDEP Estimates of Total S Deposition**

The periods cover (a) 2000–2002 and (b) 2011–2013 as well as (c) the long-term average over the full period 2000–2013.



**Figure 3. Map Showing Three-Year Average TDEP Estimates of Total N Deposition**

The periods cover (a) 2000–2002 and (b) 2011–2013 as well as (c) the long-term average over the full period 2000–2013.



## 2.3 Soil Chemistry

Soil data for this study were collected and reported by (Sullivan et al. 2013a, 2013b). Soil analyses focused largely on the O<sub>a</sub> horizon because most understory plants are shallow-rooting. Additional analyses focused on the upper B mineral horizon because this horizon can be important for supporting trees that have deeper roots and because process-based dynamic modeling of watershed response often relies on upper B horizon data (2013a, Sullivan et al. 2006b).

Soil-base saturation (BS), expressed as a percentage, is an aggregate soil acid-base chemistry metric that reflects the percent of the total cation exchange capacity that is comprised of basic, rather than acidic, cations. If the BS is low (less than about 12% to 16%; Lawrence et al. 2017, Sullivan et al. 2013b), toxic Al can be mobilized to soil solution and base-cation nutrient deficiencies can develop in vegetation. Sullivan et al. (2013b) found that *Acer saccharum* seedlings did not regenerate in the Adirondack Mountains on plots where upper B-horizon soil BS was less than 12%.

### **2.3.1 Organic Soil Sampling**

At each of five pre-selected locations situated along each overall plot centerline, opposite five seedling subplot locations, one 10 × 10-cm pin block of forest floor material was collected down to the top of an E or B horizon, whichever occurred first (Yanai et al. 2000). The surface fresh litter was gently brushed away without disturbing the O<sub>e</sub> horizon. The five pin-block samples were separated into A, O<sub>a</sub> and O<sub>e</sub> horizons, placed in zipper-locked bags by horizon, and transported to the U.S. Geological Survey (USGS) analytical laboratory in Troy, New York. Visit <https://doi.org/10.5066/F78050TR> for soil data available through the U.S. Geological Survey data.

### **2.3.2 Mineral Soil Sampling**

Three to five small reconnaissance soil pits were opened in each of the plots. From among these reconnaissance pits, the intermediate location in terms of horizon presence and thickness was selected for full-pit excavation and mineral soil sampling. At the selected site, a pit approximately 1 m<sup>2</sup> in area was excavated into the lower B or C horizon, and then photographed, described, and sampled. Horizons were identified based on observed differences in organic content, color, texture, structure, root density, rock content, and redoximorphic features according to National Resource Conservation Service protocols (Schoeneberger et al. 2002). Horizon thicknesses were measured at representative locations along the soil pit face.

Representative soil samples were collected from the face of the pit in each of the uppermost and bottom 10 cm of the B horizon, and from a representative portion of the C horizon. The relatively inert E horizon, where it occurred, was not sampled. The upper portion of the mineral B horizon was expected to best reflect differences in soil chemistry as a function of atmospheric deposition (Lawrence et al. 1995), and keeping the thickness of this increment constant assured the highest comparability among sampled locations.

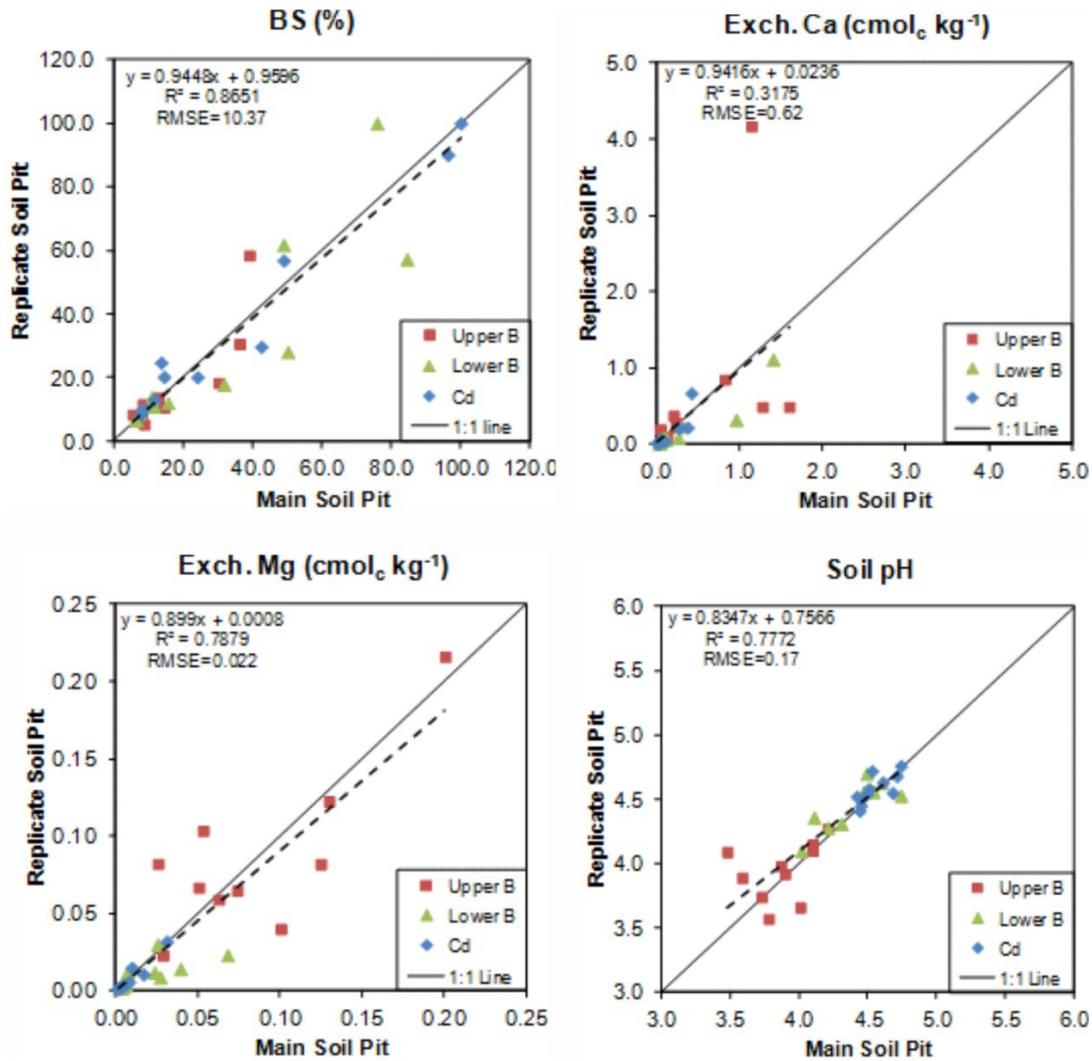
A total of 10 mineral soil pits were replicated during the course of the field sampling program to quantify local variability in soil conditions. Results for key soil parameters are plotted in Figure 4. Concentrations varied among horizons. Scatter in these plots reflects differences in soil condition between pairs of pits excavated in a given plot (Figure 4). Results of additional variables are reported by Sullivan et al. (2013a). If concentrations from each pit within the same plot were the same for respective horizons, plotting values from one pit against the other would yield a linear relationship with a slope of 1.0 and

a y-intercept of 0. Results showed reasonable agreement (correlations for %BS, Exch. Ca, Exch. Mg, pH of 0.86, 0.32, 0.79 and 0.78, respectively) between the original pits and the replicate pits.

**Figure 4. Soil Chemistry Analytical Results for 10 Replicated Mineral Soil Pits**

The pits were analyzed for (a) base saturation, (b) exchangeable calcium (Ca), (c) exchangeable magnesium (Mg), and (d) soil pH.

Data are reported by horizon for upper B (squares), lower B (triangles), and C (diamonds) horizons. None of the slopes are significantly different from 1; none of the y-intercepts are significantly different from 0 ( $p \leq 0.05$ ).



### 2.3.3 Laboratory Analyses

All soil chemical analyses were expressed on an oven-dried soil mass basis (70° C for O horizons and 105° C for mineral soils) and reported by Sullivan et al. (2013a). Analyses included loss-on-ignition (LOI); pH (in 0.01 M CaCl<sub>2</sub>); the amounts of exchangeable forms of Ca, Mg, potassium (K), sodium (Na), H<sup>+</sup>, iron (Fe), and manganese (Mn); extractable phosphorus (P; unbuffered 1 N NH<sub>4</sub>Cl), Al (KCl extraction), and SO<sub>4</sub><sup>2-</sup>; and total C and N (C-N analyzer). Quality assurance data determined through inter-laboratory sample exchange is available in Ross et al. (2015).

## 2.4 Vegetation Surveys

We sampled understory vegetation on the 50 plots (20 x 50 m each) that had been established in 2009 during the earlier study of the effects of acidic deposition and soil acidification on *Acer saccharum* trees in the Adirondack Mountains (2013a, Sullivan et al. 2013b). The plots represent a range of Ca availability, vegetation, and topographic characteristics of this forest type in the Adirondack region.

### 2.4.1 Vegetation Composition and Richness

Understory vegetation composition was characterized at each 20 x 50-m plot twice during the growing season (May–June and July–August 2015) to capture the variation between spring and summer vegetation on at least 15 subplots (1 x 1 m each) established in a 5 x 5-m grid within each plot (Figure 5). The subplots were established using a Haglof Vertex Hypsometer and distance tapes. The corners of each subplot were marked by stakes and visible flagging so that each plot could be relocated easily during the second field survey. On each subplot, all ground-layer vascular plants were identified (<1 m tall) to species (or genus when species level identification was uncertain) following Gleason and Cronquist (1991), supplemented by Holmgren (1998) and updated species nomenclature using species codes from USDA Natural Resources Conservation Service (2014). Percent cover was visually estimated individually for each vascular taxon (and for bryophytes as a group) following the plant cover estimation method of Daubenmire (1959), as used for example by Dovčiak and Brown (2014). Voucher specimens were photographed and collected outside of plots for all observed taxa. These samples were mounted and stored in the herbarium of the State University of New York College of Environmental Science and Forestry for quality control following methods described by Judd et al. (2007). In addition to species cover, the total vegetative cover and the total cover of each plant life form were estimated (forbs, graminoids,

clubmosses, ferns, bryophytes, shrubs, sub-shrubs, and tree seedlings) following USDA Natural Resources Conservation Service (2014), USDA Forest Service (2014), and Gleason and Cronquist (1991). We also estimated non-vegetative ground cover percentage on each subplot (including mineral soil, rock, and coarse woody debris) and recorded the fine-scale topography (flat, hollow, mound, or transitional).

**Figure 5. Example Plot Grid**



Plant species richness varies spatially and can therefore be influenced by the area sampled (Fridley et al. 2005). Thus, surveys of the 750 subplots (1 m<sup>2</sup>) in this study did not capture some of the rarer species. Subplot surveys were therefore supplemented with an inventory approach whereby each plot was examined, and all identified understory plant species were recorded. The plot-based approach provided quantitative measurements of herbaceous plant density and percent cover. The inventory approach identified some of the less common species that did not occur on subplots. Species richness and the degree to which species can be visually identified in the field vary temporally. Therefore, each subplot was visited twice, during both early and late summer. This improved estimates of richness for understory plant species in each plot and watershed.

## 2.4.2 Understory Light Conditions

The team characterized the light environment experienced by understory vegetation by estimating canopy openness (CO-D, Table 1) in the field using a convex spherical densiometer in opposing directions (north and south) at each of the subplots following established protocols (Dovciak and Brown 2014, Lemmon 1957). Three additional complementary measures of canopy cover and light were derived from remote sensing and canopy photographs collected or modeled within the previous study (Sullivan et al. 2013b). Total annual exposure of the ground surface to solar radiation (SolRad, Table 1) was calculated at 30 m- resolution using geographic information system (GIS) data reflecting topography, aspect, and the relative position of the sun, while correcting for the forest canopy cover (Sullivan et al. 2013a). Canopy cover (CC-ES, Table 1) was estimated by performing a spectral analysis in CorelDRAW of canopy gaps in photographs taken looking up from each soil pit. Canopy cover was also calculated at a 30 m-resolution for each plot using the USGS National Gap Analysis Program (CC-GAP, Table 1), with values based on an analysis of 1 m Landsat 7 satellite imagery (Sullivan et al. 2013a).

**Table 1. Predictor Variables (and Their Transformations When Needed)**

The predictor variables were measured or calculated from 2009 and 2015 field measurements or analyses of long-term or remote sensing data.

Symbol	Units	Transformed	Description
pH	pH units	-	Soil Acidity (pH) Measured in Calcium Chloride
T-pHb	pH units	Box-Cox, -1	Soil Acidity (pH) Measured in Calcium Chloride
BSb	%	-	Base Saturation
UB BS	%	-	Base Saturation in the upper B Horizon
T-UB BS	%	Box-Cox, -0.5	Base Saturation in the upper B Horizon
Acidityb	meq/100g	-	Exchangeable Acidity
Hb	meq/100g	-	Exchangeable H <sup>+</sup>
Al	meq/100g	-	Exchangeable Aluminum
T-Alb	meq/100g	Box-Cox, 0.5	Exchangeable Aluminum
Na	cmol <sub>eq</sub> /kg	-	Exchangeable Sodium
Kb	cmol <sub>eq</sub> /kg	-	Exchangeable Potassium
Ca	cmol <sub>eq</sub> /kg	-	Exchangeable Calcium
T-Ca	cmol <sub>eq</sub> /kg	Box-Cox, -0.5	Exchangeable Calcium
UB Ca	cmol <sub>eq</sub> /kg	-	Exchangeable Calcium in the upper B Horizon
T-UB Ca	cmol <sub>eq</sub> /kg	Box-Cox, 0.0	Exchangeable Calcium in the upper B Horizon
Mg	cmol <sub>eq</sub> /kg	-	Exchangeable Magnesium
T-Mg	cmol <sub>eq</sub> /kg	Box-Cox, -0.5	Exchangeable Magnesium

**Table 1. continued**

<b>Symbol</b>	<b>Units</b>	<b>Transformed</b>	<b>Description</b>
UB Mg	cmolesc/kg	-	Exchangeable Magnesium in the upper B Horizon
T-UB Mg	cmolesc/kg	Box-Cox, 0.0	Exchangeable Magnesium in the upper B Horizon
CaMg	cmolesc/kg	-	Ca + Mg
T-CaMgb	cmolesc/kg	Box-Cox, -0.5	Ca + Mg
LOI	%	-	% Weight Lost on Ignition
C	%	-	Total % Carbon
N	%	-	Total % Nitrogen
C:Nb	%	-	Ratio of C Divided by N
UB N	%	-	Total % Nitrogen in the upper B Horizon
S-DEP01b	kg/ha/yr	-	Mean Sulfur Deposition for 2000-2002 from TDEP
N-DEP01b	kg/ha/yr	-	Mean Nitrogen Deposition for 2000-2002 from TDEP
S-DEP07b	kg/ha/yr	-	Mean Sulfur Deposition for 2006-2008 from TDEP
N-DEP07b	kg/ha/yr	-	Mean Nitrogen Deposition for 2006-2008 from TDEP
S-DEP12b	kg/ha/yr	-	Mean Sulfur Deposition for 2011-2013 from TDEP
N-DEP12b	kg/ha/yr	-	Mean Nitrogen Deposition for 2011-2013 from TDEP
S-DEP06.13b	kg/ha/yr	-	Mean Sulfur Deposition for 2006-2013 from TDEP
N-DEP06.13b	kg/ha/yr	-	Mean Nitrogen Deposition for 2006-2013 from TDEP
CTIb	-	-	Compound Topographic Index
IMI	-	-	Integrated Moisture Index
T-IMIb	-	Box-Cox, -3	Integrated Moisture Index
CC-GAPb	%	-	% Canopy Cover from USGS-GAP
CC-ESb	%	-	% Canopy Cover from E&S Photos
CO-D	%	-	Mean % Canopy Openness from Densiometer
SoiRadb	-	-	Total Annual Solar Radiation from GIS Model
Elevationb	meters	-	From 30 m DEM (USGS, 1999)
AB-BAb	-	-	Overstory basal area proportion of <i>Fagus grandifolia</i>
AB-US	-	-	Frequency/m <sup>2</sup> of <i>Fagus grandifolia</i> in the understory
SM-BAb	-	-	Overstory basal area proportion of <i>Acer saccharum</i>
SM-US	-	-	Frequency/m <sup>2</sup> of <i>Acer saccharum</i> in the understory
RM-BA	-	-	Overstory basal area proportion of <i>Acer rubrum</i>
RM-US	-	-	Frequency/m <sup>2</sup> of <i>A. rubrum</i> in the understory

a Where not indicated otherwise, soil-chemical variables are from measurements taken in the O<sub>a</sub> horizon.

b denotes a variable included in regression model selection.

### **2.4.3 Soil Moisture Indices**

Compound Topographic and Integrated Moisture indices (CTI and IMI, Table 1) were derived following Gessler et al. (1995) and Iverson et al. (1997), respectively. The CTI was calculated by dividing the upslope (moisture contributing) area for a given point by the local slope. Higher values of CTI indicate a higher likelihood of becoming saturated with moisture (Gessler et al. 1995). The IMI also accounts for the upslope area and uses “hillshade” analysis to incorporate the extent of solar radiation in addition to local geographic curvature to account for their impact on moisture (Iverson et al. 1997).

### **2.4.4 Tree Seedling Banks and Browse Impacts**

Tree seedling bank composition was determined using seedling counts by species during the second field survey (July/August) in all 1 x 1 m-subplots if possible, given time considerations (and in five or more 1 x 1 m-subplots within each plot at the same locations as those surveyed in 2009). Within each seedling subplot, the number of seedlings was recorded by species. Seedlings included in the counts were at least 5 cm tall and had at least two fully formed leaves, but they were less than 1 cm DBH (following Sullivan et al. 2013a, 2013b). Seedling counts were enumerated by height class (<20 cm, 20-100 cm, and > 100 cm). Browse by mammalian herbivores (such as deer or rabbits) was characterized for each species and height class on a subset of the subplots as the percentage of seedlings affected by browse damage (i.e., with missing tissues and bite marks; cf., Lawrence et al. 2015b, Quant 2014). Retrospectively estimating the amount of removed plant tissue is difficult and prone to criticism. In addition, slight damage to the terminal shoot may be more significant than more substantial damage to lateral branches. Therefore, no attempt was made to quantify the damage to individual seedlings; instead, our measurement provides a population-level estimate of browse impacts (percentage of the plant population affected, ranging from 0 to 100%) to be used as a covariate in vegetation analyses. Measuring browse is important because it can potentially either mask or enhance vegetation responses to soil acidity or deposition.

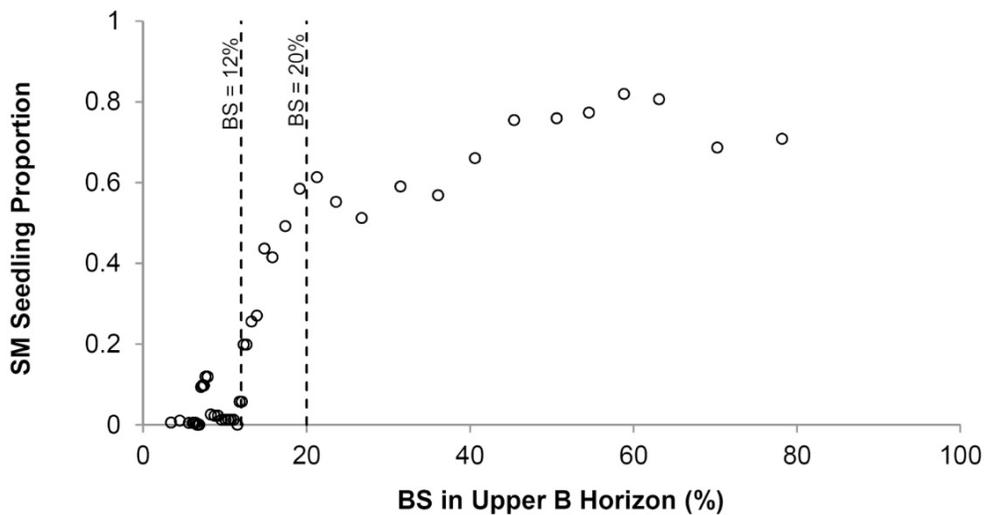
The herbaceous vegetation layer includes resident species that cannot grow taller than 1.5 m and also the seedlings, sprouts, and small saplings of woody species that will eventually grow into the higher strata of the forest. Species richness of the herbaceous vegetation layer was calculated as the total number of unique plant understory species identified on the surveyed 1 × 1-m subplots plus those tabulated in the searches of each plot and watershed.

## 2.5 Analysis

The team analyzed forest understory vegetation data to identify tipping points using approaches that are largely analogous to those used for the *Acer saccharum* assessment (Figure 6; Sullivan et al. 2013a, Sullivan et al. 2013b). We calculated mean cover, frequency, and species richness (number of species) for each plot following Dovčiak and Halpern (2010), Gurevitch et al. (2006), and Barbour et al. (1998). Species richness and vegetative cover (by functional group) per plot were analyzed relative to environmental characteristics, including soil (e.g., pH, Ca and N content, base saturation), atmospheric deposition (N and S), and light environment (overstory basal area [BA], canopy openness/cover) using linear regression (Weisberg 2005).

**Figure 6. Relationship between the Proportion of Seedlings That Were *Acer saccharum* and Soil BS in the Upper B Horizon in Adirondack Northern Hardwood Forests**

Source: Sullivan et al. (2013b)



We characterized multivariate species compositional trends across plots and measured environmental characteristics using non-metric multidimensional scaling (NMDS) ordination based on species frequency per watershed using PC-ORD v. 6.19 (McCune and Mefford 2011), following setting selections recommended by Peck (2002). Predictors of species richness were identified using ordinary

least squares (OLS) multiple regression (Fox and Weisberg 2011). In addition, an indicator species analysis (ISPAN; Dufrêne and Legendre 1997) and Peck (2010) was conducted to identify those species most closely associated with soils that may have been clearly affected by soil acidification and those soils where vegetation responses to acidification were less likely.

Statistical analyses explored the combined vegetation and soil chemistry database, with particular attention given to how the occurrences of forest understory plant species in the northern hardwood forest are related to aspects of soil acid-base chemistry, landscape characteristics, and estimates of atmospheric S and N deposition. Soil chemistry data for the upper B horizon were available at one location in each plot. However, upper soil horizon data (O<sub>e</sub>, O<sub>a</sub> and A horizons), which represent the primary rooting zone for herbs, were available at five locations within each plot. Several approaches for summarizing the upper horizon soil data by plot were investigated, including means by horizon, and the aggregation of data to develop a single number to reflect plot-representative soil chemistry values. Analyses reported herein utilized watershed level means of soil variables in the O<sub>a</sub> horizon and separately for the upper B horizon in some cases. Atmospheric N and S deposition were extracted from the TDEP spatial deposition data (Schwede and Lear 2014) based on the location of each plot and averaged to the watershed level.

### **2.5.1 Understory Community Composition**

For each understory plant species at each plot, mean species cover and frequency per site from the subplot measurements were calculated. Changes in community composition relative to environmental factors were analyzed using NMDS in PC-ORD v. 6.19 (McCune and Mefford 2011). Species composition was characterized in each watershed using a primary matrix representing the individual species frequency per m<sup>2</sup> subplot across each of 50 plots on 20 watersheds. Frequency was calculated as the number of 1 x 1 m-subplots in which a species occurred during either survey period (i.e., May–June and July–August), divided by the total number of subplots in the watershed (i.e., 30 or 45, corresponding to the number of plots per watershed [2 or 3]). Species that occurred in two or fewer watersheds were excluded from the primary matrix to reduce the effects of rare species on the analysis (McCune and Mefford 2011, Peck 2010). The analysis reflects compositional differences that were based on the occurrences of forest understory forbs, ferns, and woody species (< 1.5 m tall); graminoids were not included due to their general rarity on our plots (their mean subplot cover was only 0.4%, compared to 26% cover of all vascular plants) and because most graminoids occurred in a vegetative state (i.e., without flowers or fruits), which made them difficult to reliably identify to species.

Following Peck (2010), NMDS was run three times on autopilot (set to slow and thorough) using Sorensen distances. Scree plots and stress of solutions at each dimension suggested that a two-dimensional solution was most appropriate given the data and number of study watersheds. NMDS was then run three more times manually set to two dimensions. The distribution of plots in the ordination space were inspected for each of the three runs to confirm that distributions were consistent between the runs; we then selected the final solution using a Mantel Test in PC-ORD (which confirmed 99.9% redundancy between the selected run and all other manual runs, thus demonstrating their consistency). A secondary matrix of environmental and biotic variables (Table 1) was overlain on the NMDS ordination and the correlations between these variables and the NMDS axes were calculated to investigate the relationships between the variables and the main community compositional differences across the study watersheds.

### 2.5.2 Species Richness Models

Spatial autocorrelation in species richness at the plot and watershed level was assessed according to Moran’s I statistic based on distance thresholds of 1 km (plot level) and 26 km (watershed level). These thresholds were selected to ensure that each feature had at least one neighbor. The spatial weights matrix was developed from the inverse distance between neighboring plots/watersheds. Results are given in Table 2.

**Table 2. Spatial Autocorrelation in Plot and Watershed-Level Species Richness**

<b>Statistic</b>	<b>Plot Level</b>	<b>Watershed Level</b>
Moran's I	0.4699	0.4692
z-score	2.3987	2.6862
p-value	0.0164	0.0072

We used simple and multiple OLS regression to analyze the effects of environmental variables (Table 1) on species richness. As in the analyses of community composition, the environmental variables for each watershed were averaged. In addition, richness for each watershed as the total number of unique species identified on each plot was calculated (including species found both on and outside subplots). To limit regression analysis to the most pertinent predictors, we analyzed only those 37 variables that were strongly correlated with at least one of the NMDS compositional axes ( $r \geq 0.40$  for soil variables, and

$r \geq 0.20$  for the other variables; Table 3). Ca and Mg in the  $O_a$  horizon were highly correlated ( $r = 0.83$ ,  $p < 0.0001$ ), had nearly identical effects in multivariate models for species richness, and thus they were combined (added together) into a single variable (CaMg).

**Table 3. Pearson Correlation Coefficients ( $r$ ) and Coefficients of Determination ( $R^2$ )**

These coefficients are between untransformed environmental variables listed in Table 1 and the two NMDS ordination axes.

Axis 1			Axis 2		
Variable	$r$	$R^2$	Variable	$r$	$R^2$
Mg	0.945	0.894	Elevation	-0.652	0.425
CaMg	0.944	0.89	C	-0.626	0.392
Ca	0.939	0.882	CC-ES	-0.499	0.249
pH	0.897	0.804	LOI	-0.474	0.225
BS	0.875	0.766	AB-BA	-0.46	0.212
UB BS	0.744	0.554	UB N	-0.406	0.165
Richness	0.6	0.359	N	-0.377	0.142
K	0.57	0.325	CC-GAP	-0.351	0.123
SM-BA	0.544	0.296	Na	-0.307	0.094
N	0.482	0.232	C:N	-0.209	0.044
UB Ca	0.455	0.207	Al	-0.132	0.017
CC-GAP	0.374	0.14	K	-0.09	0.008
UB Mg	0.354	0.125	Ca	-0.065	0.004
SolRad	0.348	0.121	S-DEP12	-0.062	0.004
Na	0.294	0.086	CaMg	-0.053	0.003
Elevation	0.285	0.081	CO-D	-0.015	0
IMI	0.269	0.073	pH	0.018	0
CC-ES	0.249	0.062	Acidity	0.025	0.001
CTI	-0.044	0.002	UB BS	0.026	0.001
CO-D	-0.146	0.021	SolRad	0.051	0.003
C	-0.159	0.025	UB Ca	0.056	0.003
UB N	-0.166	0.028	N-DEP12	0.063	0.004
LOI	-0.202	0.041	Mg	0.08	0.006
AB-BA	-0.327	0.107	UB Mg	0.08	0.006
Al	-0.474	0.225	BS	0.093	0.009
S-DEP07	-0.517	0.267	S-DEP06.13	0.111	0.012
S-DEP01	-0.573	0.329	H	0.153	0.024
N-DEP12	-0.595	0.354	Richness	0.185	0.034
S-DEP06.13	-0.632	0.4	S-DEP07	0.186	0.035
H	-0.644	0.415	RM-BA	0.205	0.042

**Table 3. continued**

Axis 1			Axis 2		
Variable	<i>r</i>	<i>R</i> <sup>2</sup>	Variable	<i>r</i>	<i>R</i> <sup>2</sup>
N-DEP07	-0.647	0.419	IMI	0.273	0.074
RM-BA	-0.648	0.419	S-DEP01	0.28	0.078
N-DEP01	-0.651	0.424	N-DEP06.13	0.284	0.081
N-DEP06.13	-0.678	0.46	N-DEP01	0.319	0.102
S-DEP12	-0.684	0.468	CTI	0.355	0.126
Acidity	-0.686	0.47	N-DEP07	0.378	0.143
C:N	-0.738	0.545	SM-BA	0.384	0.147

Nitrogen, C, and LOI each appeared as important predictors in models. We included C:N ratio in model selection as a composite variable because it could be related to N availability to plants. The C:N ratio was significantly ( $p \leq 0.01$ ) positively related to the BA of *Fagus grandifolia* and negatively related to the BA of *Acer saccharum* (Appendix). As the variation in C:N could be partially explained by overstory components (BA of *Acer saccharum* and *Fagus grandifolia*; Table 1), these too were included in regression analyses. The C:N ratio was also negatively ( $p < 0.001$ ) correlated with pH, which was negatively correlated with N deposition (Appendix).

Model evaluation was carried out using the R software packages *car*, *leaps*, and *AICcmodavg* (Fox and Weisberg 2011, Lumley 2009, Mazerolle 2016, R Development Core Team 2016). Scatterplot matrices with regression lines were plotted in R, and Spearman correlations among variables were calculated using the SAS University Edition (SAS Institute Inc. 2015). Variables that had non-normal distributions (Shapiro-Wilk test  $p < 0.01$ ) were transformed to normality. The *symbox* function was used to evaluate potential Box-Cox scaled power transformations for each variable and the *bcpower* function was used to transform the variables as appropriate (see Table 1 for the specific transformations).

To avoid model overfitting given a dataset of only 20 observations (watersheds), candidate models were limited to either one or two predictor variables. This follows the recommendation in Harrell (2015) to limit predictors of continuous data to between  $n/10$  and  $n/20$ , where  $n$  is the sample size (Harrell 2015). Three global models were constructed from the selected variables, with each model including the same 18 potential predictors, but differentiated by which pair (time period) was used of the N-DEP and S-DEP variables (Table 1). We used the *regsubsets* function in R to search for the five best ( $nbest = 5$ ) two or one predictor models ( $nvmax = 2$ ) reduced from each of our three global models (using *exhaustive* search rather than *backward* or *forward* settings) (Shurin et al., 2010; Purse et al., 2012; Horrigue et al., 2016).

The top three models from each run were initially ranked using two separate criteria—Schwarz’s Information Criterion (BIC) and adjusted- $R^2$ —so that as many as 18 candidate models could result (Horrigue et al., 2016). BIC is a measure of model parsimony available within the *regsubsets* function. It approximates Akaike’s Information Criterion (AIC), with a greater penalty for inclusion of additional predictors (Schwarz 1978). This ranking procedure yielded eight candidate models (there was significant overlap of the “best” models between runs and rankings); some models that were most parsimonious (Schwarz’s Information Criterion) were not the most explanatory (adjusted- $R^2$ ). These eight “best” candidate models were further evaluated for parsimony using the *AICc* function (Akaike’s Information Criterion adjusted for small sample size; Purse et al. 2012), collinearity using the *vif* function (with the cutoff value = 4), heteroscedasticity using the function *ncvTest* and *residualPlots*, outliers using the functions *outlierTest*, *influenceIndexPlot*, and *qqPlot*, model fit using the function *marginalModelPlot*, and the effects of individual predictors on species richness using the function *avPlots* (Fox and Weisberg, 2011).

Results of diagnostic tests on the best model showed an acceptable level of collinearity based on variance inflation factors (VIF) = 2.22, or heteroscedasticity based on a plot of Pearson’s residuals against fitted values and a negative Breusch-Pagan test. Marginal model plots suggested that the “best” model’s fit was not as optimal as models two, five, six, and eight (Table 4). Several models included one or two observations with Cook’s distances between 0.2 and 0.3 (when the cutoff for the model was  $4/n = 0.2$ ; Bollen and Jackman 1990). However, removing these observations would create new outliers. A Bonferonni-corrected *t*-test of the studentized residual for each observation demonstrated that there were no statistically significant outliers. This conclusion was corroborated by examination of added-variable plots, which illustrated that removing these specific outliers alone would not clearly alter model interpretation. However, added-variable plots revealed that interpretations of the relationship between richness and S-DEP12 and N-DEP06.13 relied on a few influential points, suggesting that caution should be taken in interpreting the effects of these variables on richness.

**Table 4. Final Reduced Candidate Models for Predicting Species Richness**

Model Rank	Coefficient Estimates <sup>a</sup>							$\Delta$ AICc	Adjusted-R <sup>2</sup>	Model p-value
	Intercept	T-pH	T-CaMg	C:N	S-DEP12	N-DEP06.13	CC-ES			
1	-207.98**	268.42***	-	3.13*	-	-	-	0	0.60	0.00013
2	-104.94*	-	66.87***	-	10.20	-	-	1.3	0.58	0.00022
3	-172.82**	240.89***	-	-	9.87	-	-	1.32	0.58	0.00022
4	-89.68**	182.31***	-	-	-	-	-	1.87	0.52	0.00017
5	-36.36*	-	50.03***	-	-	-	-	2.03	0.52	0.00019
6	-98.51*	-	65.09***	2.14	-	-	-	2.6	0.55	0.00039
7	-150.93*	227.07***	-	-	-	4.20	-	3.46	0.53	0.00056
8	-33.11	195.43***	-	-	-	-	-0.70	3.56	0.53	0.00059

<sup>a</sup> Change ( $\Delta$ ) in AICc is relative to the best model. Coefficient p-values are represented as \*\*\* for  $p \leq 0.001$ , \*\* for  $p \leq 0.01$ , and \* for  $p < 0.05$ . Based on the influence of outliers, coefficient estimates for DEP variables are not considered meaningful.

Finally, we compared the effects of the individual soil predictors (measured in the O<sub>a</sub> horizon) identified in the best richness models with the effects of the same soil predictors measured in the upper B horizon. To do this, we used simple OLS regression to verify if the use of a particular soil horizon may have affected our results and inferences. In addition, although BS did not occur in any of the best richness models, we regressed richness specifically against BS (separately for the O<sub>a</sub> and upper B horizons) because BS was highly correlated to several predictors in the best models and it has been identified as an important predictor of vegetative responses to soil acidification (Sullivan et al. 2013b).

### 2.5.3 Indicator Species Analysis

We conducted indicator species analysis (ISPAN; Dufrêne and Legendre 1997) and the approach of Peck (2010) to identify those species most closely associated with upper B horizon base saturation (BS) above or below 12% at each study watershed. A BS value of 12% was selected to differentiate soils where vegetation responses may have been clearly affected by soil acidification (BS<12%), and soils where vegetation responses to acidification were less likely, based on the previous work on *Acer saccharum* (Sullivan et al. 2013a, Sullivan et al. 2013b). The ISPAN was conducted using frequency data from the same set of subplots on the same primary matrix used in NMDS, with a secondary matrix of binary values

indicating low- (BS<12%) or high- (BS>12%) base saturation in the upper B horizon in each watershed. The analysis was carried out with watersheds treated as blocks and high versus low BS as groups using PC-ORD (McCune and Mefford 2006). Species indicator values were calculated as products of relative abundance and relative frequency of each species in each group (i.e., BS>12% or BS <12%) divided by 100. Monte Carlo randomization tests were performed with 4999 iterations for each final indicator value and a species was considered an indicator of high- or low-BS if the maximum indicator value ( $IV_{max}$ ) was significant ( $P < 0.05$ ) and exceeded 25 (Dufrêne and Legendre 1997).

## 3 Results

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### 3.1 Soil Chemistry

Exchangeable Ca concentration averaged across the 50 soil pits was highest in the upper horizons, with decreasing concentrations found in progressively lower soil horizons (Figure 7a). Parameters shown include: (a) exchangeable Ca concentration, (b) base saturation, and (c) soil pH. Distributions for the remainder of the soil chemical variables can be found in Sullivan et al. (2013a). Median exchangeable Ca was 12.1 cmolc/kg in the O<sub>a</sub> horizon. The A and upper B horizons had median exchangeable Ca values of 3.1 and 0.3 cmolc/kg, respectively. The same general pattern was observed for soil % BS (Figure 7b). Upper B soil % BS was generally less than was found in surface horizons.

However, seven plots had upper B soil % BS values greater than 50%. Soil pH was typically between 3.0 and 4.0 in upper soil horizons and 3.5 to 4.5 in the B horizon (Figure 7c). Soil BS in the study plots was loosely related to the pH in the mineral soil rooting zone, mainly on sites having upper B horizon BS less than about 20%. At upper B horizon BS higher than about 20%, the pH of soil in deionized water ranged from about 4.4 to over 5.0 (Figure 8). The plots having lower BS in the upper B horizon showed pH that was in some cases as low as 4.0.

For all analyses, variation between replicate pits was highest in the upper B horizon (Sullivan et al. 2013a; Figure 4). This was expected because, compared to other mineral soil horizons, the upper B horizon has the highest level of root activity, the highest organic carbon (C) concentration, and the highest microbial activity, all factors that tend to vary spatially within the soil profile. Nevertheless, the data for all three horizons did approximate slopes of 1.0 and intercepts of 0 for nearly all of the measurements. This result confirms that a single pit is reasonably representative of the soil conditions in the study plots for these mineral soil horizons (Sullivan et al. 2013a; Figure 4). Soil BS in both the O<sub>a</sub> and upper B horizons varied spatially across the study region (Figures 9 and 10) at both the plot and watershed levels. The C:N ratio in the O<sub>a</sub> soil horizon did not show clear spatial patterns (Figure 11). The C:N of the upper B soil horizon showed evidence of higher C:N in the southwestern Adirondacks (Figure 12), the opposite of what would be expected if there was substantial N enrichment of mineral soils in the areas that received highest N deposition. This relationship may be complicated by relatively high soil C in the southwestern Adirondacks.

**Figure 7. Distribution Shown as Box-Plots of Major Soil Chemical Parameters in Organic and Mineral Soil Horizons across All 50 Sampled Plots**

Data were averaged for multiple samples that occurred within the same horizon on a plot. Parameters shown include: (a) exchangeable calcium (Ca) concentration, (b) base saturation, and (c) soil pH. Distributions for the remainder of the soil chemical variables can be found in Sullivan et al. (2013a).

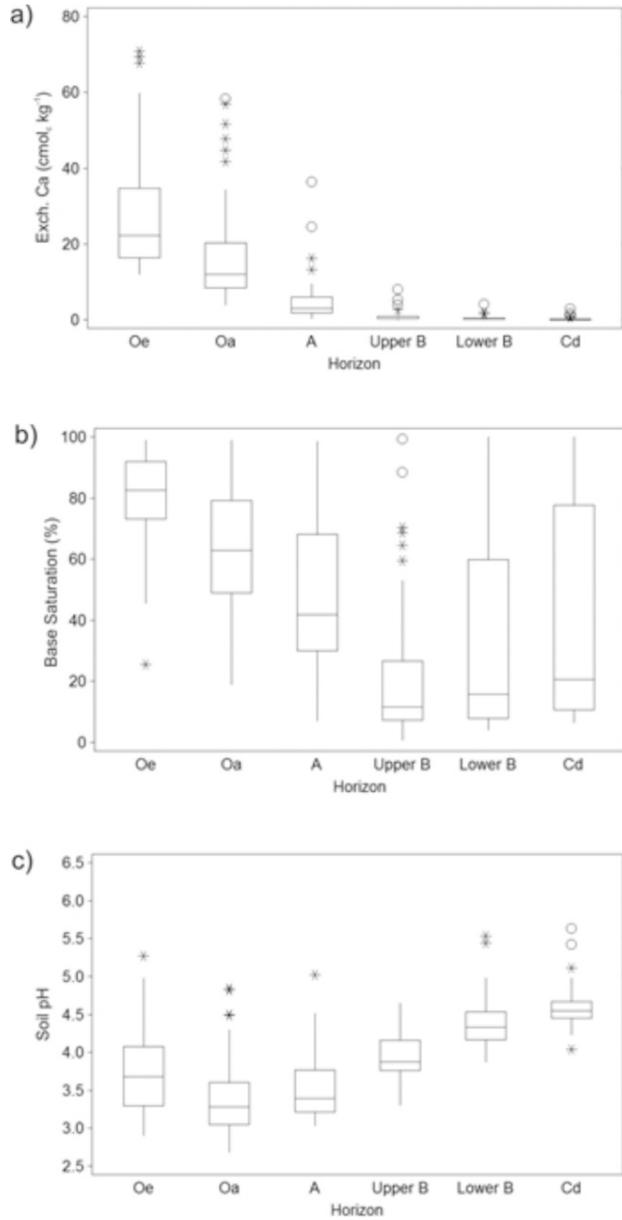
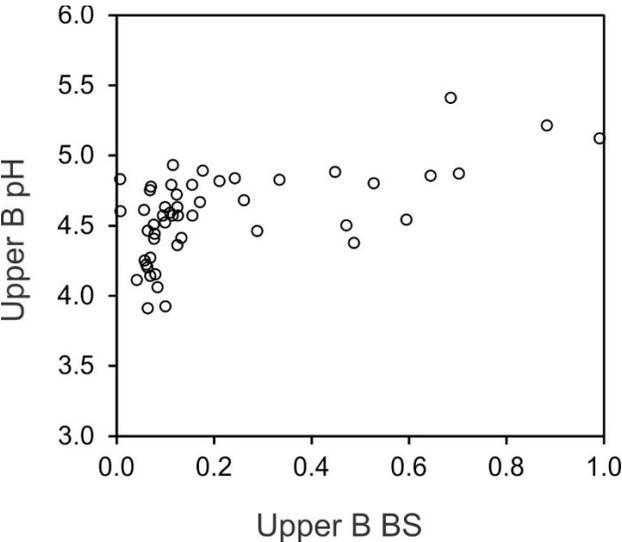
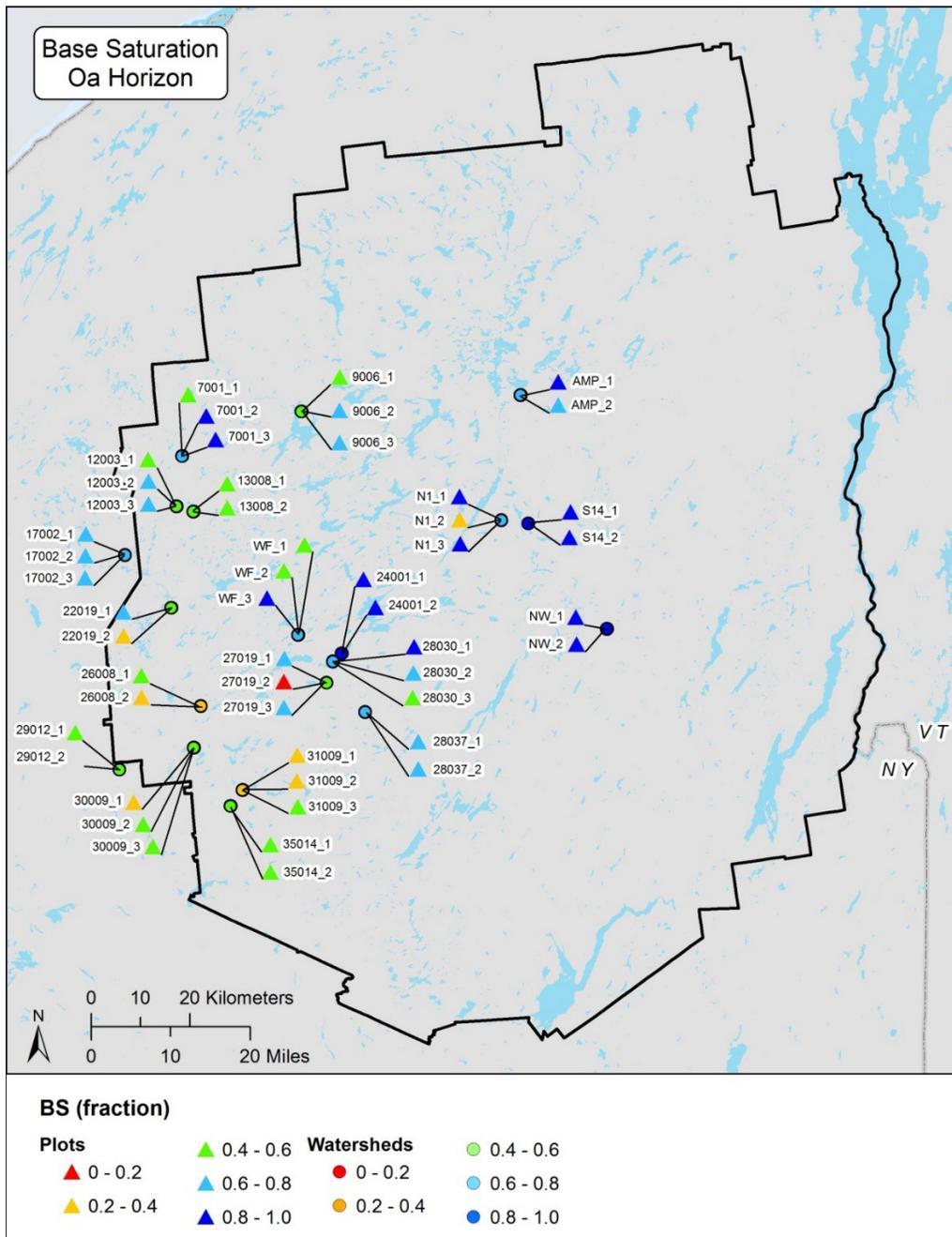


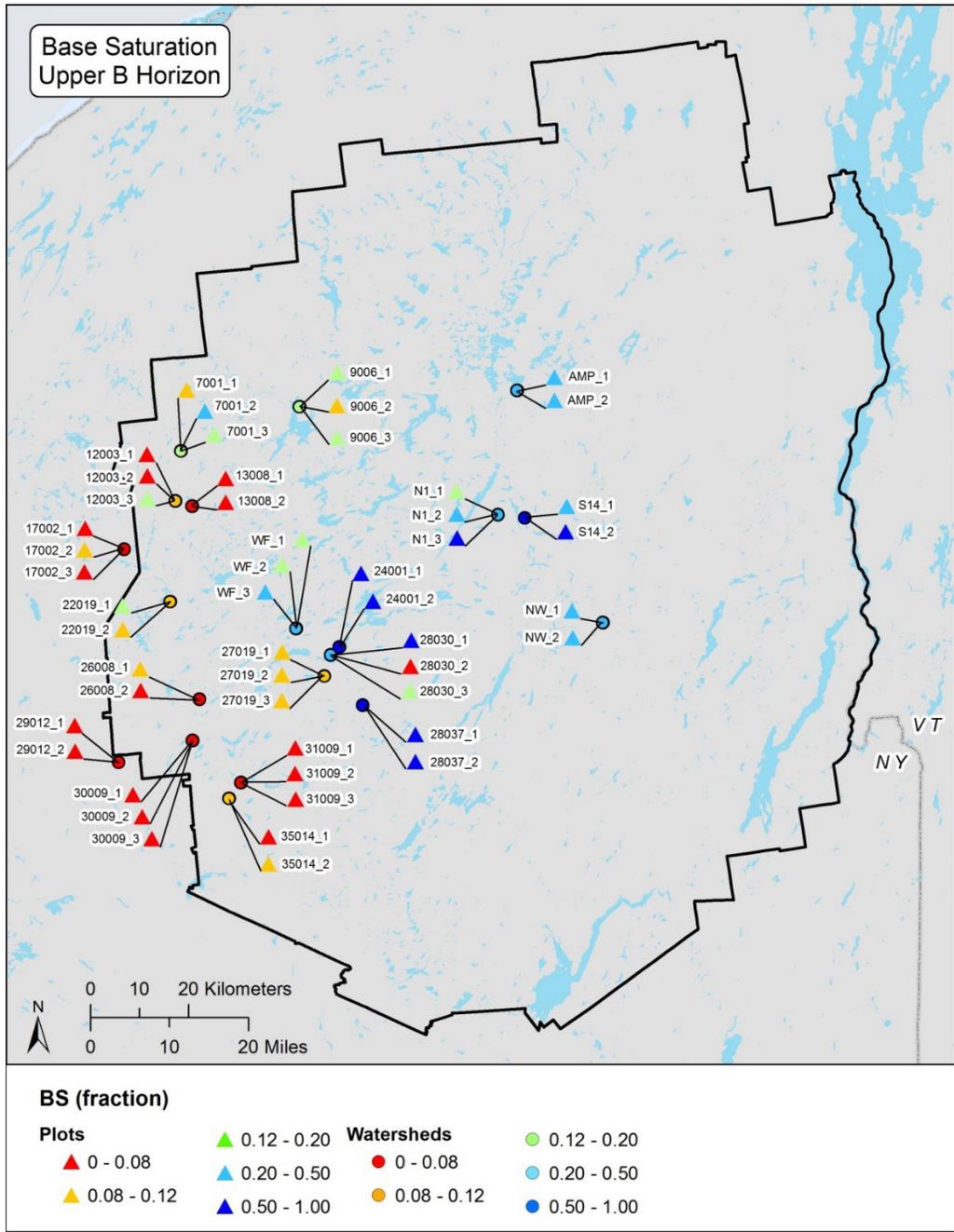
Figure 8. Plot-Level pH versus Base Saturation (BS) of the Upper B Soil Horizon



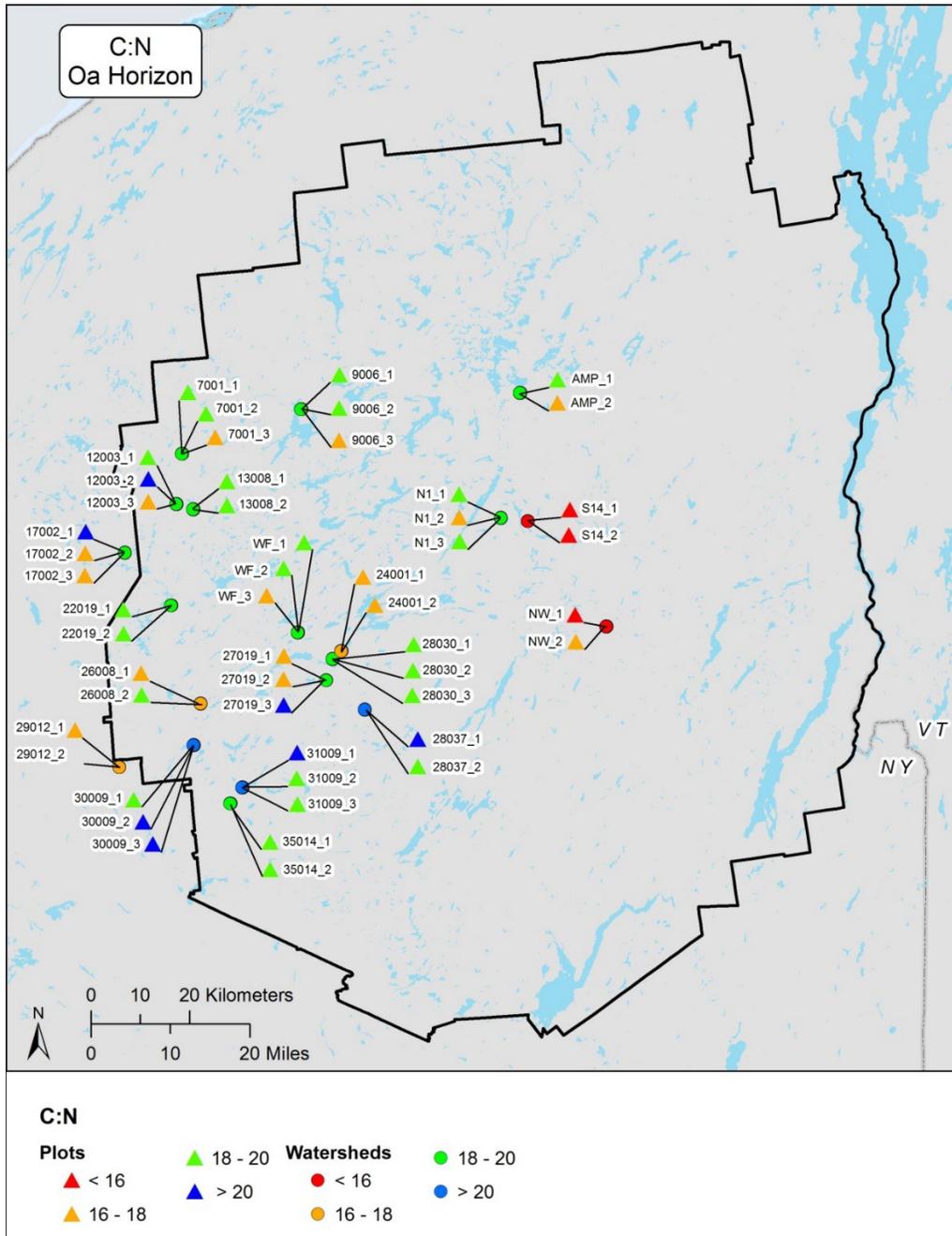
**Figure 9. Map Showing Soil-Base Saturation in the O<sub>a</sub> Horizon, Aggregated by Plot (Triangles) and by Watershed (Circles)**



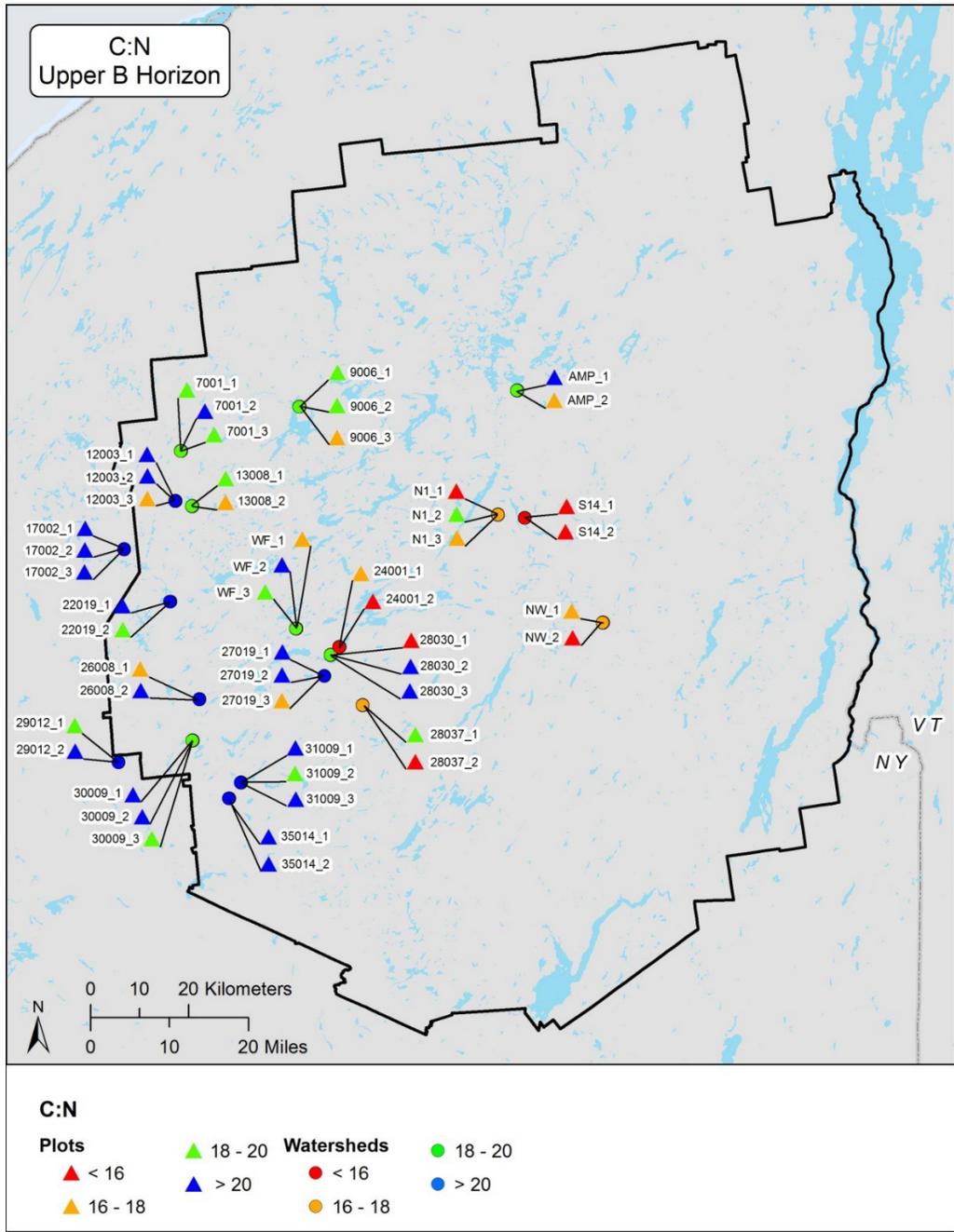
**Figure 10. Map Showing Soil-Base Saturation in the Upper B Horizon, Aggregated by Plot (Triangles), and by Watershed (Circles)**



**Figure 11. Map Showing Soil C:N Ratio in the O<sub>a</sub> Horizon, Aggregated by Plot (Triangles), and by Watershed (Circles)**



**Figure 12. Map Showing Soil C:N Ratio in the Upper B Horizon, Aggregated by Plot (Triangles), and by Watershed (Circles)**



### 3.2 Plant Species Composition and Richness

About 125 plant species were documented on the study plots (Table 5). Some (*Acer saccharum*, *Fagus grandifolia*, *Dryopteris intermedia*) occurred on all 50 plots. *Acer saccharum*, followed by *Fagus grandifolia*, was the dominant tree species in all study plots. Nevertheless, *Acer saccharum* sapling abundance was low, with nearly half of the study plots having no *Acer saccharum* saplings (Sullivan et al. 2013a, Sullivan et al. 2013b). *Acer saccharum* seedling abundance was also low on most plots, especially compared with *Fagus grandifolia*. Understory layer richness varied on most plots between about 20 and 45 species (Figure 13a). This variation in richness across plots was not associated with canopy openness in bivariate analyses (Figure 13b), suggesting that light availability was not a major determinant of richness. This result may have been due in large part to the rather narrow range of openness observed (10-20%). Photos illustrating examples of varying richness and cover are shown in Figure 14.

**Table 5. Taxa Observed and Identified to Species and Their Frequency**

Plot (n = 50) and subplot (n = 750) level (excluding graminoids)

Genus	Species	No. of Plots <sup>a</sup>	No. of Subplots	Cover % <sup>b</sup>
Fagus	grandifolia	50	540	12.79
Dryopteris	intermedia	50	491	11.07
Acer	saccharum	50	307	1.79
Acer	pennsylvanicum	49	346	2.12
Huperzia	lucidula	45	348	4.22
Prunus	serotina	43	60	1.54
Acer	rubrum	42	318	1.41
Viburnum	lantanooides	41	102	14.22
Picea	rubens	41	88	7.54
Medeola	virginiana	41	81	1.49
Betula	alleggheniensis	41	65	1.03
Trillium	undulatum	36	34	1.53
Oxalis	montana	35	85	1.52
Arisaema	triphillum	35	49	0.99
Uvularia	sessifolia	33	246	4.30
Maianthemum	canadense	33	116	2.53
Dennstaedtia	punctilobula	31	117	9.15
Streptopus	roseus	30	14	1.79
Thelypteris	noveboracensis	29	35	5.79

**Table 5. continued**

<b>Genus</b>	<b>Species</b>	<b>No. of Plots<sup>a</sup></b>	<b>No. of Subplots</b>	<b>Cover %<sup>b</sup></b>
<b><i>Mitchella</i></b>	<b><i>repens</i></b>	<b>29</b>	<b>23</b>	<b>1.54</b>
Monotropa	uniflora	28	11	0.55
Polygonatum	pubescens	27	23	1.48
Maianthemum	racemosa	27	5	0.70
Epifagus	virginiana	26	70	0.63
Viola	rotundifolia	26	61	1.66
Erythronium	americanum	23	100	1.18
Lonicera	canadensis	22	15	1.83
Trientalis	borealis	20	71	1.08
Fraxinus	americana	20	65	1.73
Oclemena	acuminata	20	10	2.20
Aralia	nudicaulis	18	31	3.47
Tsuga	canadensis	18	13	2.77
Abies	balsamea	15	2	1.00
Pinus	strobus	14	4	0.88
Dendrolycopodium	dendroidium	13	34	3.35
Tiarella	cordifolia	13	14	3.96
Prenanthes	sp.	13	7	1.57
Clintonia	borealis	11	14	3.36
Galium	triflorum	11	8	2.81
Phegopteris	connectilis	11	5	4.40
Rubus	idaeus	11	4	2.38
Trillium	erectum	11	1	0.50
Osmundastrum	cinnamomeum	10	1	1.00
Rubus	alleghehiensis	9	10	3.40
Polystichum	acrostichoides	9	9	8.94
Sambucus	racemosa	9	3	3.00
Ostrya	virginiana	8	30	3.62
Botrypus	virginianus	8	3	1.67
Panax	trifolius	8	2	1.50
Osmunda	claytoniana	8	1	1.00
Viola	renifolia	7	20	1.20
Dendrolycopodium	obscura	7	7	4.93
Rubus	pubescens	7	2	0.75
Cornus	alternifolia	7	1	1.00
Sorbus	americana	6	4	3.25
Calystegia	sepium	6	4	2.38

Table 5. continued

<b>Genus</b>	<b>Species</b>	<b>No. of Plots<sup>a</sup></b>	<b>No. of Subplots</b>	<b>Cover %<sup>b</sup></b>
<b><i>Epipactis</i></b>	<b><i>helleborine</i></b>	<b>6</b>	<b>3</b>	<b>0.67</b>
<i>Tilia</i>	<i>americana</i>	5	14	0.61
<i>Coptis</i>	<i>trifolia</i>	5	7	0.93
<i>Eurybia</i>	<i>macrophylla</i>	4	3	2.33
<i>Actaea</i>	<i>pachypodia</i>	4	0	.
<i>Platanthera</i>	<i>orbiculata</i>	4	0	.
<i>Dryopteris</i>	<i>marginalis</i>	3	3	5.33
<i>Viola</i>	<i>canadensis</i>	3	3	2.33
<i>Acer</i>	<i>spicatum</i>	3	2	0.50
<i>Caulophyllum</i>	<i>thalictroides</i>	3	1	5.00
<i>Spinulum</i>	<i>annotinum</i>	2	11	3.32
<i>Ageratina</i>	<i>altissima</i>	2	5	0.90
<i>Deparia</i>	<i>acrostichoides</i>	2	2	22.50
<i>Gymnocarpium</i>	<i>dryopteris</i>	2	2	1.00
<i>Taraxacum</i>	<i>officinale</i>	2	1	1.00
<i>Viburnum</i>	<i>cassinoides</i>	2	1	1.00
<i>Viola</i>	<i>pubescens</i>	2	1	1.00
<i>Adiantum</i>	<i>pedatum</i>	2	0	.
<i>Panax</i>	<i>quinquefolia</i>	2	0	.
<i>Polypodium</i>	<i>appalachianum</i>	2	0	.
<i>Quercus</i>	<i>rubra</i>	2	0	.
<i>Pteridium</i>	<i>aquilinum</i>	1	7	27.57
<i>Apocynum</i>	<i>androseamifolium</i>	1	3	0.83
<i>Thelypteris</i>	<i>simulata</i>	1	2	8.75
<i>Dalibarda</i>	<i>repens</i>	1	2	2.00
<b>Genus</b>	<b>Species</b>	<b>No. of Plots<sup>a</sup></b>	<b>No. of Subplots</b>	<b>Cover %<sup>b</sup></b>
<i>Solidago</i>	<i>caesia</i>	1	2	1.00
<i>Claytonia</i>	<i>virginica</i>	1	2	0.50
<i>Viola</i>	<i>incognita</i>	1	2	0.50
<i>Laportea</i>	<i>canadensis</i>	1	1	40.00
<i>Dryopteris</i>	<i>filix-mas</i>	1	1	5.00
<i>Galium</i>	<i>sylvaticum</i>	1	1	3.00
<i>Cornus</i>	<i>canadensis</i>	1	1	1.00
<i>Populus</i>	<i>tremuloides</i>	1	1	0.50
<i>Aralia</i>	<i>racemosa</i>	1	0	.
<i>Athyrium</i>	<i>filix-femina</i>	1	0	.
<i>Circaea</i>	<i>alpina</i>	1	0	.

**Table 5. continued**

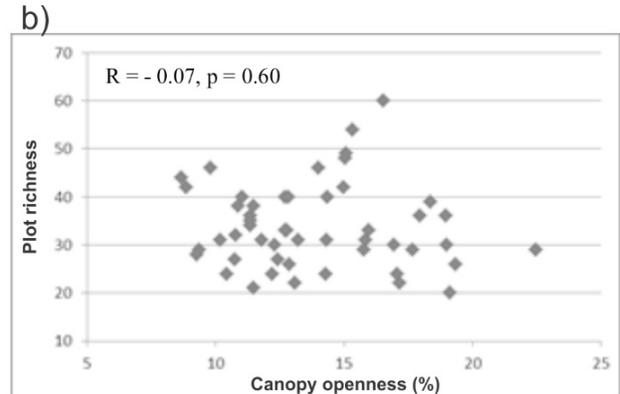
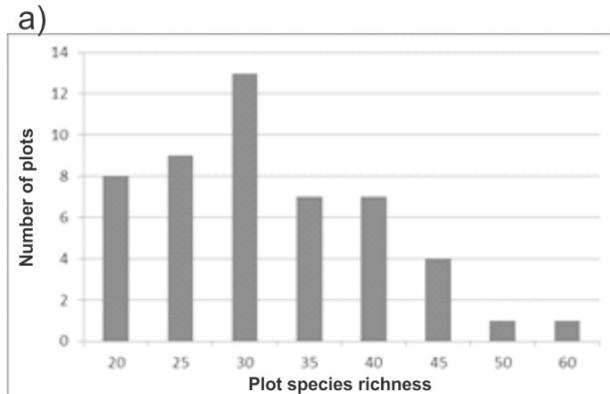
Genus	Species	No. of Plots <sup>a</sup>	No. of Subplots	Cover % <sup>b</sup>
Claytonia	caroliniana	1	0	.
Diphiastrum	digitalis	1	0	.
Dryopteris	carthusiana	1	0	.
Dryopteris	goldiana	1	0	.
Equisetum	arvense	1	0	.
Eurybia	divaricata	1	0	.
Populus	grandidentata	1	0	.
Prunus	virginiana	1	0	.
Ribes	cynosbati	1	0	.
Ribes	lacustre	1	0	.
Taxus	canadensis	1	0	.
Viburnum	acerifolium	1	0	.

<sup>a</sup> Taxa with no number of subplots reported are those identified in plot time search outside of subplots.

<sup>b</sup> Cover % calculated for subplots where each taxon occurred and averaged for rounds 1 and 2. Figure 13. Species Richness per Plot Calculated from both Subplot and Time Search Data (Excluding Graminoids)

**Figure 13. Species Richness per Plot Calculated from both Subplot and Time Search Data (Excluding Graminoids)**

They are depicted as a histogram (a) and show the lack of relationship between richness and canopy openness (b).



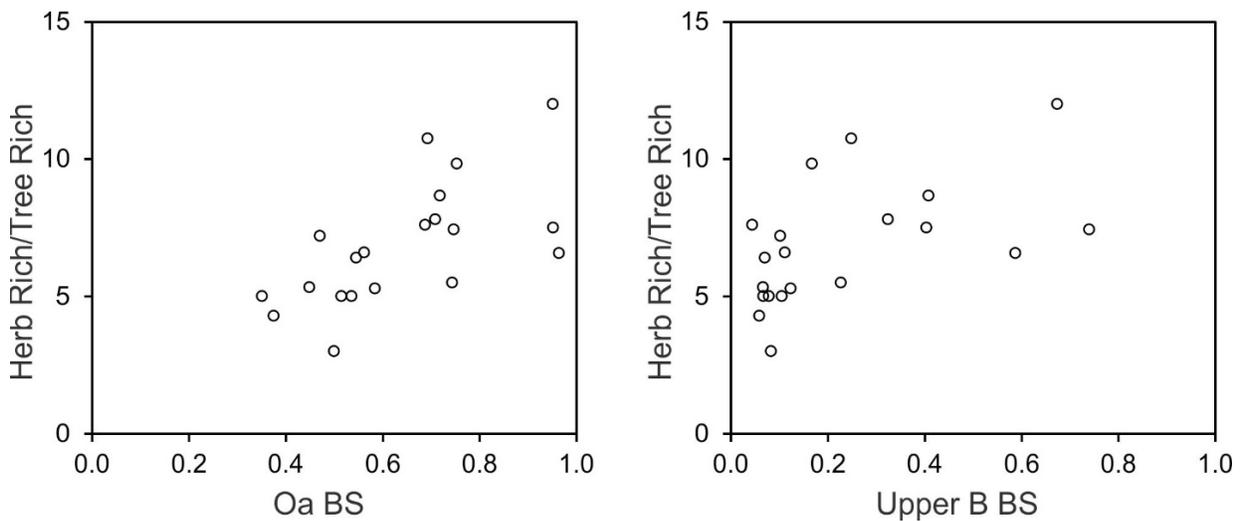
### Figure 14. Example Plots

Plots with (a) high richness, (b) high cover, and (c) low richness and cover.



In contrast, plot richness in the herbaceous layer increased with pH, Ca and Mg cations, and C:N ratio as well as with BS, using data for both O<sub>a</sub> and upper B horizons (Table 4). The ratio of plot species richness in the herbaceous layer to richness in the tree layer varied with BS in the O<sub>a</sub> soil horizon, and to a lesser extent in the upper B horizon (Figure 15). At relatively low BS, herbaceous layer richness was generally low in proportion to tree species richness in the same watershed. This suggests that low BS may be having a disproportionate impact on herbaceous layer plants.

**Figure 15. Ratio of Plant Species Richness in the Herbaceous Layer to the Tree Layer within Study Watersheds versus Base Saturation (BS) in the O<sub>a</sub> (Left Panel) and Upper B (Right Panel) Soil Horizons**



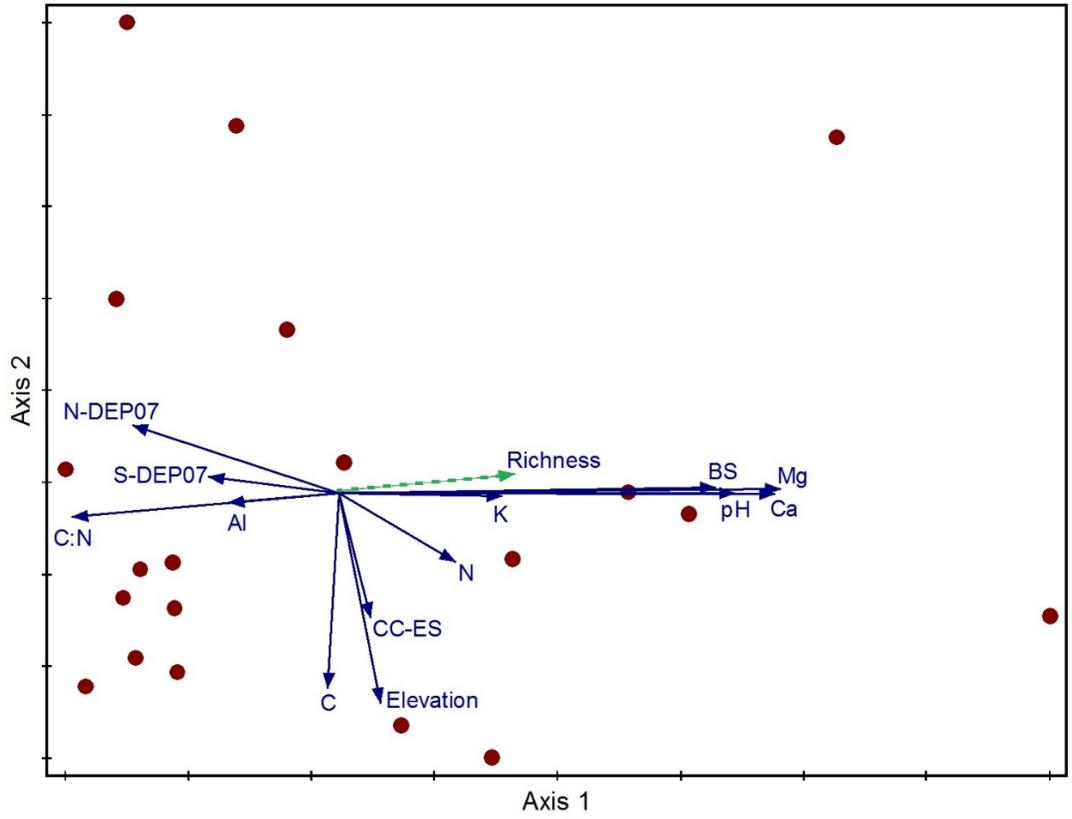
### 3.2.1 Trends in Community Composition Across Environmental Gradients

Community composition (variety of species present) varied along two distinct gradients as implied by the statistically significant final two-dimensional NMDS solution (Figure 16; randomization test  $p = 0.002$ ; stress = 11.23, well under a maximum interpretable stress threshold of 20; Horsley et al. 2008, Peck 2010). NMDS axis 1 explained 63.3% of understory compositional variation and represented a gradient of soil buffering capacity, soil acidification and atmospheric deposition: axis 1 was strongly positively correlated with pH, BS, and plant nutrients (e.g., Mg,  $r = 0.945$ ) and negatively correlated with acidic deposition and soil acidification variables (e.g., N-DEP07,  $r = -0.647$ ) as well as with C:N ratio which was positively correlated with N deposition (Figure 16, Table 3). NMDS axis 2 explained 27.8% of compositional variation and represented gradients of soil organic matter, canopy cover and elevation that were negatively correlated with this axis (e.g., C,  $r = -0.626$ ; Table 3). Interestingly, total soil N content was correlated with both axes and appears to be the main driver of the C:N vector direction (Figure 16, Table 3).

The ordination described a clear gradient of increasing species richness (number of species present) along axis 1. Richness was positively correlated with axis 1 ( $r = 0.600$ ), increasing with soil pH, BS, and base-cation concentrations (Ca, Mg) and declining with acidic deposition and soil acidification variables as well as with C:N ratio (Table 3). Similar to richness, the occurrences of eight species were strongly and positively correlated ( $r > 0.4$ ) with axis 1, suggesting positive responses to increasing pH, BS, and availability of plant nutrients. Occurrences of four species were negatively correlated with axis 1 ( $r < -0.4$ ) and positively associated with acidic deposition and soil acidification (Table 6, Figure 17). Nine species increased along the gradient of decreasing soil organic matter, canopy closure, and elevation as they were positively correlated with axis 2 ( $r > 0.4$ ). Three species were negatively correlated with axis 2 ( $r < -0.4$ ) and were positively associated with higher elevation in areas with more soil organic matter and greater canopy closure (Table 6, Figure 17).

**Figure 16. Vectors Showing Correlations of Species Richness and Abiotic Variables with NMDS Ordination of Species Composition Across Watersheds**

Only correlations having  $p \geq 0.4$  are shown. The length of each vector is drawn proportional to the strength of the respective correlation. This chart shows that axis 1 is represented by soil acid-base chemistry, with vectors of base saturation (BS), pH, and exchangeable base cations (Mg, Ca) to the right (positive relationship) and sulfur deposition (S-DEP07), and aluminum (Al) to the left (negative relationship). Axis 2 is negatively related to total percent carbon (C) and percent canopy cover (CC-ES), which reflect aspects of nutrition and carbon cycling. Deposition estimates are three-year averages centered on 2007. Watersheds are represented by filled circles.

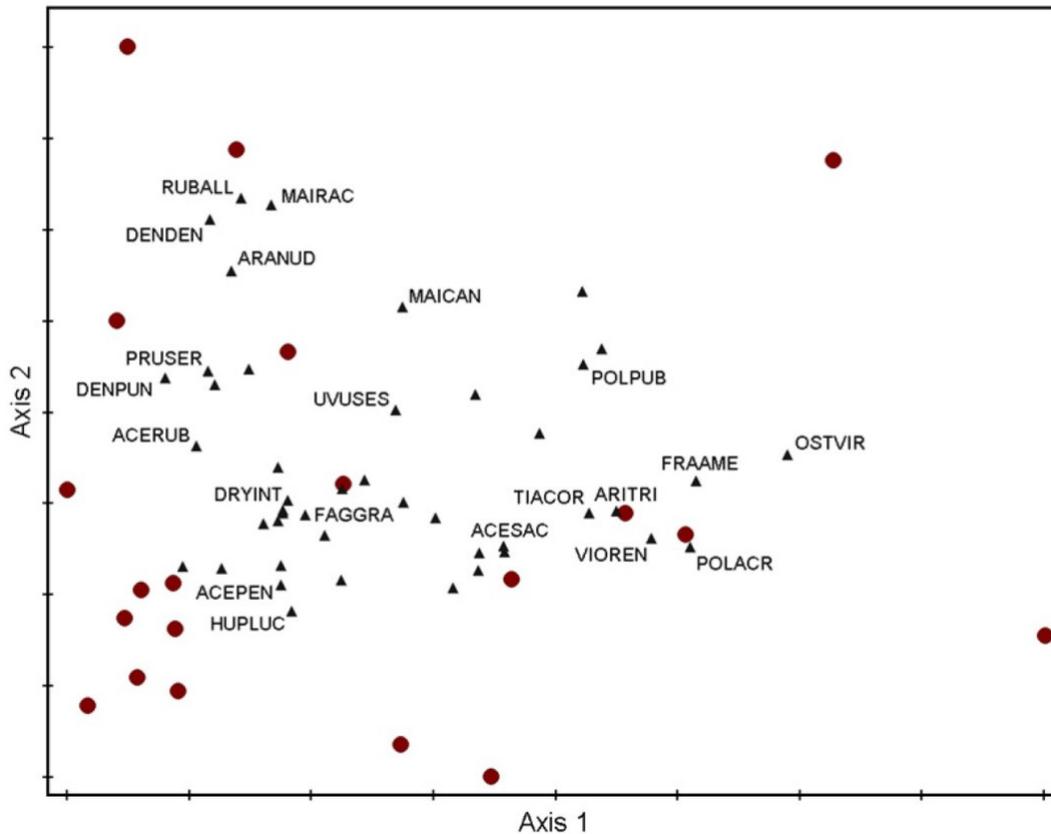


**Table 6. Correlation Coefficients ( $r \geq 0.4$ ) and Coefficients of Determination ( $R^2 \geq 0.2$ ) between Species and the two NMDS Ordination Axes**

Axis 1				Axis 2			
Genus & Species	Code	$r$	$R^2$	Genus & Species	Code	$r$	$R^2$
Arisaema triphyllum	ARITRI	0.829	0.688	Dendrolycopodium dendroidium	DENDEN	0.691	0.477
Ostrya virginiana	OSTVIR	0.754	0.569	Maianthemum canadense	MAICAN	0.69	0.476
Fraxinus americana	FRAAME	0.751	0.563	Aralia nudicaulis	ARANUD	0.609	0.371
Acer saccharum	ACESAC	0.717	0.514	Prunus serotina	PRUSER	0.6	0.36
Polygonatum pubescens	POLPUB	0.56	0.314	Dennstaedtia punctilobula	DENPUN	0.574	0.33
Tiarella cordifolia	TIACOR	0.515	0.265	Maianthemum racemosa	MAIRAC	0.539	0.291
Polystichum acrostichoides	POLACR	0.51	0.26	Uvularia sessifolia	UVUSES	0.538	0.289
Viola renifolia	VIOREN	0.469	0.22	Rubus allegheniensis	RUBALL	0.525	0.275
Dennstaedtia punctilobula	DENPUN	-0.533	0.284	Polygonatum pubescens	POLPUB	0.456	0.208
Acer rubrum	ACERUB	-0.684	0.467	Acer pennsylvanicum	ACEPEN	-0.448	0.201
Acer pennsylvanicum	ACEPEN	-0.744	0.553	Fagus grandifolia	FAGGRA	-0.461	0.213
Dryopteris intermedia	DRYINT	-0.857	0.735	Huperzia lucidula	HUPLUC	-0.697	0.486

**Figure 17. Species Distributions within the Ordination Shown in Figure 16**

Species centroids (filled triangles) describe mean species location within the ordination relative to axes and watershed locations (filled circles). For clarity, only species most correlated with at least one of the axes ( $r \geq 0.4$ ) ( $R^2 \geq 0.20$ ) are labeled by species code (see Table 6). Species on the left side of the graph tend to be negatively correlated to axis 1, while species on the right side tend to be correlated positively with axis 1. Species on top of the graph tend to be correlated positively with axis 2, while species at the bottom tend to be correlated negatively with axis 2.



### 3.2.2 Environmental Drivers of Species Richness

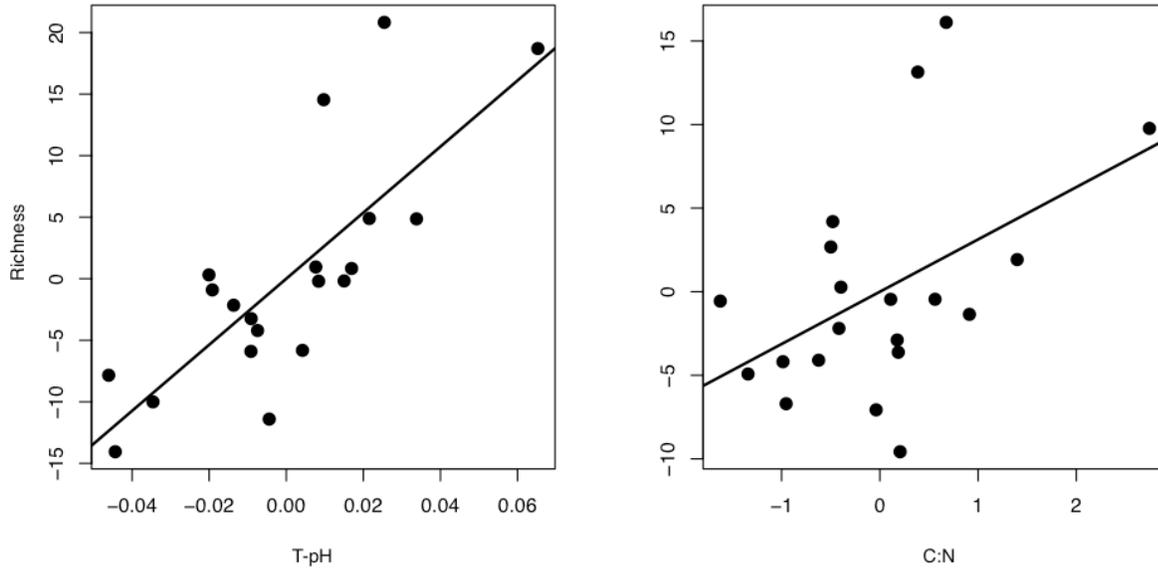
Species richness across the study watersheds was predicted best by a two-variable model (Adjusted- $R^2=0.60$ ,  $p$ -value  $< 0.001$ ) that included statistically significant positive effects of T-pH and C:N ratio (Table 4, Figure 18), and the second-best model was obtained with the related variables of T-CaMg and S-DEP12, although coefficient estimate for S deposition was non-significant at  $\alpha = 0.05$ . Overall, the most prominent predictors (in terms of frequency and ease of interpretation) were pH, CaMg, and C:N (Figures 18 and 19), with C:N ratio driven predominantly by its strong negative correlation to total soil N (i.e., C:N ratio was low where total soil N was high and vice versa). These models illustrated the overarching positive effects of Ca, Mg, and pH on species richness. The positive effect of C:N on

richness was only revealed in the multivariate regression analyses (Table 4, Figure 18) and it was masked in simpler approaches by the other stronger predictor variables (cf. Figure 16). Nitrogen and S deposition and canopy cover had statistically non-significant coefficients at  $\alpha = 0.05$ . The dramatic and positive effects of bases (Ca, Mg, and BS) on species richness were further highlighted by simple regressions of species richness against BS and individual Ca and Mg concentrations in both the O<sub>a</sub> and upper B horizons (Figure 20). Magnesium and Ca in the O<sub>a</sub> horizon had similar relationships to richness, but Mg was a weaker predictor in the upper B horizon, due largely to a few outliers (Figure 20).

While our best multivariate models of species richness included strong effects of CaMg (or pH), it is important to stress that all of these soil variables describe a composite soil gradient (axis 1 in Figure 16) in which the individual soil variables co-vary with each other. For example, pH, Mg, Ca, K, and BS in the O<sub>a</sub> horizon had generally strong ( $r = 0.44 - 0.90$ ,  $p < 0.05$ ) positive Spearman correlations with each other and with species richness. Exchangeable H and acidity were positively correlated with each other ( $r = 0.87$ ,  $p < 0.0001$ ), but they were negatively correlated with pH, Mg, Ca, BS in the O<sub>a</sub> horizon and with species richness ( $r = -0.85 - 0.53$ ,  $p < 0.05$ ). Exchangeable Al was positively correlated with exchangeable acidity ( $r = 0.65$ ,  $p < 0.01$ ) and negatively correlated with species richness, BS, Ca, and Mg ( $r = -0.48 - -0.70$ ,  $p < 0.05$ ). These relationships are corroborated by vector correlations with NMDS axis 1 (Table 3, Figure 16).

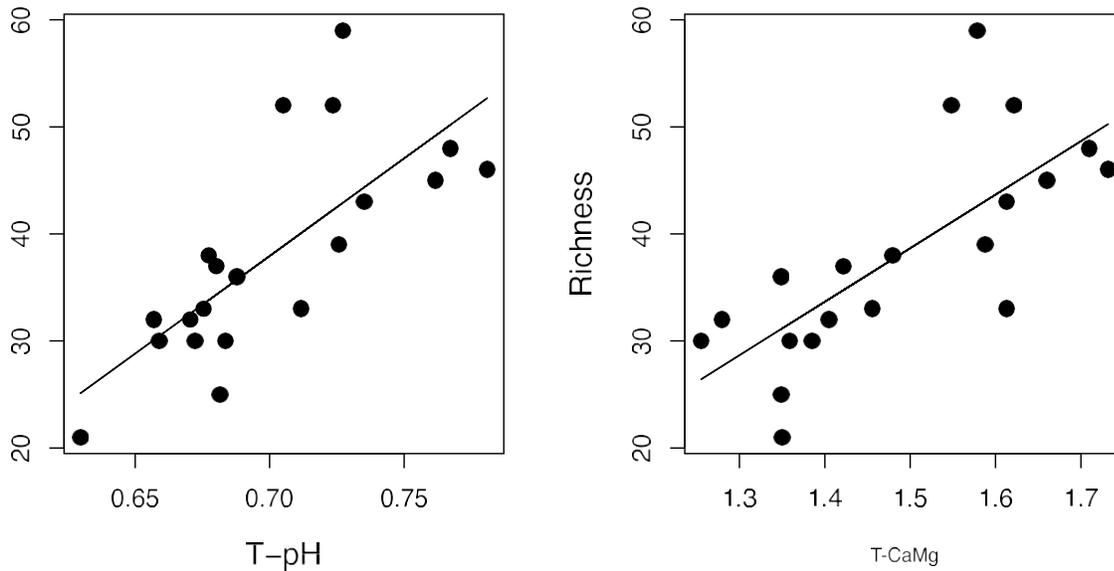
**Figure 18. Added Variable Plots for the Best Model Predicting Species Richness and Showing the Effect of each Predictor on Species Richness When the Other Predictor is Held Constant**

Table 4 provides model coefficients and p-values. Table 1 contains variable definitions. Note that residuals (which can be negative) are used in the added variable plots rather than the original variables in order to account for the effects of the other variable in the full model.



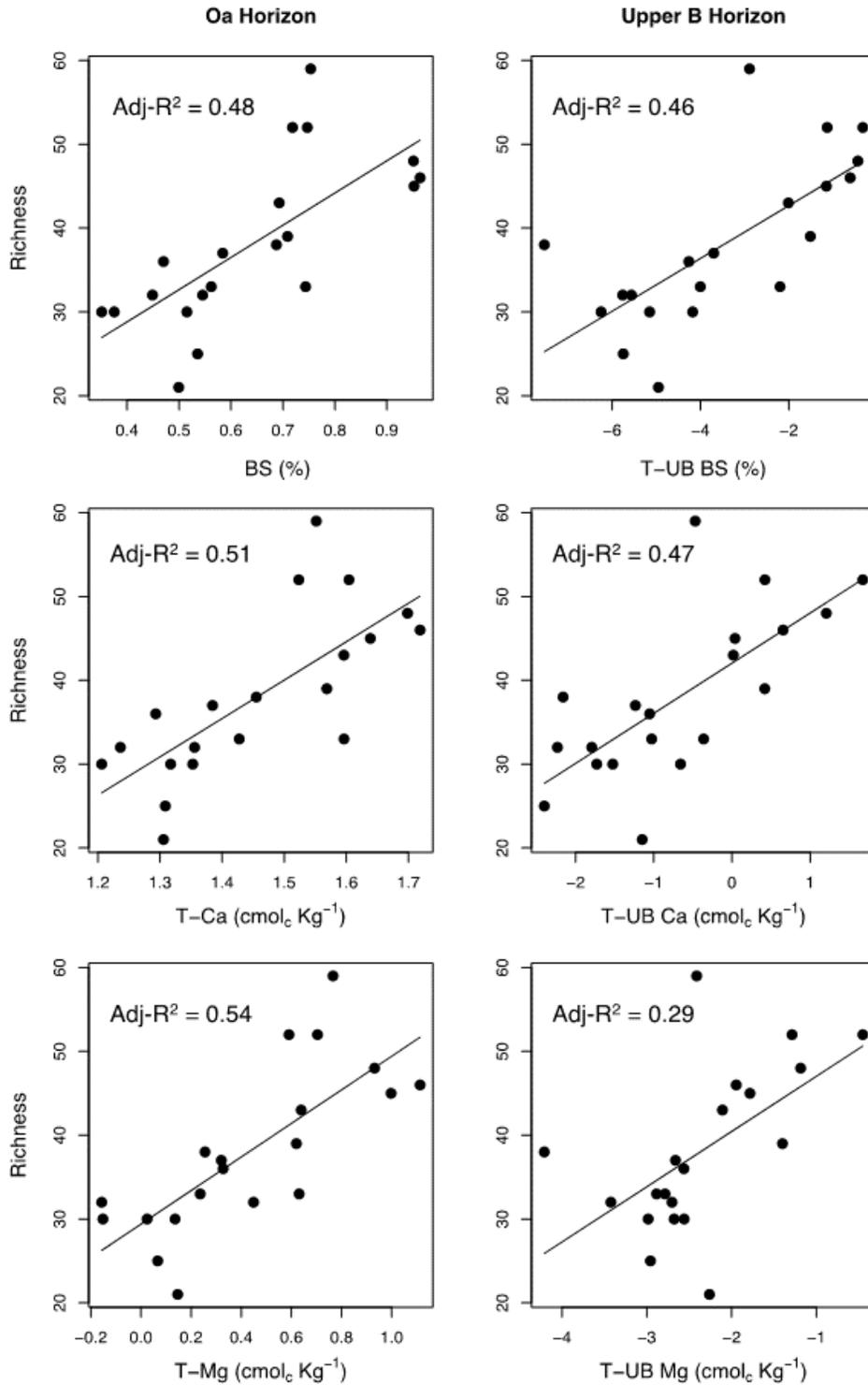
**Figure 19. Simple Regression Plots of Models 4 and 5 in Table 4**

Table 4 provides model coefficients and p-values. Table 1 contains variable definitions.



**Figure 20. Simple Ordinary Least Square Regressions of Species Richness against Soil Variables in the O<sub>a</sub> (left column) and Upper B (right column) Horizons across the 20 Study Watersheds**

“T-” indicates transformed variables.



### 3.2.3 Relationships Among Deposition and Soil Variables

While the gradient in soil acidity along axis 1 (Figure 16) may result partly from natural variation in the soil environment, atmospheric deposition of S and N (Table 1) is likely to be responsible for a significant part of the identified soil acidification gradient. This is suggested by the strong positive Spearman correlations of N-DEP07 and S-DEP07 (i.e., deposition measurements centered on 2007, prior to 2009 soil sampling) with exchangeable acidity and H ( $r > 0.65$ ,  $p < 0.01$ ), and their strong negative correlations with Ca, Mg, pH, and BS ( $r \geq 0.60$ ,  $p \leq 0.001$ ). Deposition variables measured during later periods (N-DEP12 and S-DEP12, Table 1) showed similar, but much weaker relationships to soil Ca, Mg, pH and BS (Spearman correlations  $r > 0.35$ , sometimes not significant) and to exchangeable acidity and H ( $r > 0.60$ ,  $p < 0.01$ ) due to both the decline in the deposition levels over time and the increasing disconnect between the time of soil sampling (2009) and deposition measurements (2012). Somewhat surprisingly, N in the O<sub>a</sub> horizon was significantly negatively correlated with N-DEP07 ( $r = -0.46$ ,  $p < 0.05$ ), while N in the upper B horizon was not significantly correlated with any deposition variable. There was no significant Spearman correlation between exchangeable Al and any deposition variable.

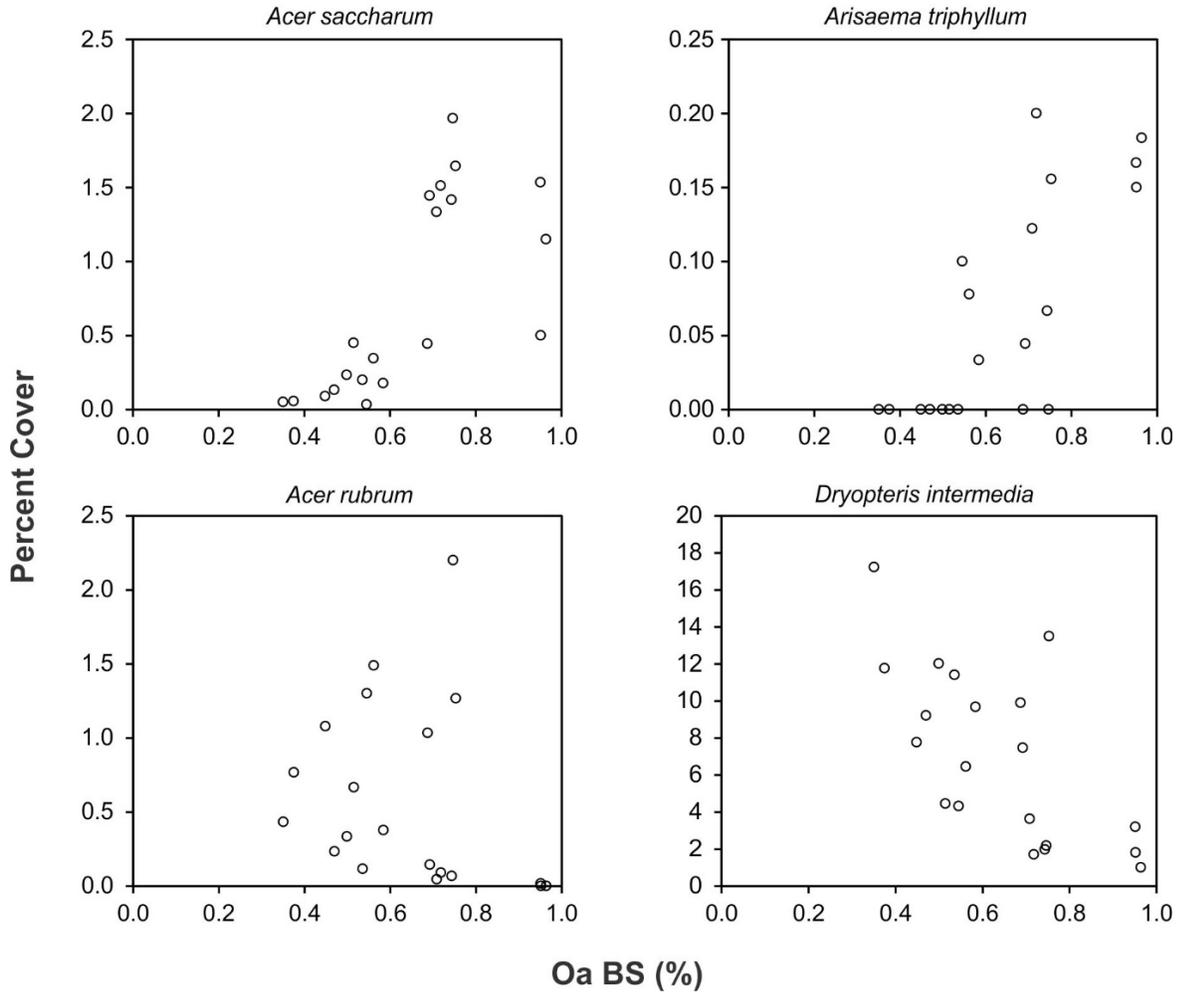
### 3.3 Patterns in Plant Cover

Four species showed some evidence of patterns of percent cover as a function of BS in either the O<sub>a</sub> and/or upper B soil horizon (Figures 20 and 21). Two of those species (*Acer saccharum*, *Arisaema triphyllum*) showed higher cover (> 0.5%) at higher BS values in both O<sub>a</sub> and B horizons (Figures 21 and 22). The other two species (*Acer rubrum*, *Dryopteris intermedia*) showed higher cover at lower or intermediate BS values in the upper B horizon (Figure 22). In each case, the tipping point of BS that appeared to affect percent cover was near 10–20% for the upper B horizon soils and near 80% for the O<sub>a</sub> horizon.

In general, there was little relationship between cover of the various plant types (ferns, forbs, bryophytes, graminoids, club mosses) and the BS of the O<sub>a</sub> or upper B soil horizons. Exceptions are shown in Figure 23, illustrating that fern and club moss covers were often higher at locations where BS was relatively low. This pattern was largely confined to the upper B soil horizon.

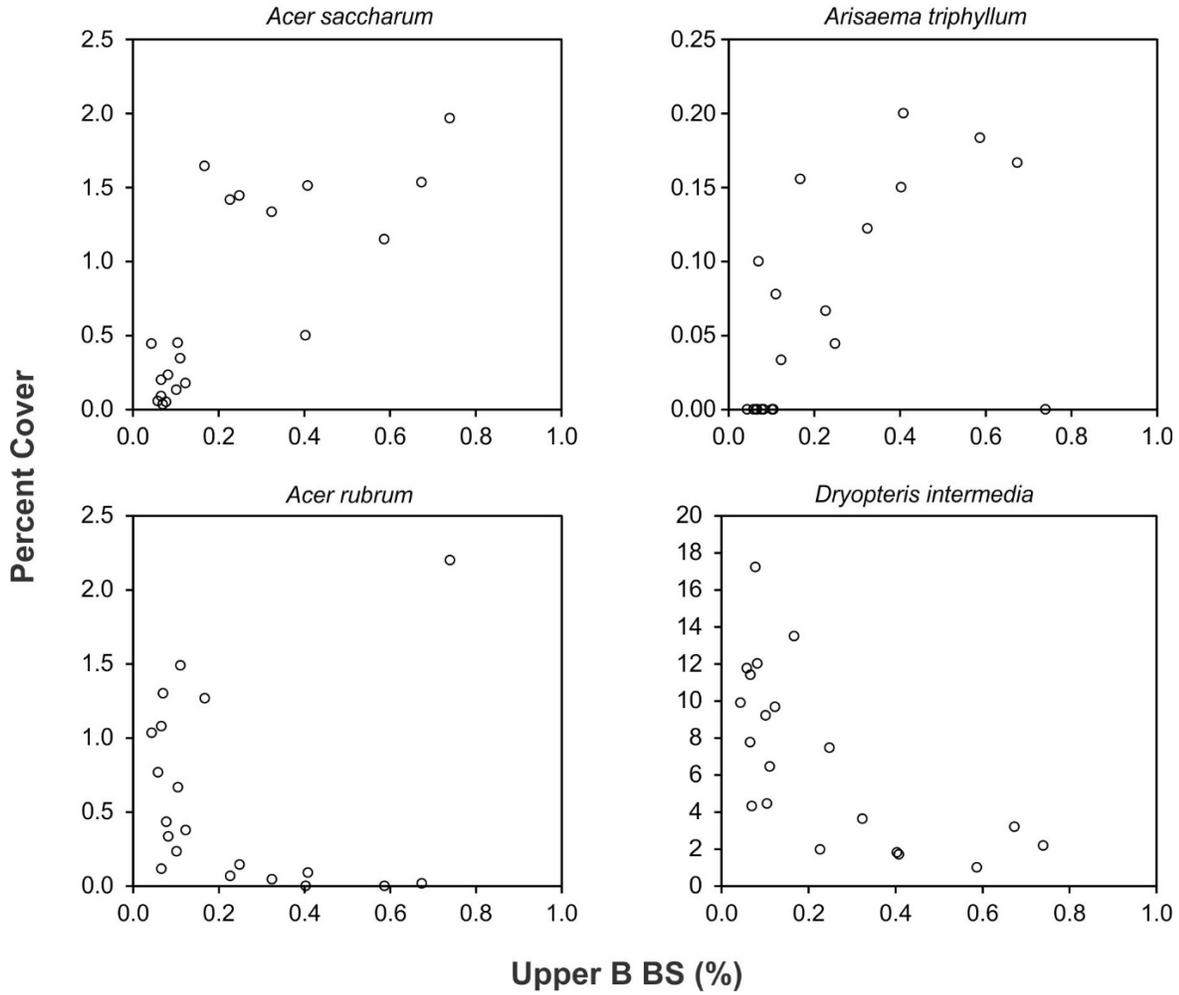
**Figure 21. Percent Cover of Selected Individual Plant Species as Functions of Base Saturation of the O<sub>a</sub> Soil Horizon**

**Species Cover (percent) vs. O<sub>a</sub> Base Saturation**



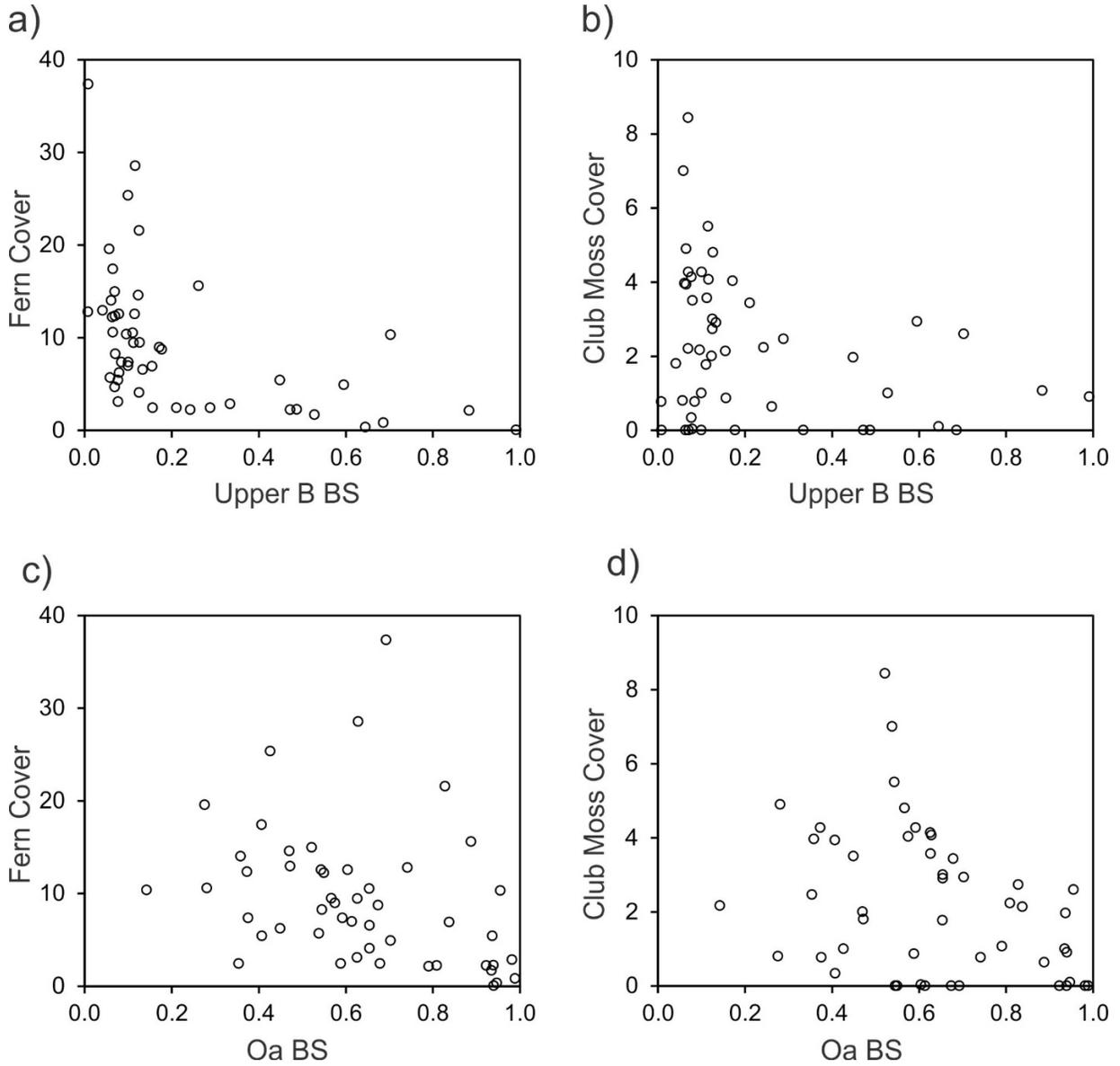
**Figure 22. Percent Cover of Selected Individual Plant Species as Functions of Base Saturation of the Upper B Soil Horizon**

**Species Cover (percent) vs. Upper B Base Saturation**



**Figure 23. Plot-Level Percent Cover of Selected Plant Types versus the Base Saturation (BS) of the Upper B and O<sub>a</sub> Soil Horizons**

Other plant types did not show evidence of clear relationships between BS and cover.



### 3.4 Browse

Across both rounds of sampling, deer browse on tree seedlings tended to intensify (accumulate) with seedling size class. It was lowest for the smallest seedlings (<20 cm tall) and often highest for the largest height class (>100 cm tall), except in cases where recruitment failure potentially due to heavy browse on intermediate size class (20 to 100 cm tall) may have led to low sapling abundance in the largest height class (Tables 7 and 8). The most intensively browsed tree species (i.e., > 50% saplings browsed in at least one of the two taller size classes) across both rounds of sampling were *Acer saccharum*, *Fraxinus americana*, *Fagus grandifolia*, and *Prunus serotina*. Tree species associated with both ends of the acidification gradient (i.e., *Acer saccharum* and *Fraxinus americana* in less acidified conditions, and *Fagus grandifolia* and *Prunus serotina* in more acidified conditions, see Figure 17, Table 6) appeared to be browsed equally and browse was thus not likely to bias patterns that we found in species composition or richness across the acidification gradient.

**Table 7. Counts of Seedling Species Observed on all Subplots of All Plots During Round 1 (n = 750)**

Grouped by size class, indicating the percent of seedlings browsed within each class.

Round 1		Size Class					
		5-20 cm		20-100 cm		> 100 cm	
Genus	Species	Total Count	Browsed (%)	Total Count	Browsed (%)	Total Count	Browsed (%)
<i>Acer</i>	<i>pennsylvanicum</i>	555	5	61	28	6	50
<i>Acer</i>	<i>rubrum</i>	839	3	37	27	0	n.a.
<i>Acer</i>	<i>saccharum</i>	1308	7	15	53	4	75
<i>Betula</i>	<i>allegheniensis</i>	76	7	7	14	0	n.a.
<i>Cornus</i>	<i>alternifolia</i>	2	0	0	n.a.	0	n.a.
<i>Fagus</i>	<i>grandifolia</i>	690	8	244	64	106	74
<i>Fraxinus</i>	<i>americana</i>	97	18	8	63	0	n.a.
<i>Ostrya</i>	<i>virginiana</i>	4	25	1	0	0	n.a.
<i>Picea</i>	<i>rubens</i>	5	0	11	9	5	0
<i>Pinus</i>	<i>strobus</i>	3	0	0	n.a.	0	n.a.
<i>Prunus</i>	<i>serotina</i>	64	8	19	84	0	n.a.
<i>Sambucus</i>	<i>racemosa</i>	4	0	0	n.a.	0	n.a.
<i>Sorbus</i>	<i>americana</i>	1	0	0	n.a.	0	n.a.
<i>Tilia</i>	<i>americana</i>	2	0	0	n.a.	0	n.a.
<i>Tsuga</i>	<i>canadensis</i>	8	0	2	0	0	n.a.

**Table 8. Counts of Seedling Species Observed on a Subsample of Five Central Subplots of All Plots**

The count was done during round 2 (n = 250), grouped by size class, indicating the percent of seedlings browsed within each class.

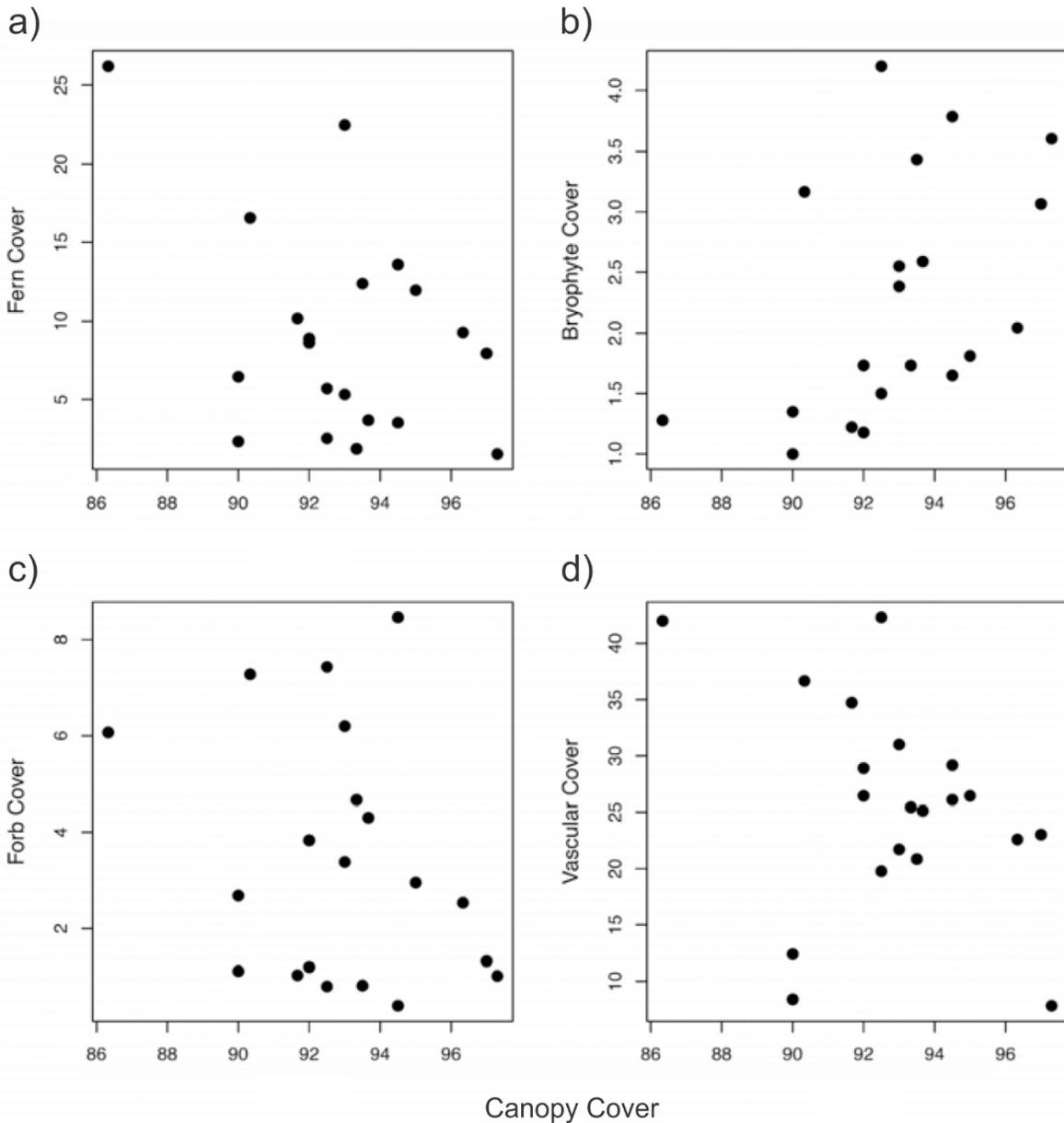
Round 2		Size Class					
		5-20 cm		20-100 cm		> 100 cm	
Genus	Species	Total Count	Browsed (%)	Total Count	Browsed (%)	Total Count	Browsed (%)
<i>Acer</i>	<i>pennsylvanicum</i>	233	3	14	14	5	40
<i>Acer</i>	<i>rubrum</i>	263	4	12	33	1	100
<i>Acer</i>	<i>saccharum</i>	418	5	2	100	3	67
<i>Betula</i>	<i>allegheniensis</i>	35	0	3	0	0	n.a.
<i>Cornus</i>	<i>alternifolia</i>	1	0	0	n.a.	0	n.a.
<i>Fagus</i>	<i>grandifolia</i>	266	5	86	59	32	59
<i>Fraxinus</i>	<i>americana</i>	28	4	4	50	0	n.a.
<i>Ostrya</i>	<i>virginiana</i>	5	0	1	0	0	n.a.
<i>Picea</i>	<i>rubens</i>	1	0	4	0	2	0
<i>Pinus</i>	<i>strobus</i>	3	0	0	n.a.	0	n.a.
<i>Prunus</i>	<i>serotina</i>	19	21	10	70	0	n.a.
<i>Sambucus</i>	<i>racemosa</i>	1	0	2	50	0	n.a.
<i>Sorbus</i>	<i>americana</i>	0	n.a.	0	n.a.	0	n.a.
<i>Tilia</i>	<i>americana</i>	0	n.a.	0	n.a.	0	n.a.
<i>Tsuga</i>	<i>canadensis</i>	4	0	0	n.a.	0	n.a.

### 3.5 Light

Most correlations to canopy openness for the various life forms were weak to nonexistent at the watershed level. Bryophytes had the strongest positive relationship to canopy cover (Figure 24) with a significant Spearman correlation of  $r = 0.57$  at  $\alpha = 0.05$ . These results suggest that light may not play a strong structuring role in these forests at the watershed scale for most life-forms, likely due partly to the narrow range of canopy openness observed in these mostly closed forests (typical canopy openness was ~10-20%). However, in concert with other variables affecting plant cover or richness, light may be more important, particularly if wind or forest management related disturbances create more open canopies and initiate greater development of the forest understory plant community.

**Figure 24. Examples of Bivariate Relationships between Canopy Cover (Measured with Photos Taken from within Plots in 2009) and Life Form Cover (%) Averaged on the Watershed Level**

Life forms examined were forbs, graminoids, lycopodium, ferns, bryophytes, shrubs, subshrubs, vines, and trees. While canopy cover did not seem to significantly affect the cover of all vascular species, it was positively related to bryophyte cover (b).



### 3.6 Indicator Species

Indicator species analysis revealed that some understory species were indicative of high- or low-base saturation. Four species (two species of ferns and seedlings of two species of maple) were indicative of base saturation in the upper B horizon < 12 % (Table 9; Figure 25). Nine species (six herbaceous and three woody, the latter including *Acer saccharum*) were indicative of upper B horizon BS > 12% (Table 9; Figure 26). Indication of BS thresholds was corroborated by species correlations with axis 1 of Figure 16 (Table 6), negative correlations being associated with acidic deposition and positive correlations associated with high pH and BS (Table 9).

**Table 9. Results of ISA Partitioned by the Condition Indicated (Groups with UB BS > and < 12%)**

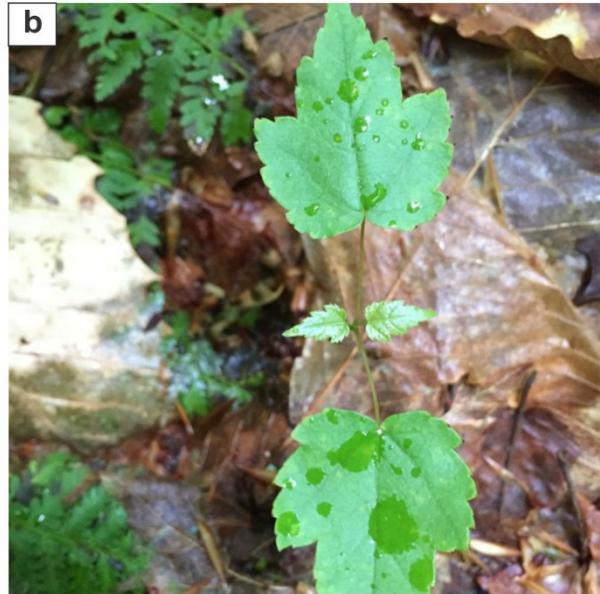
This includes Pearson correlations to NMDS axis 1, indicator values (IV), difference between the IV for each group, significance of the randomization test, and relative abundances and frequencies of each species in each group. Species codes are in Table 6, except for VIOROT, *Viola rotundifolia*; PRESP1, *Prenanthes sp.*; TIACOR, *Tiarella cordifolia*; LONCAN, *Lonicera canadensis*; and GALTRI, *Galium triflorum*.

Indicators of UB BS < 12%									
Species code	<i>r</i> Axis 1	<i>R</i> <sup>2</sup> Axis 1	IV < 12%	IV Difference	<i>p</i> - value	Rel. Abundance > 12%	Rel. Abundance < 12%	Rel. Frequency > 12%	Rel. Frequency < 12%
DENPUN	-0.533	0.284	78	71	0.004	14%	86%	50%	90%
ACERUB	-0.684	0.467	71	48	0.009	29%	71%	80%	100%
ACEPEN	-0.744	0.553	65	34	0.018	35%	65%	90%	100%
DRYINT	-0.857	0.735	60	20	0.006	40%	60%	100%	100%
Indicators of UB BS > 12%									
Species code	<i>r</i> Axis 1	<i>R</i> <sup>2</sup> Axis 1	IV > 12%	IV Difference	<i>p</i> - value	Rel. Abundance > 12%	Rel. Abundance < 12%	Rel. Frequency > 12%	Rel. Frequency < 12%
ARITRI	0.829	0.688	82	80	0.002	91%	9%	90%	20%
FRAAME	0.751	0.563	80	80	0.001	100%	0%	80%	0%
ACESAC	0.717	0.514	79	58	0.000	79%	21%	100%	100%
VIOROT	0.411	0.169	64	54	0.047	80%	20%	80%	50%
PRESP1	0.348	0.121	60	60	0.012	100%	0%	60%	0%
TIACOR	0.515	0.265	57	56	0.018	94%	6%	60%	10%
LONCAN	0.244	0.059	56	55	0.012	94%	6%	60%	10%
GALTRI	0.391	0.153	50	50	0.030	100%	0%	50%	0%
VIOREN	0.469	0.22	50	50	0.034	100%	0%	50%	0%

**Figure 25. Indicators of Upper B Horizon BS < 12%**

(a) *Acer pennsylvanicum*, (b) *Acer rubrum*, (c) *Dennstaedtia punctilobula*, and (d) *Dryopteris intermedia*

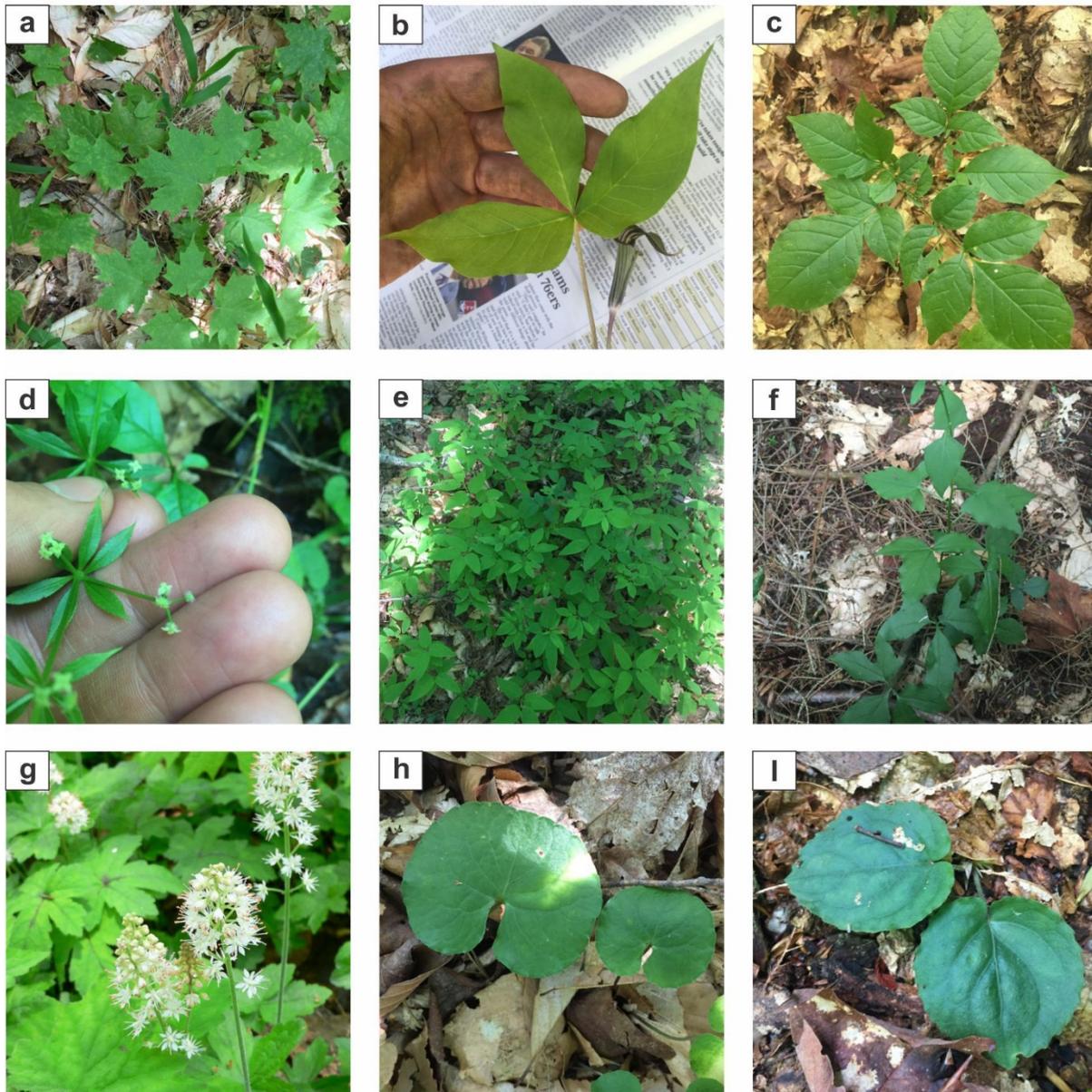
Indicators of Upper B Horizon Base Saturation < 12%



**Figure 26. Indicators of Upper B Horizon BS > 12%**

(a) *Acer saccharum*, (b) *Arisaema triphyllum*, (c) *Fraxinus americana*, (d) *Galium triflorum*, (e) *Lonicera canadensis*, (f) *Prenanthes* sp., (g) *Tiarella cordifolia*, (h) *Viola renifolia*, and (i) *Viola rotundifolia*.

Indicators of Upper B Horizon Base Saturation > 12%



Interpretation of a species' indicator value can be facilitated by consulting the differences in relative abundance and frequency of species in each group. *Acer saccharum* was present in 100% of plots in both groups. Thus, its indicator value is based solely on the differences in relative abundance of the species between those groups (79% for the group indicated and 21% for the group not). Conversely, *Prenanthes sp.* was completely absent in the upper B horizon BS < 12% group and had 100% relative abundance in the group it indicates. Differences between values for each group of those species indicating upper B horizon BS < 12% ranged from 20 to 71, while those for species indicating upper B horizon BS > 12% ranged from 50 to 80. Correlations between members of the former group and NMDS axis 1 ranged from -0.53 to -0.85, while those for the latter group ranged from 0.24 to 0.83 (Table 9).

The frequency of occurrence, by watershed, of plant species identified as indicators of either relatively high (> 12%) or relatively low (< 12%) upper B horizon BS varied spatially across the Adirondack region (Figures 27 and 28). Indicators of low BS were found in high frequency, mainly in the southwestern Adirondacks. In contrast, indicators of high BS were generally rare in the southwestern Adirondacks.

An indicator ratio was calculated by plot as the number of identified plant species that indicate relatively high BS (> 12%) divided by the number of identified indicator species of relatively low BS (< 12%). This ratio varied according to the measured soil BS in both the O<sub>a</sub> and upper B soil horizons (Figure 29) and according to estimated S and N deposition (Figure 30). The ratio generally increased with increasing soil BS in both the upper B and especially the O<sub>a</sub> horizon. Tipping points at which the ratio increased with lower deposition levels for both S and N deposition were near 10–12 kg for both S or N deposition/ha/yr. The ratio was uniformly low (less than about 1) on plots that received deposition more than 12 kg S or N/ha/yr.

**Figure 27. Species Frequency of Identified Indicators of Upper B Horizon BS > 12%**

Indicators of upper B Horizon BS > 12%

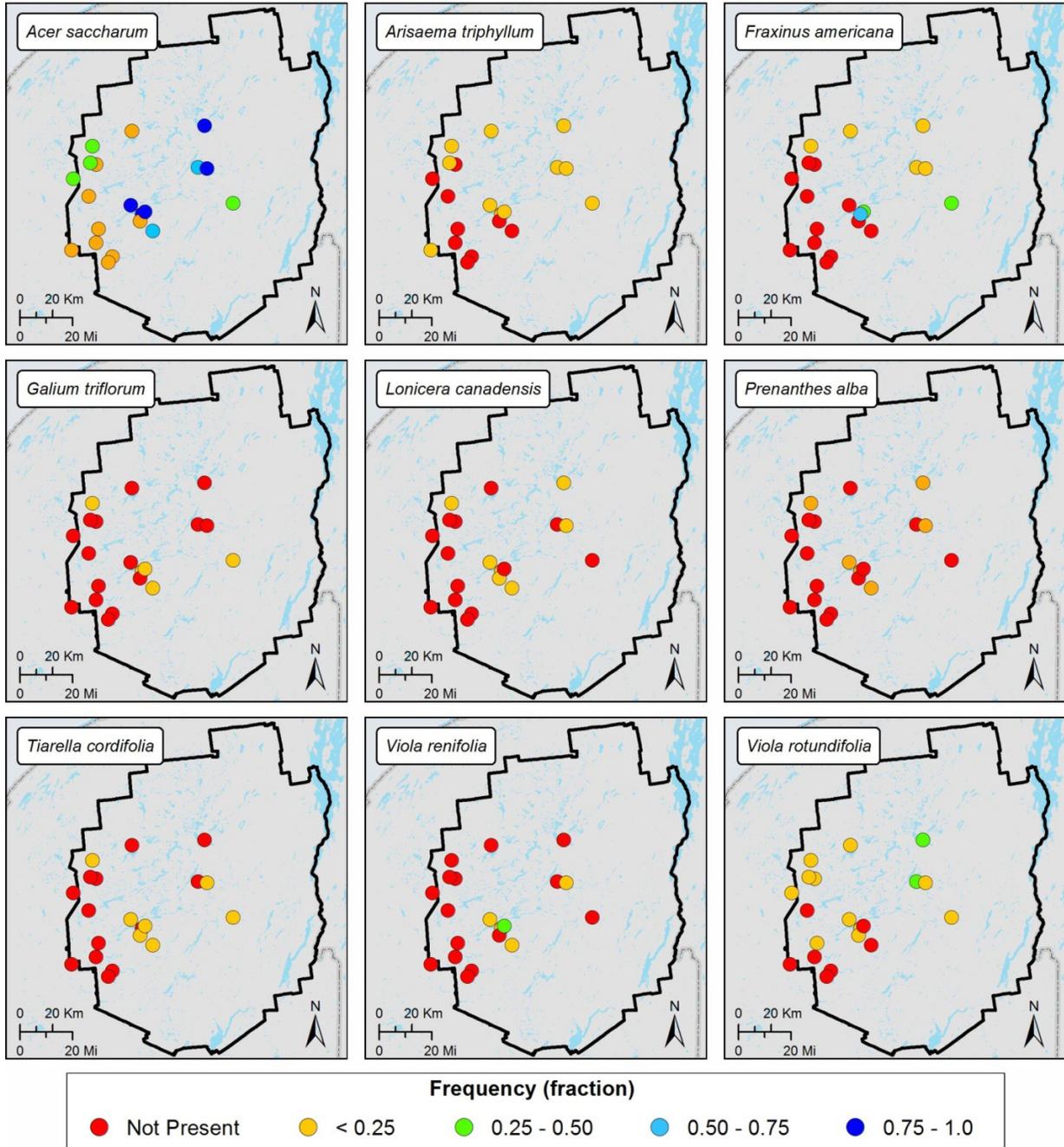
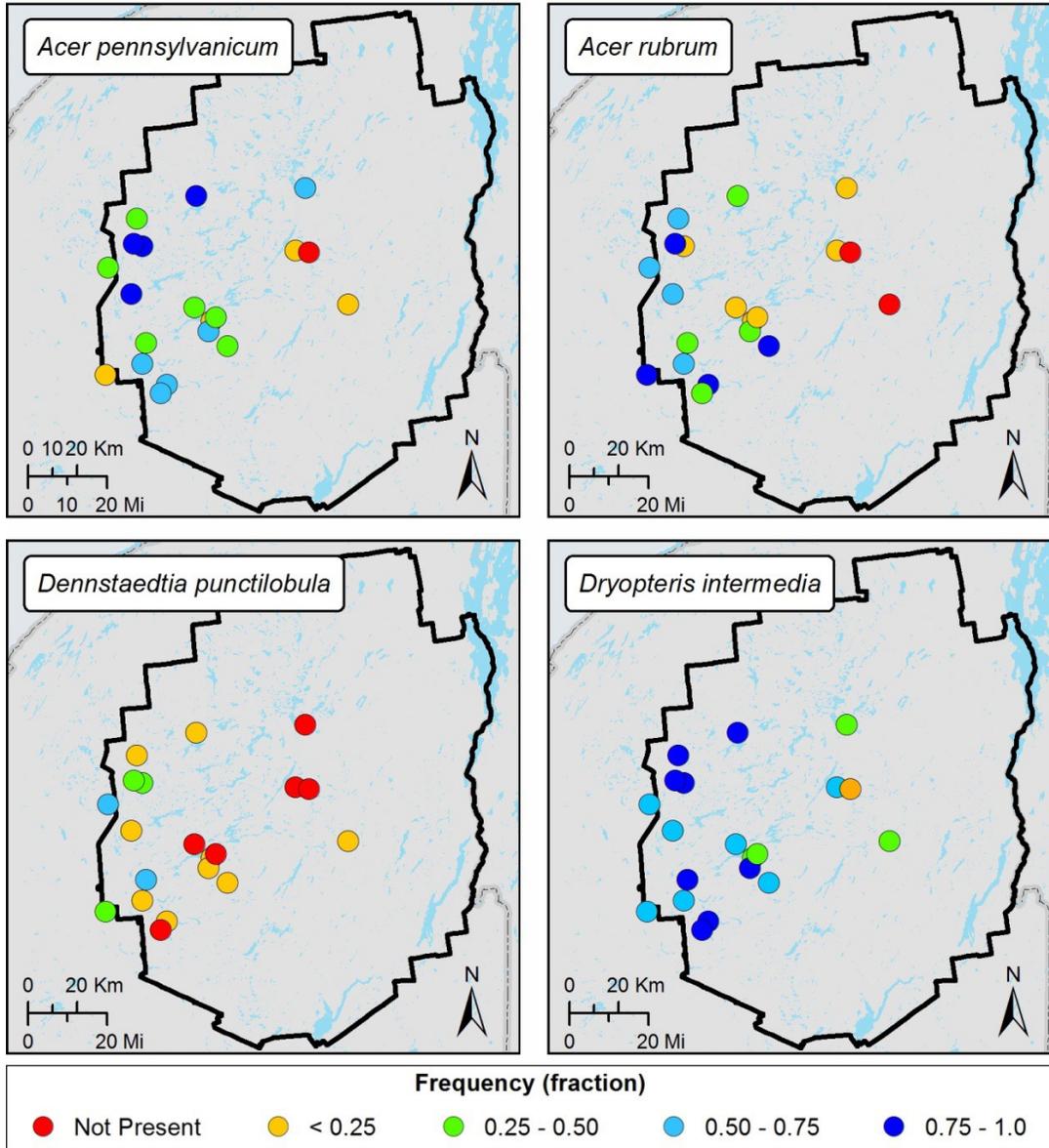


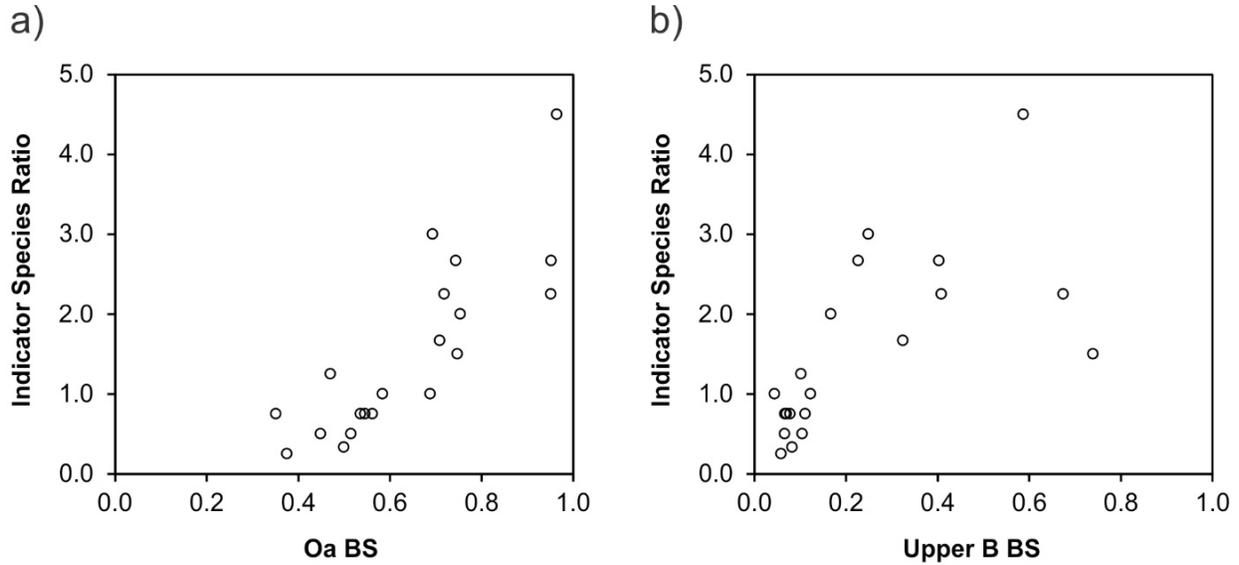
Figure 28. Species Frequency of Identified Indicators of Upper B Horizon BS < 12%

Indicators of upper B Horizon BS < 12%



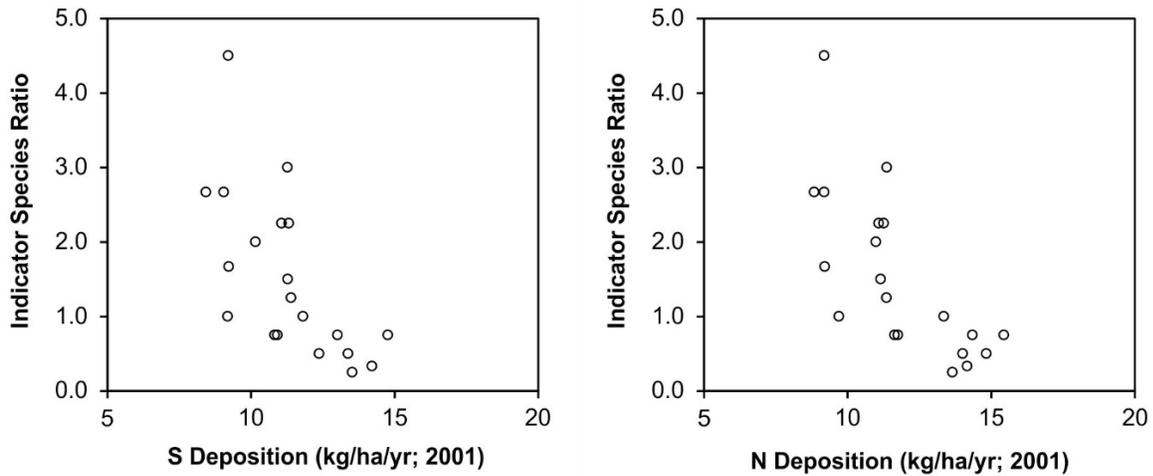
**Figure 29. Indicator Species Ratio Calculated by Plot (1)**

The number of plant species indicators of BS > 12% divided by the number of plant species indicators of BS < 12% versus (a) soil O<sub>a</sub> horizon BS and (b) soil upper B horizon BS.



**Figure 30. Indicator Species Ratio Calculated by Plot (2)**

The number of plant species indicators of BS > 12% divided by the number of plant species indicators of BS < 12% versus (a) S deposition and (b) N deposition during the period 2000–2002.



## 4 Discussion

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The herbaceous layer of the forest vegetation contributes to ecosystem structure and function disproportionate to its biomass. It commonly contains many more plant species than the overstory and contributes a litter of relatively high-nutrient content to the forest floor. It influences post-disturbance stand structure and reduces nutrient loss, especially early in the growing season (Gilliam 2007). In addition, the herb layer often responds to relatively low levels of disturbance (Gilliam 2006, Roberts and Gilliam 2003). Competition among tree seedling species that partly make up the herb layer can affect the regeneration of overstory tree species after natural or human disturbances (e.g., windthrow or logging) and it can also affect tree species recruitment into forest canopy during long-term successional responses of forest ecosystems to slower environmental changes such as changing deposition levels or climate warming.

Species richness in the herbaceous vegetation layer showed significant positive spatial autocorrelation at both the plot and watershed level (Table 2). This indicates spatial clustering in the extent to which the plots/watersheds expressed richness. Thus, plots/watersheds with low richness tended to be near to each other and plots/watersheds with high richness tended to be near to each other. These results should be considered in interpreting results of spatial patterns in soil chemistry and plant occurrences and richness.

### 4.1 Effects of Acidic Deposition on Soil Chemistry

Our results support the hypothesis that strong soil chemical-gradients in pH and cation availability exist across the Adirondack ecoregion and are related to variations in acidic deposition. Results corroborate previous work in the Adirondacks that found soil variables to be correlated with S and N deposition levels; these correlations were negative for soil exchangeable base cations and pH and positive for exchangeable Al (Sullivan et al., 2013b). Our analyses further suggested that the linkage between soil data and more recent decreased and more spatially homogenous deposition levels was weaker. Soil acidification in the northeastern U.S. contributed to decreased pH, loss of base cations through leaching (Ca, Mg), and mobilization of Al, potentially toxic to plants (Driscoll et al. 2001).

A study of acidic deposition in the Adirondack region estimated that up to 30% of Ca loss from the forest floor between 1984 and 2004 could be attributed to leaching caused by  $\text{SO}_4^{2-}$  deposition (Johnson et al. 2008). The deposition of  $\text{NO}^-$  and  $\text{NH}^+$  can potentially lead to accumulation of N in the O soil horizon (Driscoll et al. 2001), but a negative correlation between soil N and N deposition was observed in this study, perhaps due to the negative effects of acid deposition on vegetation and biological N uptake that could potentially lead to the subsequent N loss from the system by leaching.

Soil and surface water acidification are of concern to natural resource managers in the Adirondack region because of the potential for damage to sensitive terrestrial and aquatic resource receptors. These include soils, vegetation, and aquatic life. This analysis addresses soil and vegetation. As the chemistry of impacted soils changes in response to acidic deposition, several effects are of direct relevance to native plant communities. First, the supply of nutrient-base cations in the soil, including in particular Ca and Mg, can become depleted by soil acidification. This can cause increased stress for species that require considerable available base cations on the soil to support plant nutrition. This effect is reflected in the soil-base saturation measurements and calculations. Second, Al can be mobilized by acidic atmospheric deposition from soil to soil water where it can adversely affect the roots and nutrient uptake of sensitive plant species. Third, the supply of N can increase, causing some species to grow more vigorously and out-compete other species that are less able to take advantage of the added N.

## **4.2 Changes in Plant Community Composition Along the Soil-Acidity Gradient**

As soil chemistry changes in response to decades of acidic deposition, species that are unable to tolerate high acidity, high Al, and/or low-base cation supply may be stressed, show increased susceptibility to insect infestation, disease, or other stressor(s), and may show decreases in health, regeneration, and/or growth and gradually be eliminated from the ecosystem. Other species may gain competitive advantage. These environmental impacts are more thoroughly described, together with key scientific principles, by Gilliam (2006), Sullivan et al. (2011), Sullivan et al. (2012), Sullivan and Jenkins (2014), Driscoll et al. (2001), Burns et al. (2011), and Sullivan (2015).

Plant understory species composition varied considerably in relation to the gradients of base-cation availability and soil pH in our study, corroborating results of previous studies that suggested the importance of base-cation availability and soil pH in controlling the composition of herbaceous communities in northern hardwood forests of the northeastern United States (Horsley et al. 2008). While reduced base saturation across our watersheds was shown to negatively affect seedling

recruitment of *Acer saccharum* in the forest understory (Sullivan et al. 2013b), our analysis not only confirmed this trend, but identified additional forest understory species (both woody and herbaceous) that appear to respond negatively or positively to soil acidification.

### 4.3 Changes in Understory Species Richness Along the Soil-Acidity Gradient

Our analyses suggest a previously undocumented trend in the Adirondacks and a trend that has rarely been documented in forests of the northeastern United States: decreased species richness in the understory plant layer that may have occurred as a consequence of changes in base-cation availability (Mg, Ca) and pH, caused by acidic deposition. Few researchers have considered the effects of cation depletion in the Northeast on understory species richness. Beier et al. (2012) showed that both wet deposition of SO<sub>4</sub> and NO<sub>3</sub> had significant and strong negative correlations with Ca in the O<sub>a</sub> horizon in the Adirondacks, yet they found no relationship between understory species richness and Ca, potentially due to their lower sampling size (n=12 plots) versus n=20 watersheds and n = 50 plots in our study. In the Long Island resurvey by Greller et al. (1990), understory species richness of forest plant species identified as “dominant” decreased from 1922 to 1985, perhaps in response to declining pH, although other potentially limiting factors (e.g., light) were not evaluated.

Although soil pH predicted species richness, it was not as strong a predictor as base availability (Ca, Mg) in our study. This is not surprising since the mechanism for pH decrease, addition of H into the soil solution, is a precursor for Ca and Mg leaching, which has more direct impact on plants (Weil and Brady 2017). While minimal research has been conducted in the Northeast on the impacts of Mg or Ca depletion on understory forest plants, studies have suggested that decline in exchangeable Ca is detrimental to dominant canopy tree species such as *Acer saccharum* and *Picea rubens*. Calcium depletion leads to reduced vigor and growth of *Acer saccharum* (Sullivan et al. 2013b). Soil Ca is needed by plants for a range of structural and physiological roles, so changes in its availability can have important effects on forest ecosystems (McLaughlin and Wimmer 1999). For example, extracellular Ca in *Picea rubens* needles increases cold tolerance and low Ca concentrations can contribute to winter injury (DeHayes et al. 1999). Similar mechanisms may be at play for other woody understory species on our study sites.

Magnesium has been found to reduce Al toxicity in agricultural plants growing on acidified soils (Chen and Ma 2013), and Mg deficiency was implicated in the decline in *Acer saccharum* in Pennsylvania, perhaps due to the importance of Mg to chlorophyll and photosynthesis (Horsley et al. 2000).

## 4.4 Impact of Nitrogen on Species Richness and Community Composition

The effects of N on plant species composition and richness are difficult to discern given dual roles of N: a negative role in soil acidification and (up to a point) a positive role in plant nutrition (Bobbink et al. 2010). Our finding that N was negatively associated with species richness in multivariate analyses corroborates results of studies reviewed in Bobbink et al. (2010). Investigations of N deposition impacts on understory plant richness in temperate forests of the eastern United States have been limited. Experimental N additions in this region can increase plant N uptake, decrease base-cation concentrations in plant tissues, and decrease stem density of some common understory herbs (Rainey et al. 1999). Experiments in annual herbaceous communities suggested that plant diversity decreased in response to enhanced plant competition due to earlier canopy closure in plots with added N (Goldberg and Miller 1990). However, it is not clear if a similar response occurs in forest understories where light is inherently limited by the forest canopy or where background N deposition is high. Gilliam (2006) found no significant difference in understory herb richness or cover between watersheds that dramatically differed in N additions over five years (210 kg/ha added versus reference). They concluded that high-ambient N deposition caused plant responses even in the treatment without experimentally added N (Gilliam 2006). This result was corroborated by a study that found maximum changes in understory herb and tree seedling cover on sites with the lowest ambient N inputs as plant foliar N clearly responded to N additions (Hurd et al. 1998).

The literature suggests that the threshold at which N deposition begins to affect plant communities in temperate forests is between 10 and 20 kg/ha/yr (Bobbink et al. 2010). On the study watersheds here, N-DEP07 ranged from 6.27 to 9.50 kg/ha/yr and averaged 7.50 kg/ha/yr. The decline in species richness in the herbaceous layer of temperate forests in response to N addition or deposition has often been attributed to high N availability favoring a few species that can take greater advantage of high N availability at the expense of species better adapted to N utilization at low levels of availability (Gilliam 2006). On the other hand, increased N supply can contribute to other mechanisms that cause declining species richness. For example, increased foliar N can make plants more susceptible to herbivory, and greater N availability in soil can decrease mycorrhizal associations and make plants more vulnerable to pathogens or moisture and phosphorus limitation (Gilliam 2006).

This study has shown that past acidic deposition (N, S) is linked to distinct regional gradients in soil acidification (declining pH) and base-cation availability in the Adirondack Mountain region. These gradients had detrimental effects on understory plant community composition and species richness. Nitrogen was also associated with species richness, although its linkage to deposition was less clear. Soil measurements reflecting acidic deposition and soil acidification were found to exert stronger controls than other environmental variables in our analysis. Results suggest that the legacy of acidic deposition, which has likely decreased the range in Ca availability across the study region, continues to alter species composition and reduce richness of forest understory plant communities. Despite the ongoing decreases in acidic deposition levels, the start of soil recovery has only recently been observed (Lawrence et al. 2015a). These results showed that Ca availability is no longer decreasing, but increases in Ca availability were rare.

Watersheds were grouped for summary into three classes of richness (1 = low, 2 = moderate, 3 = high; Table 10). The distribution of Total N, Total C, and the C:N ratio within these richness classes are shown Figure 31. There was some evidence that total C decreased with increasing richness, but there was little change in total N with richness. Some of the watersheds with the highest richness had the lowest C:N ratios (Figure 31), indicating higher richness with increased N availability. Total N was generally higher on these low C:N ratio watersheds (i.e., those in richness class three). However, total C is also relatively low for these watersheds, so the lower C:N cannot be fully explained by higher total N. Overall, the C:N results of this study are not conclusive.

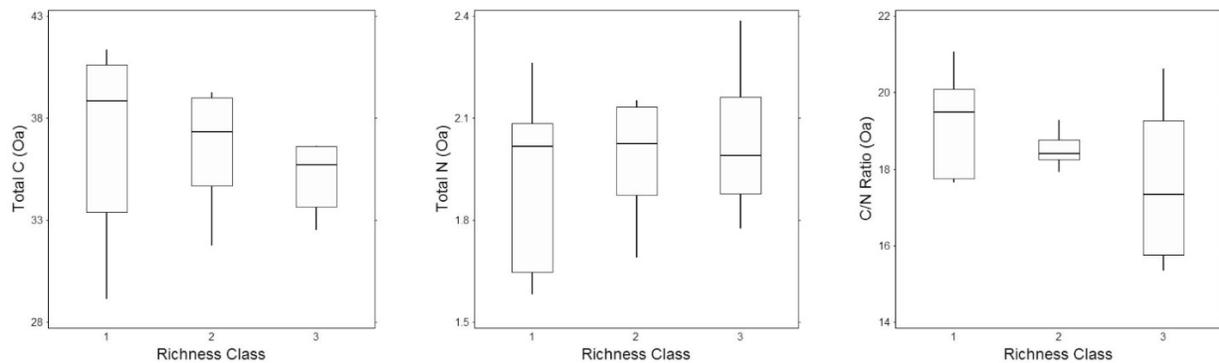
**Table 10. Watershed-level Herbaceous Layer Richness and Assigned Richness Class**

Class 1 = low, Class 2 = moderate, Class 3 = high)

Watershed	Richness	Richness Class
35014	21	1
13008	25	1
26008	30	1
22019	30	1
31009	30	1
29012	32	1
30009	32	1
AMP	33	2
12003	33	2
27019	36	2
9006	37	2
17002	38	2
N1	39	2
WF	43	2
NW	45	3
S14	46	3
24001	48	3
28030	52	3
28037	52	3
7001	59	3

**Figure 31. Total C, Total N, and C:N Ratio in the O<sub>a</sub> Soil Horizon in Species Richness Classes**

Class 1: 21-32 species, Class 2: 33-43 species, and Class 3: 45-59 species



The leaching of  $\text{SO}_4^{2-}$  remains the primary determinant of soil acidification and Al mobilization caused by air pollutant deposition in the Adirondack Mountains, but leaching of  $\text{NO}_3^-$  also continues to play an important role (Sullivan 2015, Sullivan et al. 2006b). Some of the N deposited with atmospheric deposition is taken up by vegetation and microbes and therefore does not contribute directly to  $\text{NO}_3^-$  leaching. In some Adirondack watersheds, N is more mobile (Sullivan 2015). However, atmospheric N inputs may also enhance plant nutrition in some parts of the Adirondack region.

Nutrient enrichment can occur via atmospheric N deposition where and when a key growth-limiting nutrient (in this case N) is contributed from the atmosphere to the plant rooting zone. Increased N availability from atmospheric deposition may provide a competitive advantage for species requiring or associated with higher nitrogen levels (for example, some graminoids), which could lead to shifts in community composition and a decrease in richness. This, in turn, could affect overall ecosystem resilience in the face of other environmental stressors.

Minimal information is available regarding the effects of N deposition on herbaceous plants within northern hardwood forests in the Northeast. However, Hurd et al. (1998) reported the results of experimental studies that added N at two- and four-times the ambient N deposition level at several sites in the Adirondack Mountains. Overall, herbaceous plant coverage decreased after three years of fertilization, largely in response to shading caused by enhanced cover of ferns. We found that two fern species, *Dryopteris intermedia* and *Dennstaedtia punctilobula*, were more frequent per  $\text{m}^2$  on watersheds in the southwestern portion of the sampling region (Figure 28) where N deposition has been historically greatest (Figure 3). These two species were highly correlated (Table 6) with the more acidic end of the soil gradient described by axis 1 of Figure 16.

Experimental N addition to watershed WS3 at Fernow Experimental Forest, West Virginia by Gilliam et al. (2016a) created a competitive advantage for the nitrophilic *Rubus allegheniensis*, which largely replaced the more N-efficient species *Viola rotundifolia*, a species identified here as an indicator of B horizon BS > 12%. Soil acidification and base-cation deficiency can interact with other plant stressors, including nutrient enrichment, drought, insect defoliation, and low temperatures (cf., Horsley et al. 1999). In northern temperate forest ecosystems, including northern hardwood forests in the Adirondacks, the most important nutrient that limits plant growth is often N. Bowman et al. (2006) found species

composition to be a more reliable and possibly more sensitive indicator of ecological effects of N deposition on alpine herbaceous vegetation than changes in N cycling. The use of herbaceous vegetation as an indicator of critical N deposition loads may be preferred to the use of tree response in sensitive forested settings (Burns 2003).

Recent studies by Simkin et al. (2016) and Fenn et al. (2015) have highlighted the influence of N supply on the species composition and presence of plant species at many study locations in the United States. Characteristics of the herbaceous layer and its response to N addition typically reflect legacy responses to land use history, including logging (Foster et al. 2003, Gilliam 2007). These legacy effects have altered biodiversity through the local extirpation of herbaceous species that are sensitive to the local disturbance history. Gilliam (2007) highlighted the importance of several chronic disturbances that affect the herbaceous vegetation layer: increased atmospheric carbon dioxide, increased incidence of ultraviolet radiation of wavelengths 280 to 320 nm, introduction of exotic species, and atmospheric deposition of anthropogenic N. To this list, based on the results of this study, soil acidification caused by atmospheric deposition of S and N was added.

Simkin et al. (2016) reported spatial distributions of herbaceous plants across community-scale gradients in the United States that indicated decreases in species richness as N deposition increased in 16 of 44 (36%) studied gradients. These responses were mostly along gradients having acidic soil conditions and where N deposition was higher than or equal to 7.5–9.5 kg/ha/yr. In contrast, most of the gradients in this study for which richness increased with increased N deposition received N deposition rates that averaged 3 kg N/ha/yr or less.

Gilliam et al. (2016b) reported results of a 25-year experimental N addition to a central Appalachian hardwood forest at Fernow Experimental Forest. Nitrogen was applied aerially at a high rate of 35 kg N/ha/yr to watershed WS3; WS4 served as an untreated reference. Cover of the herbaceous layer increased substantially over several years in WS3 and subsequently remained high. Herbaceous layer diversity decreased and community composition changed dramatically. In particular, there was a large increase in the cover of *Rubus* spp., normally associated with disturbance-mediated openings in the forest overstory (Gilliam et al. 2016b). These results supported the expectation that changes in N supply affect the herbaceous layer of the forest largely via increases in nitrophilic species.

## 4.5 Linkages with Atmospheric Deposition

Increased atmospheric deposition of S and/or N, caused by anthropogenic emissions sources, has contributed to ecological effects on forest plants that are reflected in soil chemistry, response to stress factors, and biodiversity. There is a need to identify plant species that serve as indicators of ecological response to ecosystem acidification and nutrient enrichment (Bowman et al. 2006). Individual indicator species can be used as the basis of calculating CLs and TLs (Belyazid et al. 2011b). Alternatively, species richness can be used as a reflection of plant diversity to specify the level of ecosystem protection achieved at a particular level of atmospheric loading of acidity or nutrients. There is some experimental evidence that changes in herbaceous vegetation composition may precede detectable changes in soil chemistry (Bowman et al. 2006).

The legacy of historical acid and nutrient deposition now gains new significance as it increasingly interacts with confounding effects of climate change which can impose additional temperature, moisture, and snowpack-related stresses on plant communities. These potential stresses add complicating interactions with the effects related to the acid and nutrient status of the soil.

The herbaceous layer is known to respond to N supply by changing aspects of biomass and species composition and richness (Small and McCarthy 2005, Strengbom et al. 2001). For example, Hurd et al. (1998) demonstrated decreased percent cover of *Oxalis acetosella*, *Maianthemum canadense*, and *Huperzia lucidula* in Adirondack hardwood forests in response to three years of experimental  $(\text{NH}_4)_2\text{SO}_4$  addition. Gilliam et al. (2006, 2007) identified the following stages of herbaceous layer response to de-acidification treatment: increase in herb layer cover, followed by decreased richness, decreased evenness, and loss of biodiversity. In this study, *Oxalis montana* showed no monotonic relationship with C:N, N, or N-DEP07. However, *Huperzia ludicula* showed a positive ( $r = 0.49$ ,  $p = 0.02$ ) and *Maianthemum canadense* showed a negative ( $r = -0.60$   $p < 0.01$ ) Spearman correlation with C:N and N respectively. Neither species showed a clear relationship with N-DEP07.

Horsley et al. (2008) identified 50 plant species in 86 northern hardwood forest stands located in northern Pennsylvania, western New York, New Hampshire, and Vermont that were indicators of sites that met the nutritional thresholds for Ca, Mg, and Mn *Acer saccharum* foliar chemistry. The purpose was to provide land managers with a diagnostic tool to determine locations where *Acer saccharum* trees were at risk or were likely to remain healthy under stressful conditions such as would be caused by drought, winter freezing, or defoliation. The goal was to determine which understory plant species responded to environmental gradients, especially those reflective of acid-base and nutritional chemistry, in a way

similar to *Acer saccharum*. The selected species were among those that typically had wide range of occurrence in mesic northern hardwood forests. Although several of those species were detected on the plots, no indicator of the nutritional thresholds found to benefit *Acer saccharum* in NY, NH, PA, or VT was found to be indicative of the threshold of 12% BS in the upper B horizon on our plots. This is likely due in part to regional differences in species composition that exist between hardwood forests in these states. Indeed, only 16 of 50 indicator species identified by Horsley were present in both regions (PA + NY and NH + VT). The northern hardwood forests in the Adirondacks may represent a relatively species-poor subset of the hardwood forests arrayed between PA and NH. While Horsley identified 234 species in the understory of 86 plots, this study identified only 116 species on 50 plots.

## 4.6 Management and Policy Implications

This research provides information on how Adirondack forests impacted by Ca depletion might recover, both chemically (soils) and biologically (vegetation), following reductions in acidic deposition. This information will help policymakers better understand and evaluate the potential benefits of current and future efforts to reduce acidic deposition in New York State and to determine locations where forest recovery is not likely to occur in the absence of restoration or other management activities.

Watersheds differ in the extent to which they respond to excess acidity or nutrient N addition. Such differences are reflected in the CLs and TLs, which reflect the thresholds of atmospheric S and/or N deposition above or below which harmful ecological effects are/are not expected. The CL is usually calculated to reflect a long-term, steady-state condition far into the future. The TL is usually specific to a particular management time frame. The data collected in this project provide part of the foundation that will allow calculation of the CLs and TLs of acidic deposition that could (1) protect sensitive Adirondack terrestrial resources from adverse impacts caused by acidic deposition, and (2) allow previously damaged resources to recover from acidification impacts. Details of CL and TL calculations can be complex and confusing, and were recently summarized by Sullivan and Jenkins (2014) and Burns and Sullivan (2015). Calculation of either requires specification of what will be protected (e.g., *Acer saccharum* regeneration or herbaceous plant species composition or richness), the critical indicator of protection (e.g., base saturation in the upper soil B horizon), the level to which the indicator will be protected (e.g., BS more than 12%), where the protection will occur (e.g., northern hardwood forests in the Adirondack Park), and the time frame of protection (e.g., year 2050). Each ecosystem will have many CLs and TLs.

Indicators of soil acid-base and/or nutrient status can provide diagnostic tools for land managers to ascertain where *Acer saccharum*, for example, are likely to be at risk to stressful conditions. Such information can inform decisions about the likelihood of success of an insect control program or other management action. Indicator species information might for example be used to prioritize pest suppression activities (Horsley et al. 2008).

Development of empirical response functions tied to S and/or N deposition for supporting CL and TL calculations in the Adirondack region is to some extent problematic because deposition levels have changed so much over the last several decades. This can be seen in the maps depicted in Figures 2 and 3 for total S and N deposition, respectively. These maps compare TDEP estimates for an early three-year average period of high deposition (2000–2002, earliest available TDEP estimates) with a more recent period of comparatively low deposition (2011–2013, TDEP estimates used here in NMDS analyses). During the earlier period, all of the study watersheds for this project exhibited N deposition higher than 8 kg N/ha/yr, and seven watersheds received more than 12 kg N/ha/yr; during the latter period, most exhibited N deposition lower than 8 kg N/ha/yr. It is likely that understory plants are in fact responding to the cumulative input of N over a sustained period of time. However, that period of time is unknown and is variable across species. Thus, N deposition as it affects plants is a moving target. This same limitation applies to calculation of CL and TL exceedances. Results of this study may be helpful to inform calculation of CLs and TLs for protecting Adirondack forest understory biodiversity against soil acidification and nutrient N enrichment, but one must be explicit about what is being protected.

## 5 Conclusions

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Results of this research suggested that plant understory richness in Adirondack hardwood forests was controlled significantly by acidic deposition and soil acid-base chemistry. Both bivariate and multivariate analyses clearly illustrated an association between the base status of the O<sub>a</sub> and upper B soil horizons and plant understory richness, cover, and species composition. In particular, richness is lower where soil-base saturation is relatively low and both sulfur and nitrogen deposition are/were relatively high. Species that indicate either relatively low- (< 12%) or high- (> 12%) base saturation were identified. These findings will assist in the development of CLs and TLs of acidic deposition for protecting plant biodiversity in the highly sensitive and impacted region. Models with which to accomplish this are under development (2011a, Belyazid et al. 2011b, Bonten et al. 2016, Reinds et al. 2014).

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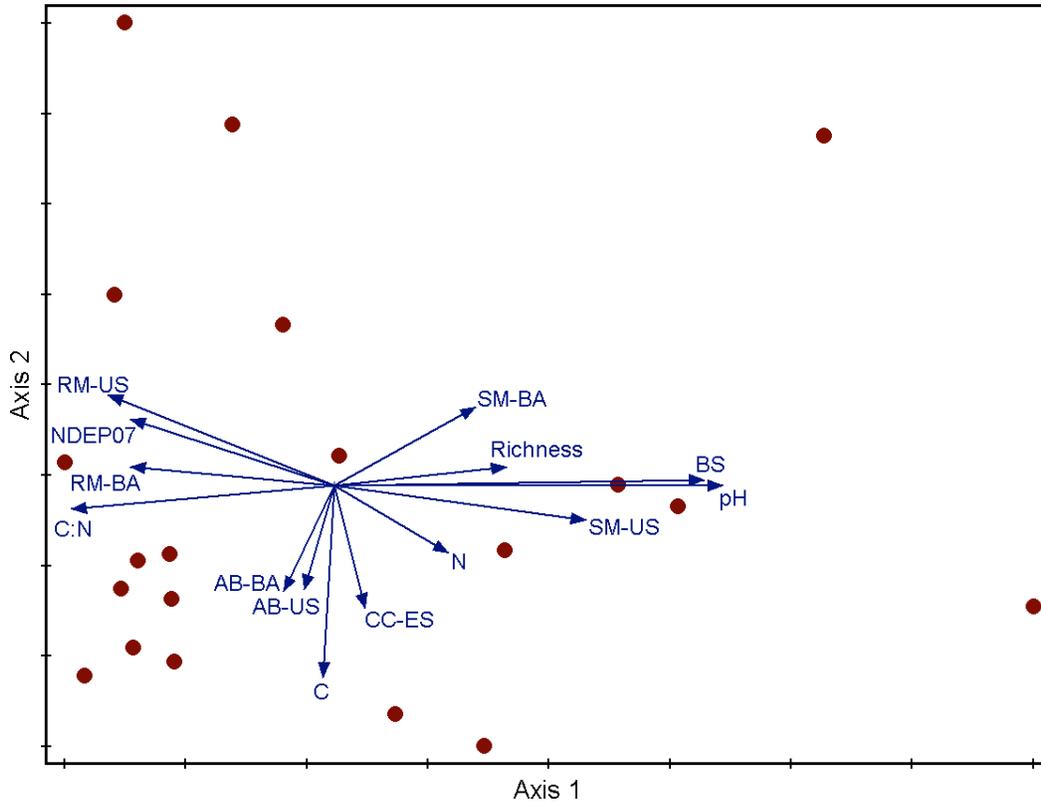
## Appendix A

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The location in ordination space of *Fagus grandifolia* (AB) is relatively opposed to that of *Acer saccharum* (SM) in the overstory (Figure A-1), a relationship that belies the soil acidity gradient. *Fagus grandifolia* is positively associated with the C and C:N vectors while pH is directly opposed to the C:N vector, supporting regression results showing that these two strongly predict C:N across the sampling area. Other correlations are given in Table A-1. *Fagus grandifolia* is experiencing a near perfect “spatial” match in recruitment between overstory and understory, while both *Acer saccharum* and *rubrum* (RM) are experiencing mismatches between overstory progenitors and understory recruits. This suggests that distributions of these species may be shifting, though a more explicitly spatial analysis will be needed to confirm the hypothesis. If a shift is occurring, the ordination would suggest it is being driven by a combination of deposition (historic and contemporary) and base-cation availability. The C:N ratio is correlated with pH (negative correlation) and the BA of both *Acer saccharum* (negative correlation) and *Fagus grandifolia* (positive correlation). The pH, in turn, is negatively correlated with N deposition (Figure A-2).

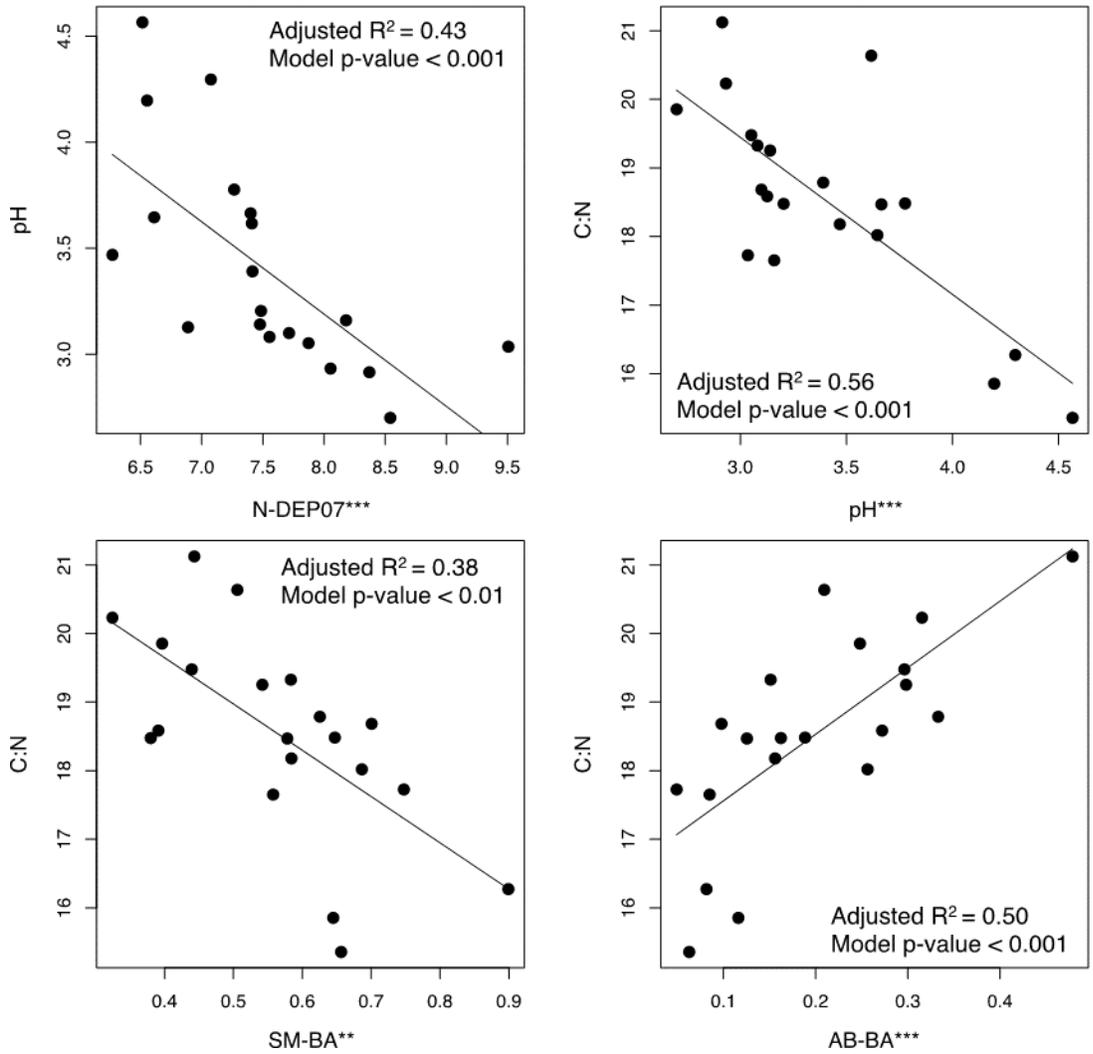
**Figure A-1. Vectors Showing Correlations of Abiotic Variables and Biotic Variables Representing the Overstory Community (-BA) and Their Understory Offspring (-US) with NMDS Ordination of Species Composition Across Watersheds**

Only correlations having  $p \geq 0.4$  are shown. The length of each vector is drawn proportional to the strength of the respective correlation. Table 1 contains variable definitions. This chart suggests that overstory species are associated with different environmental gradients. For sugar maple (SM), understory composition does not associate strongly with overstory composition.



**Figure A-2. Simple OLS Regressions Demonstrating Relationships among the C:N Ratio, Basal Area of Sugar Maple (SM) and American Beech (AB), pH, and N Deposition**

Table 1 contains variable definitions.



**Table A-1. Spearman Correlations between Variables Featured in Figure 16**

Variable	Richness	pH	BS	Ca	Mg	K	Al	C	C:N	N	NDEP-07	SDEP-07	Elevation
Richness	--												
pH	0.777***	--											
BS	0.830***	0.818***	--										
Ca	0.774***	0.839***	0.932***	--									
Mg	0.827***	0.875***	0.904***	0.907***	--								
K	0.446*	0.693***	0.556*	0.555*	0.594**	--							
Al	-0.489*	-0.409*	-0.708***	-0.614**	-0.600**	-0.399	--						
C	-0.418	-0.105	-0.226	-0.119	-0.268	-0.015	0.442	--					
C:N	-0.357	-0.681***	-0.505*	-0.621**	-0.704***	-0.642**	0.332	0.206	--				
N	0.002	0.493*	0.289	0.460*	0.352	0.453*	0.029	0.633**	-0.552*	--			
NDEP-07	-0.637**	-0.836***	-0.805***	-0.786***	-0.750***	-0.559*	0.337	0.009	0.520*	-0.468*	--		
SDEP-07	-0.509*	-0.680**	-0.731***	-0.708***	-0.600**	-0.517*	0.365	0.066	0.516*	-0.403	0.899***	--	
Elevation	0.175	0.329	0.044	0.065	0.125	0.054	0.262	0.227	0.080	0.192	-0.310	0.039	--
CC-ES	0.042	0.295	-0.035	-0.019	0.087	0.148	0.179	0.301	0.043	0.255	-0.138	0.189	0.832***
Correlation coefficient p-values are represented as *** for $p \leq 0.001$ , ** for $p \leq 0.01$ , and * for $p < 0.05$													

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