Effects of Atmospheric Deposition on Biological Diversity in the Eastern United States

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February 2007





Executive Summary

Conservation organizations have most often focused on land-use change, climate change, and invasive species as prime threats to biodiversity conservation. Though air pollution is an acknowledged widespread problem, is it rarely considered in conservation planning. This report summarizes the state of scientific knowledge on the effects of air pollution on plants and animals in the Northeastern and Mid-Atlantic regions of the U.S. Most of the information in the report is derived from a workshop that was organized by the Nature Conservancy and the Institute of Ecosystem Studies and was attended by 32 experts in air pollution science and conservation. The information from the workshop was supplemented with literature review for this report. The report considers four air pollutants (sulfur, nitrogen, ozone and mercury) and eight ecosystem types.

Effects of air pollution were identified, with varying levels of certainty, in all the ecosystems examined. The scope of the problem is illustrated in the accompanying table, which documents the level of knowledge of these impacts in the ecosystem types considered in this report. **None of these ecosystems is free of the impacts of air pollution, and most are affected by more than one pollutant**. In aquatic ecosystems, effects of acidity, nitrogen and mercury on organisms and biogeochemical processes are well documented. Air pollution causes or contributes to acidification of lakes, eutrophication of estuaries and coastal waters, and mercury bioaccumulation in aquatic food webs. In terrestrial ecosystems, the effects of air pollution on biogeochemical cycling are very well documented, but the effects on organisms are less well understood. Nevertheless, there is strong evidence for effects of nitrogen deposition on plants in grasslands, alpine areas, and bogs, and for nitrogen effects on forest mycorrhizae. Soil acidification is known to be occurring in some northeastern ecosystems and is likely to affect the composition and function of forests in acid-sensitive areas over the long term. Ozone is known to cause reductions in photosynthesis in many terrestrial plant species.

For the most part, the effects of these pollutants are chronic, not acute, at the exposure levels common in the eastern U.S. Mortality is often observed only at experimentally elevated exposure levels or in combination with other stresses such as drought, freezing or pathogens. The notable exception is the acid/aluminum effects on aquatic organisms, which can be lethal at levels of acidity observed in many surface waters in the region. Although the effects are often subtle, they are important. Changes in species composition caused by terrestrial or aquatic acidification or eutrophication can propagate throughout the food webs to affect many organisms beyond those that are directly sensitive to the pollution. Likewise, sublethal doses of toxic pollutants may reduce the reproductive ability of the affected organism or make it more susceptible to pathogens that can kill it.

We identified many serious gaps in knowledge that warrant further research. Among those gaps are the effects of acidification, ozone and mercury on alpine systems, effects of nitrogen on species composition of forests, effects of mercury in terrestrial food webs, interactive effects of multiple pollutants, and interactions among air pollution and other environmental changes such as climate change and invasive species. Unfortunately,

research funds for air pollution (other than greenhouse gases) have dwindled considerably in the last several decades, so progress on these issues will come slowly if at all.

These gaps in knowledge, coupled with the strong likelihood of impacts on systems that have not been studied in the Northeast, lead us to believe that this summary of current knowledge underestimates the true impact of air pollutants on biodiversity. It is likely that new and significant impacts will be discovered upon further research, and that known effects will turn out to be more widespread than is currently appreciated. Good examples are the recent discoveries of elevated levels of mercury in mountain-dwelling bird species and the shifts in grassland plant species composition associated with excess nitrogen deposition.

Overall, this synthesis reveals that known or likely impacts of air pollution on the biodiversity and function of natural ecosystems are widespread in the Northeast and Mid-Atlantic regions. We believe it is time for the conservation community to consider air pollution as a serious threat to conservation of biodiversity in this region. It is clear that the species, communities and ecosystems of concern to conservations cannot be protected by land preservation alone, and that action to reduce air pollution should be part of any long-term conservation strategy.

***Table 1**. Level of certainty that air pollutants result in significant negative impacts on a selected biodiversity conservation target groups based on expert review. Level of certainty was divided into four categories for ease of comparison across target and pollutant groups: known, likely, unlikely and unknown. Known = Studies documenting impacts in the region are known. Likely = Studies documenting impacts are known - but none documented for this region; and/or plausible mechanism for impacts identified, but no specific studies to confirm the plausible link were identified.*
Unlikely = Plausible links resulting in negative impacts are not supported at this time within or outside this region. Unknown = No applicable studies documenting impacts or lack of impacts were identified within or outside this region.

	Air pollutants and their products				
Conservation Target Groups	**Nitrogen**	**Sulfur**	**Ozone**	**Mercury**	**Percent (number) of air pollutants with known or likely impacts**
Alpine and subalpine ecosystems	Likely	Likely	Unknown	Unknown	50% (2)
Forests (both upland and wetland types)	Likely	Known	Known	Likely	100% (4)
Bogs and fens	Likely	Known	Likely	Likely	100% (4)
Grasslands	Likely	Unknown	Unknown	Unknown	25% (1)
High gradient headwater streams	Known	Known	Unlikely	Likely	75% (3)
Lakes and ponds	Known	Known	Unlikely	Known	75% (3)
Low gradient rivers	Likely*	Unlikely	Unlikely	Likely	50% (2)
Estuaries, bays, and saltmarshes	Likely*	Unlikely	Unlikely	Likely	50% (2)
Percent (number) of target groups with known or likely impacts	100% (8)	63% (5)	25% (2)	75% (6)	

**Nitrogen eutrophication effects are known for these systems. Although atmospheric nitrogen deposition is often a significant contributor to the total nitrogen loading in these systems, it is usually not the major source of nitrogen.*

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Acknowledgements

We would like to acknowledge all of the individuals that attended and contributed to the Nature Conservancy/Institute of Ecosystem Studies "Workshop to Evaluate the Impacts of Atmospheric Deposition on Biodiversity" held May 10 – 12, 2004 in Millbrook, NY. These individuals are listed in Appendix 1; their knowledge and ideas contributed greatly to this report. We would like especially to thank the "Contributors" listed on the cover of this report who helped considerably in summarizing the findings of the workshop or in the initial organization or writing of the report. Charlie Canham helped us conceive the project and organize the workshop, and Claudia Rosen provided excellent logistical coordination of the workshop. We thank Gene Likens for his encouragement, assistance, and participation in the workshop. This effort is possible due to a grant from the Rodney Johnson and Katherine Ordway Stewardship Fund within The Nature Conservancy.

1. Introduction

Background

The Nature Conservancy's mission is to conserve the earth's organisms by protecting the habitats they need to survive. The Conservancy's approach focuses on identifying important areas – often large landscapes - as priorities for conservation action within a larger-scale, ecoregional assessment. Once these important areas for conservation are identified, the Conservancy works with landowners and other partners in the area to insure that crucial habitats and ecosystem types remain available for the organisms that need them. Recent analysis of the status and threats to conservation in the mid-Atlantic and Northeast regions has led to the understanding that this kind of local, area-based conservation planning and action is necessary but may be insufficient. Some scientists propose that serious threats to ecosystems in the eastern U.S. arise from agents, such as air pollution and exotic species, that are regional or continental in scope and therefore beyond the control of landowners or conservation organizations working locally.

This report is a synthesis of scientific information on the impacts of air pollution on elements of biological diversity (e.g., species, natural communities, and ecosystems) in the Northeastern and Mid-Atlantic regions of the U.S. These elements – called *conservation targets* by the Conservancy - are intended to best represent biological diversity in planning efforts used to guide and focus conservation action. The report incorporates the findings of a workshop convened by the Nature Conservancy (TNC) and the Institute of Ecosystem Studies (IES) to evaluate the evidence that air pollution causes harm to conservation targets. The workshop, which was held at IES in Millbrook New York from May 10-12, 2004, was attended by 32 invited guests, including 22 academic, government and independent scientists and 10 TNC staff (see Appendix 1 for participant list). This report also includes information added by workshop participants after the workshop concluded in order to keep the information as current as possible. To the extent possible, we attempt to quantify the levels of air pollution that produce adverse impacts, and to assess the certainty of scientific knowledge on the subject.

Objectives of the report

Assessing the impacts of air pollution on ecosystems is not a new topic for science. The U.S. government created the National Acid Precipitation Assessment Program for this purpose in the 1980s, and NAPAP produced a 4-volume report in 1991 (NAPAP 1991). The European Union has focused their assessment activity on the development of "critical loads," which are defined as "the highest load of a pollutant that will not cause chemical changes leading to long-term harmful effects on the most sensitive ecological systems", according to present knowledge (Nilsson 1986). These continental-scale efforts required scores of scientists and many years of effort to complete. More locally and more recently, the New England Governors and Eastern Canadian Premiers (NEG/ECP) commissioned a study designed to determine critical loads for mercury, sulfur and nitrogen deposition for northeastern North America. (Ouimet et al. 2006, Miller 2006). Many other assessment and synthesis activities have been undertaken, ranging from scientific review papers to reports from industry groups, think tanks and NGOs.

What could we hope to add to all this prior assessment activity? Our goals are more focused in several ways than previous assessment efforts. We are interested primarily in the U.S Northeast and Mid-Atlantic regions, and we are focused on the biological responses to air pollution, specifically the species, communities, and ecosystems that comprise the set of conservation targets designated by TNC for those regions. We hoped to gain a better appreciation for the combined impacts of air pollution on multiple taxonomic groups and ecosystem types in order to better inform biodiversity conservation efforts about the relative significance of this threat. To our knowledge, this type of collective synthesis of impacts to biological diversity had not been previously attempted for multiple pollutants across multiple conservation target groups.

Our approach to the workshop was to invite experts on air pollution responses of various biological taxa (e.g. birds, salamanders, trees) and ecosystem types (e.g. forests, streams, salt marshes) to review the evidence on impacts of air pollution. The experts we invited were familiar with the primary and secondary literature so we could take advantage of prior assessment activities and include the latest research. Because we wished to limit the size of the workshop to keep it manageable, we did not have experts on every possible biological response. However, we assessed the level of knowledge within our group as we went along and focused on the taxa and ecosystem types for which we had the most knowledge. By focusing on TNC targets, we hoped to provide TNC with sufficient information to gauge the scope and severity of the threat of air pollution in the Northeast and Mid-Atlantic regions.

Air pollutants considered

The workshop considered four air pollutants: sulfur (S), nitrogen (N), mercury (Hg) and ozone (O_3). These four pollutants were agreed upon by TNC and IES prior to the workshop as the major air pollutants of concern, and were used to help narrow the focus of the workshop.

Sulfur and nitrogen are primarily released from fossil fuel combustion as S and N oxides and these gases are transformed in the atmosphere to acidic particles and acid precipitation. The gases and particles may be deposited directly to vegetation and soil surfaces in a process known as dry deposition, or they may be incorporated into cloud droplets, raindrops or snowflakes to become acid precipitation. In mountaintop and coastal areas where cloud and fog are common, highly acidic cloud droplets can deposit directly to vegetation. Sulfur oxides are released primarily from coal combustion, whereas any combustion can produce N oxides. Thus the contribution of motor vehicles to the pollution problem is greater for N oxides than for S oxides.

Nitrogen can also be released from agricultural activities as ammonia, a gas that can react with acidic gases and particles in the atmosphere to form small particles containing ammonium salts. Ammonia gas and ammonium particles can be dry-deposited to vegetation or can be dissolved in precipitation. In areas of intense agricultural activity, e.g., downwind of feedlots or heavily fertilized crops, ammonium can be the dominant form of N deposition.

The effects of S and N pollution on ecosystems are generally not caused by direct physiological effects of exposure to the gases, except in sites that are very close to pollution sources. More commonly, the effects are related to the chronic accumulation of S and N in plants and soils and the changes in soil and water chemistry caused by deposition of sulfate, nitrate and ammonium. Nitrogen and S can be transported long distances in the atmosphere and can impact ecosystems far from the emission sources. Because sulfate and nitrate ions can be easily leached from soils to surface waters, deposition of these pollutants to terrestrial ecosystems may cause a cascade of effects that includes lakes, streams, rivers, estuaries, and the coastal ocean.

Ozone is a "secondary" pollutant, formed in the atmosphere from photochemical reactions involving N oxides and hydrocarbons. Ground-level O_3 is a widespread regional pollutant in the eastern U.S. but tends to occur in particularly high concentrations downwind of major urban areas. Because O_3 and its precursors can be transported long distances, it is a threat to wildlands far removed from urban centers. Aside from its well-known effects on human lungs, O_3 is known to reduce photosynthesis in most plants and cause foliar lesions in sensitive plants (see Appendix 2 for a list of sensitive plant species). Its effects on animals other than humans and animals that serve as medical models for humans (e.g. Norway rats) have not been well studied, but are likely to be significant (Menzel 1984).

Mercury is released primarily from coal combustion and waste incineration and deposited to the earth in precipitation as well as in gaseous and particulate dry deposition. The different chemical forms of Hg in the atmosphere have varying residence times (0-300 days) and transport distances (local to global). Mercury is a known neurotoxin that biomagnifies in the food chain and bioaccumulates in individuals, thus organisms at the highest trophic levels that live the longest have the greatest risk of high exposure (Evers et al. 2005). Its most toxic form is methylmercury, which is formed primarily by S-reducing, mono-methyl bacteria, particularly under low-oxygen and acidic conditions. Such conditions are common in freshwater aquatic sediments, wetlands or saturated soils (Wiener et al. 2003).

Structure of this report

This primary source of material for this report was the information assembled and discussed by the participants in the TNC/IES workshop. We summarize those discussions here by organizing Section 2 of this report around the ecosystem types for which some knowledge was available within the group of experts assembled for the workshop. Specific biological taxa are discussed within the context of the ecosystem type with which they are most closely associated. In the discussion of each taxon or ecosystem type, we attempted to reach consensus on 1) the certainty or uncertainty of the scientific information on air pollution impacts on that target, 2) the nature of those impacts, and 3) if possible, the levels of loading of the pollutant that are known to produce the impacts.

Certainty of information. In some cases, there has been much study of air pollution effects on specific targets in the Northeast and Mid-Atlantic, and in other cases there has not. In general we reserved the highest level of confidence for targets in which air pollution impacts are known from experimental and/or gradient studies within the region. (Experimental studies manipulate the exposure to the pollutant in field or laboratory situations; gradient studies assess the impacts along a gradient of ambient exposure to the pollutant.) We had moderate confidence in conclusions inferred from studies on similar species or ecosystems outside the region. We had low confidence in conclusions drawn from mechanistic arguments about what species are likely to be sensitive to pollution, when those arguments were accompanied by little or no direct empirical support either inside or outside the region. We tried to capture even these low-confidence conclusions in our report because, in the absence of hard data, there is value in the reasoned opinion of experts on what species are likely to be sensitive. We tried to assess confidence levels no matter what the level of impact; e.g., in some cases we had high confidence that there was little or no impact on a taxon or ecosystem type.

Nature of the impacts. We considered several different types of impacts, including direct effects of pollutants on biological functioning of organisms (e.g. toxicity, mortality, effects on growth or reproduction), effects on species composition in communities, effects on abiotic ecosystem characteristics that are likely to affect the biota over the long term, and indirect effects in which species are affected through food web or competitive interactions (e.g., negative impacts on a species may benefit its prey and its competitors). We also attempted to capture specific examples of known effects on taxa or ecosystem types to help illustrate the impacts.

Loading levels that produce impacts. In some cases we felt there was sufficient information to quantify the relationship between exposure to the pollutant and impacts on the ecological systems. To do this, we followed the lead of Fox et al. (1989) in a report designed to help managers of Forest Service wilderness areas determine the potential for impacts for new air pollution sources proposed for the airshed of the wilderness area. Fox et al. proposed determining a green line and a red line of air pollution exposure (Fig. 1)—the green line is the deposition or concentration level below which there is high certainty that no adverse impacts will occur, and the red line is the deposition or concentration level above which there is high certainty of adverse impacts on at least some component of the system. Between the red line and the green line is the “yellow zone” where more information is needed to determine if air pollution will have a significant impact on the system—for instance, that information could be particularly characteristic of the site or the specifics of the exposure conditions.

> The Fox et al. (1989) approach recognizes both the difficulty in designating a single threshold for damage (i.e. a "critical load") and the possibility of substantial variation in pollution sensitivity among ecosystems of the same type. The red line and green line values in the Fox et al. report represent the collective judgment of a similar group of experts convened in 1988; our approach was to use this information as a starting point, updating it with more recent information and the findings of critical load assessments attempted by other groups. As discussed below, in some cases we were successful in specifying the red and green line values for target taxa and ecosystems, but in many cases we were not.

The ecosystem types considered in section 2 are:

Terrestrial Ecosystems (including embedded freshwater wetlands):

- Alpine and subalpine systems
- Forests (both upland and wetland types)
- Bogs and fens
- Grasslands

Aquatic Ecosystems (including freshwater, brackish, and marine):

- High gradient headwater streams
- Lakes and ponds
- Low gradient rivers
- Estuaries, bays and salt marshes

For each ecosystem type, we examined the effects of the four pollutants considered in the workshop: sulfur, nitrogen, mercury and ozone.

In section 3 of the report we discuss issues that cut across the various ecosystems and are important for understanding the full impact of air pollution on TNC conservation targets. For instance, the issues of inter-system transport of pollution and interaction among pollutants are discussed in this section. Finally, in section 4, we summarize the overall conclusions of the workshop and discuss its relevance to the Nature Conservancy's conservation mission.

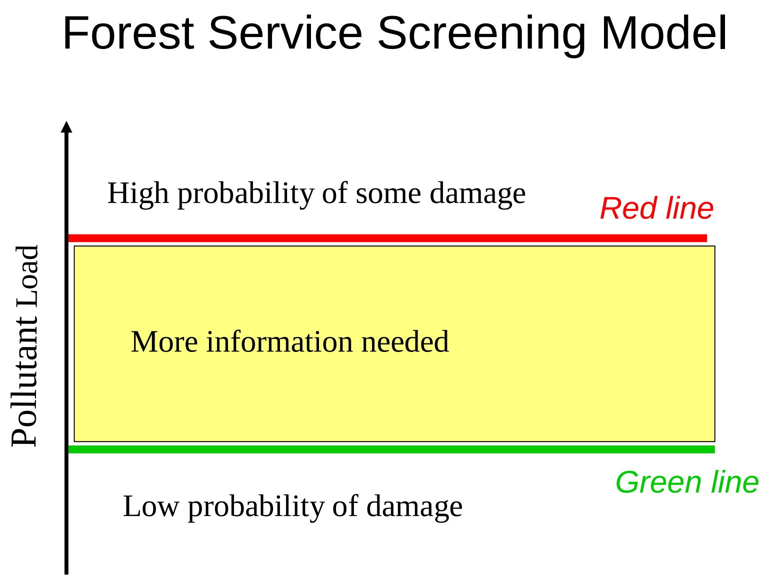

Figure 1. Red line/ green line model used by Fox et al. (1989) to screen potential air pollution impacts on Forest service wilderness areas.

2. Effects of Air Pollution

Terrestrial Ecosystems

While the public is generally aware of the effects of air pollution on aquatic ecosystems because of media coverage of acid-rain damaged lakes and Hg-contaminated fish, the public is much less aware of effects on terrestrial ecosystems. In some ways the terrestrial effects are more subtle because many soils are well buffered against acid inputs and the long life span of many terrestrial plants means that biological community changes play out in slow motion. Terrestrial researchers have tended to focus on microbial and geochemical effects in the soil as indicators of ecosystem sensitivity; with a few exceptions, effects on the plant and animal communities have received less research attention. (The exceptions include the direct physiological effects of O_3 on plants and of acid deposition on certain trees, especially red spruce (*Picea rubens*).) As a result, while much is known about deposition, accumulation and mechanisms of damage of air pollutants in terrestrial systems, much less is known about thresholds of impact on biota, in particular the ultimate threshold of death for an organism. Regardless, evidence from many terrestrial ecosystems indicates that the significance, severity and scope of this threat is worthy of conservation concern.

In general, the biogeochemical impacts of S and N on ecosystems depend upon their mobility in the canopy and soils to which they are deposited. If the anions (negatively charged ions) they form (sulfate and nitrate) are leached through the canopy and soils, rather than being retained, they can strip the foliage and soils of valuable nutrient cations (positively charged ions) such as calcium and magnesium. The leaching of sulfate and nitrate can cause acidification of soils and surface waters and mobilization of aluminum. Aluminum is a natural component of soils, but in acid conditions it becomes more soluble and thus more concentrated in soil water, where it can be toxic to roots, and it can leach into surface waters, where it is toxic to fish.

Both S and N can also accumulate in the vegetation and soil, leading to delayed effects as the accumulated material bleeds out slowly years or decades after its initial deposition. Accumulation of N in terrestrial ecosystems can cause shifts in species composition as N-loving species outcompete those species better adapted to less fertile soils (Gough et al. 2000). Nitrogen accumulation may also lead to a condition known as N saturation, in which overabundance of this key nutrient results in a cascade of impacts on microbial and plant production and N cycling (Aber et al. 1998).

Ozone is a well-studied pollutant known to be toxic to plants and animals. In plants, O_3 appears to affect membrane function, leading to reduction in photosynthesis, slower growth and in severe cases, death. In animals, O_3 effects have mainly been studied in humans, where it damages lung tissue and exacerbates respiratory problems such as asthma.

Mercury is known to accumulate in soils, but effects research has primarily focused on aquatic ecosystems where anaerobic conditions facilitate the production of the highly toxic form called methylmercury. The main terrestrial organisms considered to be at risk were animals that feed on other animals from the aquatic food web, such as birds feeding on aquatic insects or raccoons that eat aquatic invertebrates. Only recently have researchers begun to examine the methylation and bioaccumulation of Hg in terrestrial food webs, and more conclusive information is likely forthcoming in the next few years.

The following sections highlight specific ecosystem types, summarizing the discussion at the workshop about what is known about air pollution effects in those ecosystems, and also identifying many areas where additional research is warranted..

2.1 Alpine Ecosystems

Nitrogen

The workshop participants knew of no direct studies from the eastern U.S. on the effects of N deposition on the herbaceous and shrub communities that constitute the alpine zone of northeastern mountains. However, there have been studies on the effects of N on alpine ecosystems in the Rocky Mountains and in Europe. At Niwot Ridge in the Rocky Mountains of Colorado, an N enrichment study in an alpine meadow showed that N addition increases overall plant diversity, primarily by increasing the abundance of a sedge, *Carex rupestris*, and several other species (Bowman et al. 2006). This study concluded that species composition is a more sensitive indicator of changes due to N deposition than is than soil chemical response, and the plant responses are evident at N deposition rates as low as 4 kg N/ha/y. The authors speculated that higher levels of N deposition or long-term accumulation of N in the system may cause a decrease in plant species diversity as nitrophilous species start to dominate over those species less responsive to N (Bowman et al. 2006).

Because of the effects of N shown in the experiments in the Rockies and the overall floristic and structural similarity of alpine ecosystems in the Rockies and the eastern U.S., we have moderate confidence that N deposition is affecting alpine ecosystems in the eastern U.S. Deposition loads in eastern alpine zones probably range from 10-20 kg N/ha/y, and have probably been at that level for several decades, so it is possible that productivity and species shifts have already occurred in these ecosystems. However, in the absence of direct experimental evidence, gradient studies, or long-term monitoring of vegetation in these ecosystems, the nature and magnitude of the effects remain highly uncertain.

Sulfur, acidity, mercury and ozone

No direct studies of the effects of S deposition, acid deposition, Hg, or O_3 on alpine ecosystems are known by this group, either in the eastern or western U.S. Because of their high elevation, these ecosystems are exposed to high deposition rates of all of these pollutants. For red spruce trees in isolated patches within the alpine zone, one might expect a sensitivity to acid-induced calcium leaching as for red spruce in forests (see discussion in Forest section below); however, this has not been demonstrated experimentally in alpine red spruce. Most alpine plants have never been tested for sensitivity to O_3. Likewise, we know of no studies of Hg accumulation in food chains in alpine systems. Small wetlands and frequently saturated soils in alpine ecosystems may offer an opportunity for the methylation reaction which transforms inorganic Hg into highly toxic methylmercury. Thus, for all of these pollutants we consider the potential exposure levels to be high and impacts to be likely, but we have low confidence in any prediction of specific impacts because of the lack of relevant studies.

2.2 Bogs and fens

Nitrogen

Bogs and fens may be among the most sensitive ecosystems to the eutrophication effects of N deposition because they tend to be nutrient-poor, and ombrotrophic bogs in particular receive all of their nutrients from atmospheric deposition. Bogs and fens are listed by Bobbink et al. (1998) as among the ecosystems at highest risk of species compositional shifts due to N deposition. This subject has received extensive research attention in Europe, where increases in N deposition have been associated with decline in typical bog species such as the sundew *Drosera* and certain species of *Sphagnum*. Often favored are graminoids such as *Deschampsia* and *Eriophorum* that can grow tall and outcompete the bog species for light. Bedford et al. (1999) suggest that most North American wetlands are more likely to be limited by phosphorus (P) than by N, but marshes and swamps are the wetland types most likely to show N limitation or N and P co-limitation. However, species adapted to low-N environments may be quite sensitive to inputs of added N. A N enrichment study in bogs in New England showed substantial effects on growth and reproduction of the pitcher plant *Sarracenia purpurea* (Ellison and Gotelli 2002). If there is no change in current N deposition rates, these changes suggest a substantial probability of extinction of local populations within 100-250 years (Gotelli and Ellison 2002, 2006, see Box 1).

Box 1. Nitrogen impacts on the pitcher plant.

The pitcher plant (*Sarracenia purpurea*), a common sight in northeastern bogs, is a carnivorous plant that has adapted to low nutrient conditions by evolving the ability to capture insects and digest them in its "pitcher," a modified leaf. Research in bogs in Massachusetts and Vermont has shown that addition of excess nitrogen to pitchers, simulating N-enriched rainfall, changes pitcher plants by causing them to have fewer and smaller pitchers and more photosynthetic leaves (Ellison and Gotelli 2002). Models using the results of these experiments showed that even slight increases in N deposition will increase the risk of extinction of pitcher plants in the bogs studied (Gotelli and Ellison 2002, 2006). Other carnivorous plants, such as the common bladderwort (*Utricularia macrorhiza*), have also been shown to be sensitive to nutrient enrichment of their environments (Knight and Frost 1991).

Recent results reported from a long-term Canadian experiment suggest that chronic N deposition may initially lead to enhanced carbon uptake as the microbial community changes and decomposition slows (Basiliko et al. 2006). However, in the longer term, there may be a shift to decreased carbon sequestration and increases in CO_2 and CH_4

emissions as vegetation changes associated with higher N availability lead to production of plants that decompose more rapidly. These results, combined with the accumulated evidence from Europe and elsewhere and the direct experimental evidence from New England, give us high confidence that N deposition will strongly affect bog and fen ecosystems. The evidence suggests a red line value of 5 kg N/ha/y. Because most of the eastern U.S. receives deposition at that level or higher, it is probable that N effects are already occurring in many areas. We were not able to estimate a green line value, because most of these ecosystems are already above the red line and N removal experiments have not been attempted. However, because bogs are so sensitive to N inputs, it is possible that any increase over background levels of N deposition has an effect.

Sulfur and acidity

One biogeochemical response to S deposition in wetlands is important and well understood. As more S is deposited, the activity of S-reducing bacteria is increased. These bacteria gain energy from the chemical reduction of sulfate to sulfide in anaerobic conditions such as those that occur in wetland soils and sediments. Because these bacteria also methylate Hg, the increase in their activity increases the potential for the formation of methylmercury. This interaction between the S and Hg cycles results in increased toxicity of Hg in high-S wetlands (Heyes et al. 2000).

Mercury

The workshop participants were not aware of any direct study of Hg on the organisms of bogs and fens. However, the role of acidic wetlands in Hg cycling is well known (Wiener et al. 2003). Because of the anaerobic conditions in their soils and sediments, wetlands are hotspots for methylation of Hg in the landscape (Grigal 2003). Thus the less toxic inorganic Hg draining from a watershed can be converted to methylmercury in a wetland, where it can then be transported to a stream or lake or consumed in the wetland and transferred up the food chain. We would expect the higher-trophic level consumers in bogs and fens (e.g., birds that consume bog insects) to be at high risk for Hg accumulation.

Ozone

To the best knowledge of the workshop participants , the effects of O_3 on the herbaceous plants, shrubs and mosses of bog and fen ecosystems have not been studied. However, several of the tree species that are commonly found in or around wetlands in this region are considered sensitive to O_3 (e.g. green ash, *Fraxinus pennsylvanica* and speckled alder *Alnus rugosa*) (See Appendix 2), suggesting that primary and secondary impacts are plausible, but relatively undocumented.

2.3 Forests

Forests have received more air pollution-related research attention than any other terrestrial ecosystem type. However, the studies have largely focused on biogeochemical responses, and the links to species composition are often unclear. This is probably because the dominant organisms in forests— trees-- are so long-lived that studying the population and community responses to a chronic stress such as air pollution requires long-term research. Nonetheless, some recent studies have begun to reveal a web of actual and potential biological responses that are a cause for concern.

Nitrogen

There has been much research on the effects of N deposition on forests, both within the eastern U.S and elsewhere, particularly the western U.S. and western Europe. This research has caused a major shift in the way forest ecologists think about N. Previously, N was considered solely as a limiting nutrient for forest production, and fertilization with N was used to enhance production. In the last 20 years, however, research has shown that chronic N addition can have toxic effects that alter plant, soil, and microbial interactions and can lead to loss of soil fertility, reduced productivity, and even tree death. The basic processes involved have been organized in a conceptual framework referred to as “nitrogen saturation” (e.g. Aber et al. 1998). While this is still an active area of research, most scientists agree that continued accumulation of N in terrestrial ecosystems causes significant responses in ecosystem function.

Temperate-zone forests in unpolluted areas are usually limited by N, which means that additions of N can stimulate productivity. Most of the N that is deposited from the atmosphere is taken up by plants or microbes and retained in the vegetation or in soil organic matter. Leaching of N from these forests in drainage water is usually minimal, except in the case of older or damaged forests, which have reduced N uptake capacity because of slower growth rates. As deposition of N increases due to air pollution, N accumulates in the soils and vegetation, increasing the rate of N cycling in the ecosystem. The increased cycling increases the opportunity for N leaching, which occurs primarily as the mobile anion nitrate. Foliar and wood N concentrations increase, and the microbial processes that transform N in the soil are enhanced. In the U.S., there is little evidence for increased tree growth from the fertilizing effect of this added N, probably because most of the N appears to be retained in the soil organic matter where it is unavailable to the plants (Nadelhoffer et al. 1999). However, increased nitrate leaching is observed in some (but not all) forested ecosystems in the Northeast as N deposition levels increase (Aber et al. 2003). The differences between those ecosystems that show increased N leaching and those that do not is probably related to forest history (e.g. fire, logging, etc.), tree species composition and soil properties, especially the carbon:nitrogen ratio (Goodale and Aber 2001, Lovett et al. 2002). Similar results have been found in Europe, where the most important factors controlling the amount of nitrate leaching are the amount of N deposition and the carbon:nitrogen ratio of the forest floor (MacDonald et al. 2002). Nitrate leaching is important because it acidifies soils, stripping away important nutrients such as calcium and magnesium and mobilizing aluminum. In this regard, it acts in concert with sulfate leaching, thus N and S pollution can have additive effects.

The effects of N saturation on species composition of forests are not as well studied as the biogeochemical effects. Shifts in tree species composition under ambient deposition levels would be difficult to assess because of the long generation time of trees. Even if long-term studies revealed such shifts, it would be difficult to attribute them unambiguously to N deposition to eastern forests, which are simultaneously being exposed to many new stresses (e.g., O_3, climate change, and exotic pests) in addition to N deposition. Changes in abundance and composition of understory shrubs and herbs might also be expected in response to N deposition, as has been shown in Europe (Bobbink et al. 1998). In the eastern U.S. the data are not as clear-- the few studies that have examined this effect have used fertilization experiments as opposed to gradient studies or long-term measurements, and the studies have shown varying responses (Jordan et al. 1997, Hurd et al. 1999, Rainey et al. 1999, Gilliam 2006). It is known from studies in the eastern U.S. that N addition shifts the activity of soil microorganisms, with some responding positively to N addition while others respond negatively (e.g. Carreiro et al. 2000). Across a gradient of N deposition in the eastern U.S., changes in microbial N cycling activity are seen in some forest types but not others (McNulty et al. 1991, Lovett and Rueth 1999). Shifts in abundance and species composition of mycorrhizal fungi, which form the crucial interface between roots and soil for most plants, have been observed in response to N deposition in Europe, Alaska and southern California (Arnolds 1991, Lilleskov et al. 2001, Siguenza et al. 2006). Herbivorous insects tend to prefer plants with higher N concentration, and there is some evidence that increased N may be predisposing trees to attack by insect pests (e.g. McClure 1991, Latty et al. 2003). Increased susceptibility to pests could be a serious liability for eastern forests, given the number of exotic insect pests that are being introduced continually through enhanced global trade (Lovett et al. 2006).

In the last 15 years, experimental studies of N addition to forest stands or watersheds have been reported from Maine, New Hampshire, Vermont, Massachusetts, New York and West Virginia (Norton et al. 1994, Mitchell et al. 1994, McNulty et al. 1996, Adams et al. 1997, Magill et al. 1997, Templer et al. 2005). The N application rates vary from about 2 – 15 times ambient N deposition levels. A few stands show nearly compete retention of N with little biological or biogeochemical response, but most show increases in plant N content, microbial N cycling, production and leaching of nitrate, and leaching of cations such as magnesium and calcium. In three cases, a high-elevation spruce-fir forest on Mt. Ascutney, VT, a red pine forest in central Massachusetts, and a mixed-oak forest in southern New York, the N addition resulted in declines in productivity and increases in tree mortality (McNulty et al. 1996, Magill et al. 1997, Wallace et al. in press). The mechanism of this effect is not yet understood, but in all three cases soil acidification and the resulting aluminum toxicity to roots is a strong possibility (Aber et al. 1998). It is alarming to see tree mortality in response to the addition of a nutrient that was previously thought to be beneficial, but it must be remembered that these are experiments with artificially enhanced N deposition, and mortality does not appear to be a widespread response to N deposition under the current ambient deposition loads in the eastern U.S. What remains unclear, and will be extremely important to resolve, is whether forests will respond the same way to long-term accumulation of N from atmospheric deposition as they do to experimental N additions.

Little is known about the response of forest animals in the eastern U.S. to N deposition, although one might expect that increases in the N content of plant tissue and shifts in soil microbial activity would cause subtle ramifications throughout the above-ground and below-ground food webs.

The workshop participants had high confidence in the conclusion that N deposition produces both biogeochemical and biological effects in forests. The best available criteria for setting red and green line values is nitrate leaching, which appears to be very rare in forests receiving < 5 kg N/ha/y and increasingly common as deposition levels increase beyond 8 kg/ha/y (Aber et al. 2003). Similar thresholds have been reported for European forests (e.g. Dise and Wright 1995). Because we considered the nitrate leaching as a symptom that indicates current microbial response and may result in vascular plant response over a time frame of decades, we estimated the green and red line values at 5 and 8 kg N/ha/y, respectively.

Sulfur

Much research has also been done with regard to the effects of S in forest ecosystems. Because S is usually not a biologically limiting element, the responses are in many ways less complex than those of N. Atmospherically deposited sulfate enters plant and microbial pools, but the S itself does not appear to cause any direct biological responses other than the stimulation of S-reducing bacteria in anaerobic environments. Because S deposition in the eastern U.S. far exceeds the biological requirement for the element, most of the deposited S is either leached from the ecosystem or retained in the soils in both inorganic and organic forms. In glaciated regions of the Northeast, soils have little sulfate adsorption capacity, so most of the deposited sulfate leaches through the canopy and soils, stripping nutrient cations such as calcium and magnesium in the process. The resulting acidification of the soils mobilizes aluminum, which can be toxic to tree roots and, when it enters surface waters, to fish and other aquatic organisms (Cronan and Grigal 1995, Driscoll et al. 2001).

In unglaciated areas, the sulfate leaching is mitigated to varying extent by sulfate adsorption in the subsoil, although even the low levels of sulfate leaching in these ecosystems can acidify streams in sensitive areas (Galloway et al. 1983, Webb et al. 1994). Some of the sulfate retained in the soil may be re-mobilized in the future as S deposition levels decline, leading to a long-term legacy of elevated sulfate in stream water that would slow the rate of recovery of streams in response to declining S emissions.

Thus the biological effects of S deposition in forests are largely due to the acidification and cation losses caused by sulfate leaching. In areas of high base cation supply, such as areas with calcium-rich bedrock (e.g. limestone), the soil cation losses are less of a problem, and the soils and streams are buffered against acidification. In more sensitive areas, loss of soil cations can be a problem for plants that require a high calcium or magnesium supply, such as sugar maple (*Acer saccharum*), white ash *(Fraxinus americana)*, basswood *(Tilia americana)*, and flowering dogwood *(Cornus florida)*. Declines in sugar maple have been observed in calcium-poor areas in central and western Pennsylvania, attributed to a combination of acid deposition and insect outbreaks (Horsley et al. 2002). Fertilization of plots with calcium and magnesium appears to reverse the decline (Long et al. 1997).

In systems without substantial amounts of base cations in the bedrock or till, replenishment of these nutrient cations by rock weathering and atmospheric deposition is a very slow process. Therefore, soil acidification and base cation depletion are long-term processes that may take decades or even centuries to reverse after the leaching losses are stopped. The recovery time is further lengthened by the continued slow release of accumulated S and N from within the ecosystem after deposition of S and N is reduced.

In the mountains of the eastern U.S. red spruce has been shown to be sensitive to acid deposition because the acidity leaches calcium from the foliage. The loss of foliar calcium, especially the small portion of that calcium that is membrane-bound, renders the tree less able to develop frost hardiness in the autumn, leading to winter damage and in many cases, tree death (DeHayes et al. 1999) (See Box 2). This mechanism is thought to be responsible for the widespread spruce decline observed in northeastern mountains during the 1980s, a problem that continues to this day (Hawley et al. 2006).

Animals may also be affected by soil acidification. Earthworms, slugs, millipedes, centipedes, slugs, collembolans and isopods are among the soil animals known to be sensitive to acidity, although most of the studies are from high-deposition areas in Europe (Rusek and Marshall 2000). One recent study reports that productivity of Wood Thrush *(Hylocichla mustelina)* populations is negatively correlated with acid deposition levels across the northeastern U.S. (Hames et al. 2002). This is purely a correlative result, but the proposed mechanism for the response is plausible— that acid rain reduces the quantity of quality of the soil invertebrates that are the main source of calcium for wood thrushes.

The workshop participants did not estimate red and green line values for S deposition because it was considered too simplistic an approach given the more advanced state of our knowledge of the biogeochemical effects. Much more sophisticated calculations and models have been applied to forests throughout the region to project soil and stream acidification, taking into account such crucial factors as soil and bedrock chemistry (Miller et al. 2006, Gbondo-Tugbawa and Driscoll 2003, Cosby et al. 1985). Our recommendation is that these models be applied to sites of interest to TNC to estimate potential acidification responses.

Box 2. High-elevation forest damage.

High-elevation forests of the eastern U.S. are subject to high levels of acid deposition, partly because they are frequently bathed in acidic clouds. The acid deposition depletes some nutrient ions (such as calcium and magnesium) from the soil at the same time it strips those nutrients from the foliage. This "one-two punch" can knock out sensitive species, particularly red spruce (*Picea rubens*). Research in Vermont and elsewhere has shown that the loss of calcium from red spruce needles reduces their ability to develop cold-hardiness in the autumn and leads to freezing damage during cold winters (DeHayes et al. 1999, Schaberg et al. 2000). This acid-induced cold sensitivity is probably the main cause of the observed decline of red spruce in the mountains of the Northeast during the 1980s.

Mercury

Mercury is a widespread pollutant in the forests of the eastern U.S. It can accumulate in soils and is converted to its most toxic form, methylmercury, in anaerobic environments such as wetlands, riparian zones, and any other upland area with moist soils. Plants appear to be insensitive to methylmercury, but in animals it is a potent neurotoxin that can cause physiological, behavioral, and ultimately reproductive impacts. Mercury is biomagnified in food webs; thus, animals that are at highest risk of Hg toxicity are those feeding relatively high on the food chain, especially if their food originates from habitats with moist soils or water that are conducive to methylation. Animals that are long-lived are also at high risk, particularly in individuals where the input of methlymercury exceeds its ability to depurate or demethylate Hg.

Wildlife in both wetland and upland forests were previously considered safe from the impacts of methlymercury because of conventional thought that only aquatic systems have the ability to biomagnify methlymercury and that a fish-based food web was the only one of concern. Recent findings now show that species that are not linked to the fish food web can contain surprisingly elevated levels of methlymercury. Elevated methylmercury levels have been found in birds of subalpine ecosystems, such as the blackpoll warbler and the endemic Bicknell's thrush (Rimmer et al. 2005). Apparently moist, acidic soils of high-elevation forests provide an environment conducive to potentially high levels of Hg deposition (Miller et al. 2005) and Hg methylation. Rimmer et al. (2005) documented the strong and predictive relationship of litterfall Hg values modeled by Miller et al. (2005) and the blood Hg values of the Bicknell's Thrush.

The workshop participants had high confidence that Hg pollution is affecting biogeochemical processes (methylation) and animals of eastern forests. However, we did not set red and green line values, because the science is still young and not yet quantified at the confidence level needed.

Ozone

Ozone has been the subject of much research because it is a federal "criteria" pollutant, that is, the concentration regulated by the EPA, and states are required to comply with those regulations. The regulatory standards are based primarily on the effects of O_3 on human health, but effects on plants are also well known. Ozone is a potent oxidant, and once it enters a plant through stomata it reduces photosynthesis and alters carbon allocation. Ozone at the levels found in the eastern U.S. often does not kill plants outright, but slows their growth and may make them more susceptible to other fatal stresses such as insect or pathogen attack. Ozone exposure can also reduce flowering (Bergweiler and Manning 1999) and alter the decomposition rate of leaves after they are shed from the plant (Findlay and Jones 1990). Because species vary in their sensitivity, O_3 can shift the competitive balance in plant communities to the detriment of sensitive species (Miller and McBride 1999). Further, because individuals of a given species vary in their sensitivity, O_3 exposure can cause changes in genetic structure of populations, reducing or eliminating sensitive genotypes (Taylor et al. 1991, Davison and Reiling 1995).

At a broad scale, sensitivity of plants to O_3 is dependent on level of exposure, species, and soil moisture status. The dependence on soil moisture reflects the fact that O_3 enters the plant through the stomates, and in dry conditions the stomates are more often closed. Thus, O_3 exposure in a dry year or at a dry site may be less damaging than the same exposure in more moist conditions.

The complexity of the physical and chemical sources and sinks for atmospheric O_3 results in complex patterns of exposure in space and time. In lowland areas subject to air pollution influence, O_3 concentration tends to increase during the day and reach a peak in late afternoon, then decline during the night to a minimum in early morning. On mountaintops this daily cycle may be absent, resulting in higher exposures for montane plants, especially in the morning hours. Because O_3 reaches its greatest concentration downwind of, rather than within, major urban areas, O_3 sensitive trees may actually grow better in large cities than in the surrounding suburban and exurban areas (Gregg et al. 2003).

Many plants have been screened for O_3 sensitivity, but the screening is usually based on the development of visible foliar injury rather than on the more subtle responses of reduced photosynthesis or pathogen resistance. Appendix 2 is a list of plants on U.S. National Park Service properties that are known to be particularly sensitive to O_3 exposure (National Park Service 2003).

Despite the considerable research on plants, there is little information on the effects of O_3 on animals other than *Homo sapiens* and the animals that serve as its medical models, such as the Norway rat. Given the effects of O_3 on the human respiratory system, one might expect significant impacts of O_3 exposure on any animals with similar respiration mechanisms (Menzel 1984). However, we know of no information on O_3 effects on animals in natural ecosystems.

The O_3 research community has devoted considerable effort to synthesizing information on effects of O_3 on plants. Several different indices of O_3 exposure are used, but one that is used commonly in plant research is the Sum06-- the maximum, rolling 90-day sum of the average daytime (0800-1959) hourly concentrations of $O_3 \geq 0.06$ ppm for the year. A conference held to review O_3 exposure research and identify threshold levels of exposure that produce impacts on plants identified a Sum06 level of 8-12 ppm-hr as likely to produce foliar injury to some plants in natural ecosystems (Heck and Cowling 1997). Following the recommendation of the experts at that conference, we recommend 8-12 ppm-hr as a red line value for TNC. Because any O_3 can be injurious to sensitive plants (Fox et al. 1989), the best green line value is probably the background, unpolluted level of O_3 exposure, but there is yet no consensus on what that background O_3 level was in the eastern U.S.

2.4 Grasslands

Grasslands are a minor ecosystem type in the northeastern U.S., and there is little information on the effects of air pollution on either the biota or the biogeochemistry of these systems. Grasslands develop distinctly different communities depending upon whether their soils are acidic or calcareous. Acid grasslands are more common but calcareous grasslands tend to have more rare species (Stevens et al. 2006).

Nitrogen

We are aware of no direct studies on N effects on grasslands in the eastern U.S. However, experimental and gradient studies from elsewhere give us moderate confidence that effects on species composition are likely (Dise and Stevens 2005). In Minnesota, N fertilization of an acid grassland (at a level of 100 kg N/ha/y) resulted in a 40% reduction in species richness over 12 years (Wedin and Tilman 1996). In Great Britain, a recent comparison of species composition in acid grasslands along a gradient of N deposition showed that species composition was affected at N deposition rates as low as 5 kg N/ha/y (Stevens et al. 2004). This deposition level is below the mean N deposition for the eastern U.S., suggesting that current levels of N deposition are currently affecting grassland species composition in many areas. Thus, we have moderate confidence in the conclusion that N deposition is affecting acid grasslands in the eastern U.S., and we chose 5 kg N/ha/y as a preliminary green line value, bearing in mind that no data are available from within the region. At the levels of deposition found in this region, the effects are likely to be shifts in relative abundance of species, favoring the nitrophilic species (such as *Agropyron repens,* Wedin and Tilman 1996), rather than loss of species or local extinction.

We know of no studies of N deposition on calcareous grasslands in the U.S., Biogeochemically, they are likely to be less sensitive to acidification because the calcareous soils buffer the acidity. However, in Europe, species composition of calcareous grasslands is quite sensitive to N enrichment (Stevens et al. 2004). Species compositional shifts due to N enrichment may be more likely to cause species extinctions in calcareous grasslands because they tend to contain more rare species.

Sulfur, ozone and mercury

We know of no studies of the effects of S, O_3, or Hg deposition on eastern U.S. grasslands. Because there are many plant and animal species that require grassland habitat, the lack of information on pollution effects is disquieting. However, grasslands are generally considered to have minimal abilities to methylate Hg and data from a few studies indicate low Hg body burdens of grassland bird species (Evers et al. 2005).

Aquatic Ecosystems

The four air pollutants are very different in their effects on aquatic ecosystems. Sulfur is largely an agent of acidification through the mechanisms discussed above. Nitrogen can contribute to acidification but also can cause eutrophication (over-enrichment with nutrients) in aquatic systems that are limited by N supply. Mercury is a potent neurotoxin that accumulates in aquatic food webs to alter the behavior and reproduction of organisms at high trophic levels. Ozone has little effect in the water, but may have effects on emergent aquatic plants or air-breathing animals that are part of aquatic ecosystems. These potential effects of O_3 on aquatic plants and animals have not, to our knowledge, been studied, so we will ignore O_3 in the following discussion .

The effects of acid deposition on the chemistry and biology of aquatic ecosystems have been well known since the 1970s, and there is little doubt about the serious impact acidification has on a wide range of aquatic organisms. The research has primarily focused on small lakes and streams, and has included comparative studies across acid deposition gradients, experimental acidification of lakes and streams, and long-term studies of acidification or recovery in lakes or streams subject to increases or decreases in acid loading. Many of the key studies have been done in the target area of this report (Northeastern and Mid-Atlantic regions of the U.S.). We have high confidence that acid deposition is adversely affecting aquatic ecosystems in this region.

Effects of acidic deposition on water quality include reduced pH (increased acidity), reduced acid neutralizing capacity (ANC)[1], and increased aluminum (Al) concentrations. (Driscoll et al. 2001). The primary variables of concern to organisms are pH and Al concentration. In gill-breathing organisms, Al interrupts gas and ion transport across respiratory membranes, leading to disruption of the five major functions of the gill: 1) ion transport, 2) osmoregulation, 3) acid-base balance, 4) N excretion, and 5) respiration (Brakke et al. 1994). The effects of Al on fish were known as early as the mid-1970s (Schofield 1978). Other physiological effects also occur in aquatic organisms, including altered hormonal and behavioral responses (Brakke et al. 1994). Aquatic organisms vary widely in their sensitivity to acidification. The most sensitive organisms tend to be adversely affected when pH drops below about 6, while some tolerant organisms can survive in waters as acid as pH 4. The sensitivity of various taxonomic groups to acidification has been well researched and some general patterns have been observed. These general patterns are listed in Box 3.

It is important to note that stream and lake acidification can be chronic or episodic, with episodic acidification usually occurring during large water flow events such as large storms or snowmelt periods. The chemistry may be different in chronic vs. episodic acidification—for example, in the Northeast, N leaching is more important in episodic than in chronic acidification (Murdoch and Stoddard 1993, Driscoll et al. 2001). Nonetheless, episodes of acidification can be as damaging to aquatic biota as chronic acidity because a single event can kill an organism.

In addition to the direct toxic effects of pH and Al on aquatic organisms, indirect effects in lake and stream ecosystems can be important. For instance, lowered pH can reduce the concentration of dissolved organic carbon (DOC) in lakes, allowing light to penetrate further into the lake. This increases the light available for macrophytes and benthic algae that grow on lake bottoms, and in addition the increased visibility alters the relationship between predators and prey in the lake. Dissolved organic carbon is important for another reason: it complexes aluminum and makes it less toxic, so a decrease in DOC increases the toxicity of Al. Indirect food web effects can also occur; for instance, if a predator is tolerant of acidity but its prey are not, the predator will not be able to survive in an acidified lake.

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[1] Acid Neutralizing capacity (ANC) is the ability of water to neutralize strong acids, and is one of the primary measures of surface water acidification and recovery. Waters with ANC < 0 μeq/L (micro-equivalents per liter) are considered chronically acidic, those with ANC between 0 and 50 μeq/L are considered sensitive to acidification, and those with ANC > 50 μeq/L are often considered relatively resistant to acidification. While ANC does not directly affect aquatic organisms, it is an integrative measure for the propensity of an ecosystem to experience high acidity and Al concentrations, which do affect organisms.

Research on atmospheric deposition effects in lakes and streams clearly show that certain characteristics make lakes more susceptible to inputs of strong acids (Stoddard et. al, 1998). In general, streams and lakes at higher altitudes, with thin till depth, non-carbonate geology, associated wetlands, and low ANC are considered sensitive to acidification. Perched seepage lakes recharged by rain water are also considered sensitive (Young and Stoddard, 1996). Other factors influencing sensitivity to acid deposition include the ability of watershed soils to retain sulfate and nitrate. While some S is retained through biotic immobilization in soils and vegetation, most retention is through adsorption of sulfate on iron and aluminum oxides in the soil, and is usually highest in unglaciated soils (Galloway et al. 1983). In contrast, N retention is largely biological and is most complete in watersheds with rapidly growing forests. Forest type and previous land use or disturbance history can also influence N retention. Hydrology also comes in to play in stream acidification because flow paths that route water directly to the stream and minimize contact with the soil reduce the capacity for neutralization. In addition, there is considerable biodiversity present in intermittent streams and ephemeral ponds, but little research has been done on the factors controlling acidification in these environments.

Streams and lakes are not homogeneous environments, rather they encompass a range of habitat types that can vary in their acidification. For instance, many streams increase in pH as water moves downstream. Even in headwater streams, some sections may be influenced by seepage from well-buffered ground water and may represent a refuge for fish in an otherwise acidified stream. Similarly, some invertebrates in a lake may escape from acidified water by sheltering in the well-buffered sediments on the bottom of the lake. Thus spatial heterogeneity in aquatic systems is important for both the tolerance of and recovery from acidification. Further, this heterogeneity indicates that behavioral responses of organisms- e.g., the propensity of fish to drift downstream or invertebrates to burrow into the sediments during acid episodes—can influence the tolerance of the biota to acidification.

Mercury is deposited to aquatic ecosystems and their watersheds primarily in inorganic form. However, Hg's toxic effects are caused by its organic form, methylmercury; therefore those factors that influence Hg methylation also influence the extent to which systems are harmed by Hg deposition. The methylation process often proceeds with the involvement of sulfate-reducing bacteria and so conditions conducive to these bacteria, such as high sulfate, low oxygen, and low pH, also promote more accelerated rates of methylation (Wiener et al. 2003). Most methylation of Hg occurs in the anoxic sediments of lakes, streams, and wetlands. Levels of DOC also appear to influence Hg methylation but these effects are not completely understood and are the subject of current research. Methylmercury production and availability are also dictated by hydrology; on water bodies where large areas of substrate undergo wetting and drying, methylmercury levels are elevated.

Mercury is particularly dangerous in aquatic food chains where biomagnification is common. Food chain lengths are primarily dictated by zooplankton diversity and abundance (Chen and Folt 2005, Chen et al. 2005). Greater zooplankton diversity can result in an order of magnitude increase in methylmercury in higher trophic level organisms, while in lakes with algal blooms, a "biodilution" effect can occur whereby methylmercury levels are dampened (Chen et al. 2005).

Box 3. Sensitivity of aquatic taxa to acidification (from Baker et al. 1990).

pH Change	**General Biological Effects**
6.5 to 6.0	Little community change; possible effects on highly-sensitive fish species (e.g. fathead minnow, striped bass)
6.0 to 5.5 	Loss of sensitive species of minnows and dace (fathead minnow, blacknose dace). Perhaps decreased reproduction of walleye and lake trout; increased accumulation of filamentous green algae. Changes in species composition and decrease in species richness in phytoplankton, zooplankton, and benthic invertebrate communities. Loss of some zooplankton species and many species of clams, snails, mayflies, amphipods, and some crayfish.
5.5 to 5.0 	Loss of lake trout, walleye, rainbow trout, smallmouth bass, creek chub. Further increase in filamentous green algae. Loss of many zooplankton species as well as all snails, most clams and many species of mayflies, stoneflies, and other benthic invertebrates.
5.0 to 4.5 	Loss of most fish species. Further decline in the biomass and species richness of zooplankton and benthic invertebrate communities. Loss of all clams and many insects and crustaceans. Reproductive failure of some acid-sensitive amphibians, including spotted salamanders, Jefferson salamanders, and the leopard frog.

The known biological effects of methylmercury are numerous and likely affect all major vertebrate taxa at individual, population, and potentially at metapopulation levels. Effects can be categorized as physiological, behavioral, and reproductive. They are relatively well-described for fish-eating wildlife and increasingly so for fish (see Evers 2005). Although traditional emphasis of Hg in fish has been on exposure to determine human and ecological effects, recent efforts have increasingly been placed on direct effects of methylmercury on fish that include inhibition of normal growth and gonadal development (Friedman et al. 1996), predator avoidance (Webber and Haines 2003) and on reproduction (Hammerschmidt et al. 2002). There are few exposure and effects studies on herpetofauna, although Hg is sometimes considered among the possible causes of long-term and widespread declines in amphibian populations.

Efforts with birds have been more comprehensive and have included both laboratory and field studies. Bird species in which the effects of Hg are well known from laboratory studies include the Mallard (*Anas platyrhychos*) (Heinz 1979) and Ring-necked Pheasant (*Phasianus colchicus*) (Fimreite 1971). Symptoms of mercury exposure in birds include reduced reproductive success, behavioral changes such as a reduction in time spent hunting, and neurological problems such as brain lesions, spinal cord degeneration and tremors (Evers 2005). Until recently, results from Hg dosing studies on mallards have been used by the USEPA (USEPA 1997) and other agencies for setting universal threshold levels or lowest observed adverse effect levels (LOAELs) for all bird species. Now, it is well understood that bird species vary in their sensitivities to methylmercury exposure. Sensitivity appears to be grouped by foraging guild – strict granivores appear to be most sensitive, while insectivores are more sensitive than omnivores, which are more sensitive than piscivores. Much of the effects literature is focused on piscivores, and for good reason, as piscivores have some of the most at-risk species. The species with the greatest literature on exposure and effects is the Common Loon (*Gavia immer*). Lab and field studies on both individuals and populations have developed national exposure profiles (Evers et al. 1998, 2003) as well as regional risk profiles (Evers et al. 2004) that are now related to biological hotspots (Evers 2006). Lakes within these hotspots are now viewed as population sinks. Connectivity of these population sinks within the regional metapopulation of loons is currently being assessed. Other piscivorous birds in which Hg has been shown to harm reproductive success of populations include the Bald Eagle (*Haliaeetus leucocephalus*) in Maine (DeSorbo and Evers 2005) and wading birds such as the Great Egret (*Ardea alba*) in Florida (Bouton et al. 1999, Spalding et al. 2000) and Snowy Egret (*Egretta thula*) in Nevada (Henny et al. 2002).

Recent studies suggest that the terrestrial invertebrate food web may have the ability to biomagnify Hg as much or more than the aquatic food web. Similar to the zooplankton food web, the transfer of methylmercury from one trophic level to the next (or from one secondary consumer to another) provides the ability for methylmercury concentrations to increase one order of magnitude. Spiders are predators in invertebrate food webs, and large spiders may carry as much of a methylmercury body burden as gamefish. As a result, insectivorous birds such as songbirds and rails are likely at much higher risk than previously realized, even in strictly terrestrial habitats (Rimmer et al. 2005). Other more novel forage pathways for methylmercury are also coming to light and include food webs with periphyton and mollusks.

Mammal Hg exposure and effect levels, particularly for piscivorous species, are relatively well-known. The best-studied species include mink (*Mustela vison*) and river otter (*Lontra canadensis*)., for which sublethal effects include impairment of motor skills and weight loss. Yates et al. (2005) summarized exposure levels for the past two decades for much of northeastern North America. Laboratory studies on mink that establish LOAELs indicate effects in the wild are highly likely (Aulerich et al. 1974, Wren et al. 1985, 1987, Dansereau et al. 1999).

With this background information in mind, we proceed to summarize the effects of air pollution in various aquatic ecosystem types in the region of study.

2.5 High gradient headwater streams

Sulfur and Nitrogen

Sulfur and N deposition have two principal effects on headwater streams. First, if sulfate and nitrate leach through watershed soils, they can mobilize acidity and aluminum which have direct effects on stream ecosystems. Second, N is often a limiting nutrient in aquatic ecosystems, and thus added N can produce eutrophication. In the past, headwater systems in the temperate zone have usually been found to be limited by phosphorus, thus it has generally been assumed that the eutrophication effects are primarily expected in downstream ecosystems such as bays and estuaries that are more commonly N-limited. Recently, however, some headwater systems have been reported to be N-limited, and the eutrophication issue is currently being re-assessed. (Bernhardt et al. 2005). With little information available, however, we will confine this discussion to acidification effects of sulfate and nitrate.

As stream acidity increases, sensitive species (see Box 3) will either die out or will seek refugia in less-acidified sections of the stream. Mobile species such as fish and invertebrates will often “drift”, essentially allowing themselves to be carried downstream in search of better habitat conditions. If the increase in acidity is brief (e.g., in response to heavy rainfall or snowmelt), there may be little fish mortality unless species are prevented from leaving the system. When streams become chronically acidic, fish species can be lost from the system. There is strong evidence from many studies in this region and elsewhere that acidification can result in loss of fish populations and decline in fish species diversity (Jenkins 2005). Research at Shenandoah National Park in Virginia suggests that one fish species is lost for approximately every 21 μeq/L decrease in ANC (Sullivan et al. 2002).

Effects on benthic species such as mussels and snails are not well studied. Naturally acidic headwater streams at high elevation do not normally support many mussel species..

In episodically acidic streams mussels may close up to avoid toxic effects. Mussels would likely be eliminated from chronically acidic streams.

Mercury

Only recently has methylmercury in biota been measured in headwater streams. Salamanders have shown elevated Hg levels (Bank et al. 2005) and absence of some salamander species has been linked to potential chemical changes such as greater acidification and increased methylmercury availability (Bank et al. 2006). Further work has shown that crayfish in low order streams generally have higher Hg burdens than crayfish in rivers, lakes, and reservoirs within the same watershed (Pennuto et al. 2005). There is compelling evidence that the high input of Hg and S in the Appalachian Mountains could have negative population-level impacts on the high diversity of salamander species that reside in upper watershed streams and ponds. (Bank et al. 2006)

2.6 Lakes and ponds

The region under review at the workshop included the lake and pond-rich glaciated regions of the Northeastern United States, as well as the unglaciated, lake and pond-depauperate regions of the mid-Atlantic. Northeastern lakes were the focus of the workshop discussions, as insufficient information is available for the small number of natural lakes in the mid-Atlantic. Atmospherically deposited S and N are both significant contaminants to this system. Mercury is also a significant contaminant, affecting a number of taxa across trophic levels.

Sulfur and Nitrogen

The workshop participants had very high confidence that acidic deposition is affecting the biota of lake and pond ecosystems in the study area, particularly in the Northeast. Comparative studies of high- and low-acidity lakes within the region and experimental lake acidification studies elsewhere provide a scientifically coherent picture of the effects of acidification. Animal species differ in their sensitivity to acidification (Box 3), but in general as pH drops below 6, taxa are progressively lost. In the Adirondacks, one fish species is lost for every 0.8 unit decline in lake pH (Jenkins 2005). In lakes of the Adirondacks and the White Mountains of New Hampshire, an average of 2.4 crustacean species were lost with each pH unit decrease (Confer et al. 1983). Remaining species may suffer directly from the effects of acidification but also indirectly if some important food sources disappear as a result of acid stress, or species may respond positively if their predators are sensitive to acidity. In fact, the experimental removal of fish from unacidified lakes brings about some of the same changes that occur with acidification. Invertebrate predators like corixids and C*haoborus* become abundant along with a concomitant change in species composition and a decrease in biodiversity (Eriksson et al. 1980). Increased acidity is also linked to increased water clarity and, consequently, increased light penetration. This results in warming of the water column, and altered stratification and seasonal turnover regimes.

Establishing one contaminant deposition threshold for all lakes across a diverse landscape is extremely difficult, since there is a range of variability in natural ANC, pH, and base cation supply. Several available models, such as MAGIC (Cosby et al. 1985) and PnET-BGC (Gbondo-Tugbawa and Driscoll 2003) predict stream and lake acidification based on deposition levels and watershed characteristics. Although the parameter-intensive nature of these models has allowed their application to only a limited number of watersheds in the region, a current TNC effort is aimed at broader extrapolation of the modeling results.

Atmospherically deposited N may have a eutrophying effect in addition to an acidifying effect. Export of N to estuaries can have important consequences, as discussed below. Nitrogen is not usually a limiting nutrient in lakes and ponds (Driscoll et al. 2003), however, there is some evidence that very low-N surface waters may be limited or co-limited by N and therefore respond to N additions. Examples are streams in the New Jersey Pinelands (Morgan and Philipp 1986), and coastal plain ponds on Cape Cod (Kniffen et al. 2007) and possibly on Long Island as well.

Mercury

Atmospheric deposition, directly on the lake surface as well as on the watershed, is a significant source of Hg in lakes, A recent synthesis of Hg efforts from the Northeast showed that Hg concentrations in fish tend to decrease with increasing pH, sulfate, and ANC in lakes (Chen et al. 2005). Land use also affects the sensitivity of lotic systems to Hg deposition, with a tendency for lower Hg levels in fish from aquatic ecosystems with higher residential and urban development in the watershed (Chen et al. 2005).

Much work has been conducted on piscivores residing in lakes including the summary of large Hg exposure data for fish (Kamman et al. 2005), birds (Evers et al. 2005), and mammals (Yates et al. 2005) for northeastern North America. This effort provided insight into what species are at greatest risk. Fish species with the higher Hg levels include primarily introduced species such as walleye, northern pike and both largemouth and smallmouth bass. Other species with elevated levels were yellow and white perch and lake trout. Although actual impacts from Hg on native fish species in lakes of the Northeast may be of lower concern than the ability of fish to transfer methylmercury to people, the known and potential impacts to fish-eating birds and mammals is of high conservation concern. There are documented impacts from methylmercury on the reproductive success of several piscivorous bird species including the Common Loon and the Bald Eagle. Other species of concern based on compilations of Hg exposure levels and their piscivorous diet include the Belted Kingfisher, Great Blue and Green Heron, and Common and Hooded Mergansers and mammals such as the mink and river otter (Evers et al. 2005, Yates et al. 2005).

There was a high degree of confidence at the workshop that Hg has significant impacts on aquatic biota in the study area. Because the toxicity of Hg depends on the extent to which it is methylated, and there is a wide variation in methylation abilities among lakes of different types, it is difficult to determine a threshold of Hg deposition that affects biota. Even relatively low levels of Hg deposition may have significant impacts if methylation rate is high and biomagnification occurs in the food web. Current modeling efforts will hopefully provide an ability to predict the propensity of Hg methylation in watersheds.

Box 5. Mercury impacts to the Common Loon.

Common Loons are among the best-studied animals for mercury exposure. Loons are especially susceptible to mercury contamination because they eat fish and are thus subject to the results of biomagnification of mercury in the aquatic food web. High mercury levels in loons can cause behavioral effects that can lead to reduced reproductive rates and thus to declining populations.

2.7 Low gradient rivers

Sulfur and Nitrogen

Larger, low gradient, lower elevation streams and rivers in the Northeast and Mid-Atlantic do not generally show impacts from acid deposition. In larger watersheds, effects of atmospheric deposition are buffered by in-stream processes and the neutralizing capacity of the watershed. However, rivers may be sensitive to N pollution, especially as they near the sea and become estuaries or tidal rivers. We discuss the issue below under "Estuaries, bays and salt marshes."

Mercury

The forested floodplains of large rivers have substantial ability to methylate Hg, and recent work at three Hg-contaminated rivers in the region (the Sudbury River in Massachusetts and branches of the Shenandoah and Holston Rivers in Virginia) has demonstrated the importance of floodplain forests and riparian wetlands for generation of high methylmercury levels (e.g. Waldron et al. 2000). Insectivorous bird species that live in these floodplains such as the Carolina Wren, Worm-eating and Yellow-throated Warblers, Northern and Louisiana Waterthrushes, Red-winged Blackbird, and Song and Swamp Sparrows have blood Hg levels that well exceed known toxic levels for songbirds (Evers et al. 2005).

2.9 Estuaries, bays, and salt marshes

Sulfur and Nitrogen

Estuaries, bays and salt marshes are generally not severely impacted by acidic deposition, but they are subject to eutrophication caused by excess loading of N from atmospheric deposition and other sources (Boyer et al. 2002). These ecosystems are usually directly on, or receive water from, large rivers where there are high levels of N (and other nutrients) from a diversity of point and non-point sources, including agricultural and urban runoff, industrial and municipal wastewater, and atmospheric deposition to the estuary and to its watershed. The mix of these sources is unique to each watershed but typically atmospheric deposition accounts for 25-40% of the total (Boyer et al. 2002). Thus atmospheric deposition is not the major source of N pollution in these systems and it is expected that only a modest improvement would be achieved by reducing levels of atmospheric deposition. However, point sources and agricultural runoff of N are generally decreasing as better controls are put in place, while atmospheric N deposition is holding steady (Driscoll et al. 2003). Thus, the percentage contribution of atmospheric deposition to this problem is increasing over time.

Most estuaries and bays in this region have some degree of eutrophication due to excess N loading (Scavia and Bricker 2006). The eutrophication leads to excess algal growth, and when the algae die and decompose, low oxygen concentrations may result, especially in deeper waters (Driscoll et al. 2003). The low oxygen is a danger to fish and shellfish, among other organisms.

Salt marshes are well known for their ability to incorporate inorganic N, often responding with higher plant growth (Valiela et al. 1975). High plant growth and large accumulations of litter allow for substantial immobilization of N directly in plant tissue, microbial biomass and organic matter accumulating during detritus decay (Findlay et al. 2002). A significant amount of research, much of it in the study area, has shown that nutrient additions to salt marshes can change species composition, generally allowing tall-form *Spartina alterniflora* to expand in coverage at the expense of higher marsh species, and that the plant species change has measurable effects on animal consumers. (Sarda et al. 1996 , Levine et al. 1998, Emery et al. 2001). These experiments typically involve levels of N deposition well above typical loading rates, so extrapolating to ambient conditions is difficult. Nonetheless, if the systems are N limited, even small increments in N loading will probably have effects, perhaps subtle, on production and species composition Comparative studies of salt marshes in Rhode Island show a negative relationship between N loading (much of the variation is driven by sewage loads) and plant species richness such that over a range of watershed N loadings (~ 1 to 30 kg N/ha marsh area/yr) species richness declines from roughly 10 to 5 species/transect (Wigand et al. 2003). The relationship is confounded to some degree by a covariation between N load and marsh physical characteristics.

Submerged aquatic vegetation (SAV) is known to be very sensitive to water quality with well-documented effects of eutrophication on water clarity and growth of epiphytes (Dennison et al. 1993, Stevenson et Al. 1993). SAV supports a diversity of invertebrates and fishes and is almost always a key variable in assessments of estuarine "condition" or "health". There have been several attempts to determine critical levels from either cross-system comparisons of N loads and SAV extent (e.g. Short and Burdick 1996). Values known to cause shifts in species composition (usually towards a macroalgal-dominated system) occur at loadings of about 25 kg N/ha/y and possibly less (see Hauxwell et al. 2003). These loadings are probably several-fold higher than loadings 100 years ago and this N is derived from multiple sources with a predominance of wastewater (Roman et al. 2000).

Mercury

It is well known that freshwater wetlands generally serve as areas of high Hg methylation, thus making obligate birds especially vulnerable to high levels of Hg contamination (Evers et al. 2005). The role of saltmarsh habitats in methylating Hg and enhancing its bioavailability (Marvin-DiPasquale et al. 2003), however, is less well documented, but is of increasing concern especially in urban areas. Saltmarsh Sharp-tailed Sparrows are obligate saltmarsh passerines with $\approx$ 95% of their global population breeding within the Northeast. Spending their entire annual cycle in saltmarsh habitats makes them excellent indicators of Hg contamination. Saltmarsh Sharp-tailed Sparrow blood Hg concentrations tend to be higher than other songbirds (Lane and Evers 2006). It is likely that Saltmarsh Sharp-tailed Sparrows have significantly higher blood Hg levels because they feed at a higher trophic level or consume different prey than sympatric Nelson's Sparrows (Shriver et al. in press).

3. Synthesis and Linkages

In the previous section, we summarized the known effects of air pollution, ecosystem type by ecosystem type and pollutant by pollutant. This approach obscures issues and themes that cut across ecosystem boundaries and pollutant types. In this section we explore some integrative themes that emerged from the workshop.

3.1 Intersystem transfer of pollutants

Many of the pollutants we discussed here are mobile and can be transported through a landscape, most often by moving water. This has two principal consequences: (1) an atom of pollutant (S, N or Hg) can have multiple effects as it moves from ecosystem to ecosystem, and (2) “upstream” ecosystems can alter the rate, timing and form of pollutant inputs to “downstream” ecosystems. We cite here several examples of these phenomena.

The nitrogen cascade

An atom of N released from fossil fuel combustion can have multiple effects as it works its way through the environment. First, while in the atmosphere, it is a contributor to the formation of O_3 and photochemical smog, harming both human health and ecosystem function. Next, if it is deposited to a terrestrial ecosystem, it can contribute to N saturation and its attendant effects—principally species compositional shifts and soil acidification. If the atom of N is denitrified in the soil and released to the atmosphere as nitrous oxide, it can contribute to the greenhouse effect. If, instead, it is leached through the soil into surface waters, it contributes to soil and stream acidification. Finally, as the N reaches estuaries and the coastal oceans, it can cause eutrophication, resulting in algal blooms, hypoxia, and other severe disruptions of the aquatic ecosystem. This series of effects of N in the environment has been termed the “nitrogen cascade” by Galloway et al. (2003), and is the reason why N pollution is so dangerous to the environment. It is also the reason why reduction of N emissions is so cost-effective in terms of environmental benefit per dollar spent in emission control costs.

Mercury methylation and transfer

Throughout most of the eastern U.S. Hg deposition is high enough to be dangerous if the deposited Hg is converted to organic forms (by methylation) and incorporated in the food chain. The main factor controlling the exposure to Hg is therefore the rate of methylation, which is a microbial process occurring primarily in anaerobic environments. The concentration of the dangerous methylmercury in surface waters is determined both by methylation in those surface waters and in the surrounding watershed. In particular, presence of wetlands in the watershed increases the delivery of methylmercury to lakes because of the anaerobic soils in wetlands (Grigal 2002). Thus Hg transformations in a terrestrial wetland can affect the rate of Hg bioaccumulation in a lake further downstream.

Aluminum in soils and surface waters

As discussed above, deposition of S and N can acidify soils. Aluminum, an abundant natural component of soils, is in higher concentration in soil water from acidic soils because of its increased solubility in acidic solutions. Aluminum is toxic to roots because it can inhibit the uptake of nutrient cations such as calcium (Cronan and Grigal 1995). The soluble aluminum can also be leached into surface waters where it interferes with respiration of fish by binding to their gills (Cronan and Schofield 1979). Thus, a natural constituent of soils is mobilized by acid pollution and moves downstream to be toxic in an ecosystem some distance from where it originally resided. Moreover, the terrestrial ecosystem regulates the rate and timing of delivery of Al to surface waters by retaining or releasing sulfate and nitrate, the mobile anions that must accompany the Al. Changes in acid deposition rate may not be immediately reflected in proportional changes in Al leaching if S and N are stored in watershed soils and later released.

3.2 Interaction of pollutants

Although we discussed pollutants individually in section 2, in reality they are all present simultaneously in most ecosystems in eastern U.S., and they can interact, sometimes in complex ways. Theses interactions can occur in the formation, deposition, or effects of the pollutants.

An example of an interaction effect on the formation of pollutants is the well-known role of N oxides in the photochemical reactions that form O_3. Thus the emission of one pollutant (nitric oxide) affects the formation of another (O_3). This process is complex and nonlinear, depending on the air temperature and the presence of hydrocarbons and sunlight.

An example of interaction in the deposition of pollutants is the role of ammonia in enhancing deposition of S. As sulfur dioxide gas is deposited to leaf surfaces, it acidifies those surfaces, which tends to slow down the sulfur dioxide deposition process. In the presence of ammonia (a pollutant gas released from agricultural operations) however, the alkaline nature of the ammonia gas counteracts the acidifying effect of the sulfur dioxide, leading to enhanced S deposition (Fowler et al. 2005).

There are many examples of interaction of pollutants after they are deposited to ecosystems. Perhaps the simplest is the additive interaction of S and N deposition on soil acidification. Soil acidification is primarily driven by leaching of anions, which strip the soil of basic cations such as calcium, magnesium and potassium. Both sulfate and nitrate are anions that can cause acidification, and their effect is additive. (However, the situation becomes more complex if we try to predict the leaching of these ions based on their deposition rates, because of the many biological and abiotic processes that control the retention of deposited S and N in ecosystems.)

Another example of the interaction of pollutants is interactive biogeochemical cycling of S and Hg. Deposition of sulfate stimulates the activity of a certain type of anaerobic bacteria that derive energy from the chemical reduction of sulfate. These same bacteria also methylate Hg, producing the organic form of Hg that accumulates in food chains. Thus the deposition of S stimulates the biogeochemical pathway that enhances the toxicity of Hg.

Interactions among pollutants can also be positive. Though not considered here, carbon dioxide is also a combustion-derived air pollutant. Increased concentrations of carbon dioxide tend to cause plants to reduce their stomatal opening, and this may make the plants less sensitive to other gaseous pollutants such as O_3 and sulfur dioxide.

In general, much less research has been done on the interaction of pollutants than on the effects of single pollutants. The interactions are often complex, nonlinear, and poorly understood. Our understanding of the effects of air pollution will not be complete until we understand these interactions in much more detail and can predict their consequences.

3.3 Time lags and legacies

Ecosystems are complex amalgamations of biotic and abiotic materials, some of which respond quickly to environmental change and some of which respond very slowly. If air pollution affects one of the slowly changing components of an ecosystem, the pollutant effect is likely to endure for a long time. This seems obvious, but it bears some elaboration in examples that illustrate the ubiquity and time scale of these effects. For biotic effects, the issue of life span is critical. Effects of air pollution have primarily been demonstrated on short-lived organisms (e.g. aquatic invertebrates, mycorrhizae, grasses) and are much harder to demonstrate on long-lived organisms such as trees. Nonetheless, if air pollution does produce changes in tree species composition, it may take centuries for the ecosystem to recover because of the long generation time of trees. A similar example is the accumulation of S, N and Hg in the organic matter of soils and lake sediments which can have very slow decomposition rates. The accumulated S and N can "bleed" out slowly from the soils over many decades after the cessation of the pollutant input. Recovery from base cation depletion in soils can also be a very long-term process if the geologic substrate is low in these cations. If the pool of exchangeable cations has been depleted by years of acid deposition, the recovery of that pool requires inputs from atmospheric deposition and rock weathering that exceed outputs from leaching and accumulation in plants. The net rates are often low compared to the total pool, so this recovery can take decades or centuries (Driscoll et al. 2001).

Aquatic ecosystems are also subject to lag effects. A prime example is the recovery of biota in acidified surface waters. If acidification has caused local extinction of fish or invertebrates in a pond, and if reduction of pollutant deposition causes chemical recovery of the water quality, there may still be a time lag in the biotic response because dispersal and recovery of the organisms can be slow. Before a planktivorous fish population can be re-established in a formerly acidified pond, first the chemical quality of the water must improve, then the invertebrates that the fish consumes must disperse to and re-establish in the pond, and finally the fish population itself must re-colonize the pond in sufficient numbers to insure a viable population. All of these steps can take time. This problem is compounded by the fact that as acid deposition is reduced, acidification of surface waters tends to become less chronic and more episodic, but often a single acid episode can kill the biota and require the recovery process to start from the beginning again.

3.4 Food web effects

The discussion above leads to consideration of how food webs can control the expression of, and recovery from, pollutant effects. Many examples of this were illustrated at the workshop. In lakes, for example, if a particular invertebrate species is acid-sensitive, the loss of that species as a lake acidifies will have ramifications not only for that species but also for the species that consume it, and likewise through the links of the food web. In addition to direct pollution effects, the biological effects of acidification include altered predator-prey interactions following the decline and disappearance of fish.

Bioaccumulation of Hg also depends strongly on food webs. Mercury toxicity is most often seen in animals of high trophic levels, because Hg concentrations tend to increase with each step up the food chain. Similar food web effects may occur in terrestrial ecosystems, though they are less well documented. For example, the primary hypothesis for the effects of acid deposition on land birds is that soil acidification can reduce the abundance of ground-dwelling invertebrates that some birds require for adequate calcium supply (Hames et al. 2002).

3.5 Interactions between atmospheric deposition and other environmental changes

Just as the various pollutants that we considered interact with one another, their effects also interact with those of other environmental changes that are happening concurrently. It was clear from the discussions at the workshop that this is considered an important and understudied issue, though we did not dwell on it for lack of time. There are myriad examples. Changing temperature affects every biological and chemical process in ecosystems, from respiration of the leaves at the top of a forest canopy to microbial methylation of Hg in the sediment at the bottom of a lake. Microbial processes and activity of poikilothermic (cold-blooded) organisms are expected to be especially sensitive. Examples include the increase in bacterial nitrification with increasing temperature (Murdoch et al. 1998) and the effect of warming temperatures on the seasonal onset of calling in various species of frogs (Gibbs and Breisch 2001). Temperature also effects the duration of ice cover on lakes (Likens 2000), the frost-hardiness of spruce trees subject to acid deposition (DeHayes et al. 1999), and many other aspects of ecosystem function. Temperature and moisture strongly affect the distribution of organisms (e.g. Iverson and Prasad 2000), so the whole biotic assemblage of ecosystems can change as climate shifts. Consequently it is extremely difficult to predict the effects of pollutants on ecosystems, and the recovery of those ecosystems from reduced pollution, against the background of a changing climate.

Invasion of exotic species also interacts with air pollution. Deposition of N may make some habitats more suitable for weedy invasive plants (Howard et al. 2004, Jordan et al. 1997), and may make trees more susceptible to exotic pests (e.g. Latty et al. 2003). Invasive aquatic species can radically change the community composition of surface waters, thus altering the effects of acid deposition on the biota.

Land use changes also influence the effects of air pollution, both by changing the distribution of emission sources and by changing the nature of the receiving ecosystems. Again, there are many examples, and we only list a few here. Most forest ecosystems in the northeastern U.S. are in a phase of regrowth from a period of heavy clearing in the 19th and early 20th centuries. Their successional state strongly affects their retention and processing of N and their species composition. Harvesting of timber and acid deposition both deplete crucial base cations from forest soils (Federer et al. 1989). Land use changes in watersheds affect pollutant loading to aquatic ecosystems; for example, N from atmospheric deposition, agricultural runoff and sewage treatment facilities all contribute to the eutrophication of estuaries (Fisher and Oppenheimer 1991).

In general, while we may understand the effects of pollutants from controlled studies, the concurrent imposition of multiple forms of environmental change—air pollution, climate change, land use change, and exotic species—makes prediction of the responses of ecosystems to changing pollutant loading very challenging.

4. Conclusions

4.1 Air pollution has significant impacts on the biodiversity and functioning of many ecosystem types.

Effects of air pollution are known or likely to occur in all the ecosystems examined (Table 1). Thus, <u>none of these ecosystem types is free of the impacts of air pollution, and most are affected by more than one pollutant.</u> In aquatic ecosystems, effects of acidity, N and Hg on organisms and biogeochemical processes are well documented. Air pollution causes or contributes to acidification of lakes, eutrophication of estuaries and coastal waters, and Hg bioaccumulation in aquatic food webs. In terrestrial ecosystems, the effects of air pollution on biogeochemical cycling are very well documented, and the effects on species composition are less well understood. Nevertheless, there is strong evidence for effects of N deposition on plants in grasslands, alpine areas, and bogs, and for N effects on forest mycorrhizae. Soil acidification is known to be occurring in some northeastern ecosystems and is likely to affect the composition and function of forests in acid-sensitive areas over the long term. Ozone is known to produce reductions in photosynthesis in many terrestrial plant species. <u>Overall, we believe that air pollution is having a serious impact on the biodiversity and function of natural ecosystems of the eastern U.S</u>.

4.2 Air pollution impacts may be subtle but are important

For the most part, the effects of these pollutants are chronic, not acute, at the exposure levels common in the Northeast. Mortality is often observed only at experimentally elevated exposure levels or in combination with other stresses such as drought, freezing or pathogens. The notable exception is the acid/aluminum effects on aquatic organisms, which can be lethal at levels of acidity observed in many surface waters in the region.

The effects of these pollutants are subtle but they can be serious. Changes in plant species composition due to N enrichment may not cause immediate extinctions, but the effects can propagate through a food web to affect many organisms in an ecosystem. Likewise, increasing the N content of a tree may not kill it, but it may make it more susceptible to pests and pathogens that can kill it. Mercury may not kill fish, but may reduce the reproductive success of the loons that eat them. Further, the effects of air pollution can interact with those resulting from other environmental changes, including climate change, land use change, and introduction of exotic species, to produce severe stress on natural ecosystems.

4.3 Critical loads are important but often difficult to identify

One of the goals of this effort was to identify levels of pollution that could help identify areas at risk of damage—the red line and green line values discussed above. While we are aware of the problems with setting simple "critical load" values for complex and heterogeneous ecosystems, we know that identifying red and green line levels would be of considerable value to the conservation community, providing a basis for mapping impacts and thus allowing focus on sensitive areas and specification of target loading levels. We identified these levels where we could, but unfortunately in many cases the lack of specific information rendered us unable to specify a particular value (Table 2). Often we were able to say with high or moderate certainty that impacts of a pollutant are occurring, even though we did not have sufficient information to identify a critical exposure level.

4.4 There are major gaps in our knowledge

Our discussions exposed major gaps in knowledge that will require much future research to fill. Among these gaps are:

- The effects of S and N deposition on species composition of terrestrial ecosystems, especially forests
- Controls on Hg methylation in lakes, wetlands, terrestrial ecosystems
- Atmospheric dry deposition rates of pollutants, especially Hg
- Exposure and effects of Hg on organisms in terrestrial ecosystems
- Base cation weathering rates in soils
- Effects of O_3 on grassland, wetland, and alpine plants and on wild animals
- Interactive effects of pollutants
- Factors controlling recovery rates from acidic deposition in lakes, streams and soils

Filling these knowledge gaps will require a sustained investment in research. Unfortunately, funding for air pollution research (other than greenhouse gases) has declined precipitously since the 1980s, and shows no sign of increasing in the foreseeable future. This puts us in a precarious situation of knowing enough to be very concerned about the effects of air pollution on natural ecosystems, knowing that there is much that we don't understand, and being unable to improve that situation for lack of funding.

Table 1. *Level of certainty that air pollutants result in significant negative impacts on a selected biodiversity conservation target groups based on expert review. Level of certainty was divided into four categories for ease of comparison across target and pollutant groups: known, likely, unlikely and unknown. Known = Studies documenting impacts in the region are known. Likely = Studies documenting impacts are known - but none documented for this region; and/or plausible mechanism for impacts identified, but no specific studies to confirm the plausible link were identified.*
Unlikely = Plausible links resulting in negative impacts are not supported at this time within or outside this region. Unknown = No applicable studies documenting impacts or lack of impacts were identified within or outside this region.

	Air pollutants and their products				
Conservation Target Groups	**Nitrogen**	**Sulfur**	**Ozone**	**Mercury**	**Percent (number) of air pollutants with known or likely impacts**
Alpine and subalpine ecosystems	Likely	Likely	Unknown	Unknown	50% (2)
Forests (both upland and wetland types)	Likely	Known	Known	Likely	100% (4)
Bogs and fens	Likely	Known	Likely	Likely	100% (4)
Grasslands	Likely	Unknown	Unknown	Unknown	25% (1)
High gradient headwater streams	Known	Known	Unlikely	Likely	75% (3)
Lakes and ponds	Known	Known	Unlikely	Known	75% (3)
Low gradient rivers	Likely*	Unlikely	Unlikely	Likely	50% (2)
Estuaries, bays, and saltmarshes	Likely*	Unlikely	Unlikely	Likely	50% (2)
Percent (number) of target groups with known or likely impacts	100% (8)	63% (5)	25% (2)	75% (6)	

**Nitrogen eutrophication effects are known for these systems. Although atmospheric nitrogen deposition is often a significant contributor to the total nitrogen loading in these systems, it is usually not the major source of nitrogen.*

One particular type of research is especially crucial and deserves special mention. The U.S. does not have an integrated biological monitoring system. Without monitoring data, we are in many cases unable to say if populations are declining, or, if pollution is reduced, if they are recovering. Chemical monitoring of precipitation and surface waters is sparse but has been used very effectively in policy formulation (Lovett et al. in press). Biological monitoring is primarily an ad-hoc activity by individual scientists who try to sustain the necessary long-term funding. We need an equivalent emphasis on biological monitoring to track the status of the biological resources of the nation.

Table 2. *Compilation of red line and green line values for the four pollutants and eight Conservation Target Groups. The green line (values in green in the chart) is the deposition or exposure level below which there is high certainty that no adverse impacts will occur, and the red line (values in red in the chart) is the deposition or exposure level above which there is high certainty of adverse impacts on at least some component of the system. "U" indicates that red and or green line values are unknown, "Model" indicates cases in which critical loads can be calculated more accurately by existing models that incorporate characteristics of specific sites. Gray shading indicates cells in which effects are unlikely (see Table 1).*

	Air pollutants and their products			
Conservation Target Groups	**Nitrogen (kg N/ha/y)**	**Sulfur (kg S/ha/y)**	**Ozone (Sum06 index, ppm-hr)**	**Mercury**
Alpine and subalpine ecosystems	4/U	U/U	U/U	U/U
Bogs and fens	U/5	U/U	U/U	U/U
Forests	5/8	Model	U/8-12	U/U
Grasslands	5/U	U/U	U/U	U/U
High gradient headwater streams	U/U	Model		U/U
Lakes and ponds	U/U	Model		U/U
Low gradient rivers	U/U			U/U
Estuaries, bays, and saltmarshes	U/U			U/U

4.5 Air pollution impacts are most likely being underestimated

It is apparent from this review that we currently have limited understanding of some potential effects of specific air pollutants (e.g. effects of N deposition on alpine ecosystems, effects of O_3 on wildlife), the strength of interactions among pollutants, the extent and implications of time lags, the relative amount of primary and secondary food web effects, and nature of interactions with other environmental threats. Unfortunately, there are many areas of research that have been largely discontinued (e.g., ground-level O_3 impacts to plants), and other areas of inquiry that illustrate impacts are much more pervasive than previously thought (e.g., Hg). Taken together, it seems likely that our current knowledge, as summarized in this report, represents an underestimation of the problem.

5. Implications for Conservation

The impacts of air pollution on humans and the natural world have been known for a long time. However, in most cases these impacts have been studied as smaller pieces of a larger puzzle – such as a single pollutant's impact to an individual species or ecosystem. Foe effective conservation of biodiversity we must look across multiple species and ecosystems and assess the scope and severity of the threat presented by multiple pollutants at the same time This report attempts, for the first time to our knowledge, to look broadly at the impacts of air pollutants to those species, ecological communities, and large-scale ecosystems that are the focus of biodiversity conservation. Our assessment revealed that in the Northeast and Mid-Atlantic regions, the impacts are significant and widespread across many ecosystems types, disrupting the functioning of many of these ecosystems to varying extents. Impacts to humans have been the driving force behind most air quality regulation in the United States (NRC 2004). However we believe it is time to consider the impacts of air pollution on biodiversity conservation, to protect the wildlife species at risk, the ecosystems that provide valuable services to our society, and the centuries of personal and financial investments made to preserve these ecosystems for humans and wildlife.

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Appendix 1. List of attendees at TNC/IES workshop

TNC = The Nature Conservancy, IES = Institute of Ecosystem Studies

Aquatic Group

Linda Green	U. Virginia
Bill Brown	TNC
Chris Bruce	TNC
Art Bulger	U. Virginia
Celia Chen	Dartmouth College
Jack Cosby	U. Virginia
Chuck DeCurtis	TNC
Judy Dunscomb	TNC
Stuart Findlay	IES
Gene Likens	IES
Winsor Lowe	IES
Bill Shaw	Independent
Mark Smith	TNC
Dave Strayer	IES
Tim Tear	TNC

Terrestrial Group

Michelle Brown	TNC
Charlie Canham	IES
Nancy Dise	Manchester Metropolitan U.
Charley Driscoll	Syracuse U.
Aaron Ellison	Harvard U.
Dave Evers	Biodiversity Res. Inst.
Charles Ferree	TNC
Melany Fisk	Appalachian State U.
Stefan Hames	Cornell U.
Jerry Jenkins	Independent
Robert Kohut	Boyce Thompson Inst.
Gary Lovett	IES
Frank Lowenstein	TNC
Linda Pardo	USDA Forest Service
Kathie Weathers	IES
Rick Webb	U. Virginia
Alan White	TNC

Appendix 2. Plant Species Sensitive to Ozone

Plant species on National Park Service or Fish and Wildlife Service properties that are considered sensitive to ozone. Species considered sensitive are those that typically exhibit foliar injury at or near ambient ozone concentrations in fumigation chambers and/or are species for which ozone foliar injury symptoms in the field have been documented by more than one observer (National Park Service 2003).

Species	Common name
Aesculus octandra	Yellow buckeye
Ailanthus altissima	Tree-of-heaven
Alnus rubra	Red alder
Alnus rugosa	Speckled alder
Amelanchier alnifolia	Saskatoon serviceberry
Apios americana	Groundnut
Apocynum androsaemifolium	Spreading dogbane
Apocynum cannabinum	Dogbane, Indian
Artemisia douglasiana	Mugwort
Artemisia ludoviciana	Silver wormwood
Asclepias exaltata	Tall milkweed
Asclepias incarnata	Swamp milkweed
Asclepias syriaca	Common milkweed
Aster acuminatus	Whorled aster
Aster macrophyllus	Big-leaf aster
Cercis canadensis	Redbud
Clematis virginiana	Virgin's bower
Corylus americana	American hazelnut
Eupatorium rugosum	White snakeroot
Fraxinus americana	White ash
Fraxinus pennsylvanica	Green ash
Gaylussacia baccata	Black huckleberry
Krigia montana	Mountain dandelion
Liquidambar styraciflua	Sweetgum
Liriodendron tulipifera	Yellow-poplar
Lyonia ligustrina	Maleberry
Oenothera elata	Evening primrose
Parthenocissus quinquefolia	Virginia creeper
Philadelphus coronarius	Sweet mock
Physocarpus capitatus	Ninebark
Physocarpus malvaceus	Pacific ninebark

Pinus banksiana	Jack pine
*Pinus jeffreyi***	Jeffrey pine
*Pinus ponderosa****	Ponderosa pine
Pinus pungens	Table-mountain pine
Pinus radiata	Monterey pine
Pinus rigida	Pitch pine
Pinus taeda	Loblolly pine
Pinus virginiana	Virginia pine
Platanus occidentalis	American sycamore
Populus tremuloides	Quaking aspen
Prunus serotina	Black cherry
Prunus virginiana	Choke cherry
Quercus kelloggii	California black
Robinia pseudoacacia	Black locust
Rhus copallina	Winged sumac
Rhus trilobata	Skunkbush
Rubus allegheniensis	Allegheny blackberry
Rubus canadensis	Thornless blackberry
Rubus cuneifolius	Sand blackberry
Rubus parviflorus	Thimbleberry
Rudbeckia laciniata	Cutleaf coneflower
Salix gooddingii	Gooding’s willow
Salix scouleriana	Scouler’s willow
Sambucus canadensis	American elder
Sambucus mexicana	Blue elderberry
Sambucus racemosa	Red elderberry
Sapium sebiferum	Chinese tallowtree
Sassafras albidum	Sassafras
Solidago altissima	Goldenrod
Spartina alterniflora	Smooth cordgrass
Symphoricarpos albus	Common snowberry
Vaccinium membranaceum	Huckleberry
Verbesina occidentalis	Crownbeard
Vitis labrusca	Northern fox
Vitis vinifera	European wine

** *P. jeffreyi* and *P. ponderosa* may hybridize, making identification difficult.
*** *P. ponderosa* var. *ponderosa* is the more sensitive variety; *P. ponderosa* var. *scopulorum* is not as sensitive