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Effects of Nitrogen Deposition and Empirical Nitrogen Critical Loads for Ecoregions of the United States

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Abstract

Human activity in the last century has led to a significant increase in nitrogen (N) emissions and atmospheric deposition. This N deposition has reached a level that has caused or is likely to cause alterations to the structure and function of many ecosystems across the United States. One approach for quantifying the deposition of pollution that would be harmful to ecosystems is the determination of critical loads. A critical load is defined as the input of a pollutant below which no detrimental ecological effects occur over the long-term according to present knowledge.

The objectives of this project were to synthesize current research relating atmospheric N deposition to effects on terrestrial and freshwater ecosystems in the United States, and to estimate associated empirical N critical loads. The receptors considered included freshwater diatoms, mycorrhizal fungi, lichens, bryophytes, herbaceous plants, shrubs, and trees. Ecosystem impacts included: (1) biogeochemical responses and (2) individual species, population, and community responses. Biogeochemical responses included increased N mineralization and nitrification (and N availability for plant and microbial uptake), increased gaseous N losses (ammonia volatilization, nitric and nitrous oxide from nitrification and denitrification), and increased N leaching. Individual species, population, and community responses included increased tissue N, physiological and nutrient imbalances, increased growth, altered root:shoot ratios, increased susceptibility to secondary stresses, altered fire regime, shifts in competitive interactions and community composition, changes in species richness and other measures of biodiversity, and increases in invasive species.

The range of critical loads for nutrient N reported for U.S. ecoregions, inland surface waters, and freshwater wetlands is 1-39 kg N ha^{-1} y^{-1}, spanning the range of N deposition observed over most of the country. The empirical critical loads for N tend to increase in the following sequence for different life forms: diatoms, lichens and bryophytes, mycorrhizal fungi, herbaceous plants and shrubs, trees.

The critical load approach is an ecosystem assessment tool with great potential to simplify complex scientific information and communicate effectively with the policy community and the public. This synthesis represents the first comprehensive assessment of empirical critical loads of N for major ecoregions across the United States.

Key words: air pollution, atmospheric N deposition, critical nitrogen loads, biodiversity, nitrate leaching, nitrogen saturation, plant nitrogen cycling, natural resource protection, vegetation type conversion

1. Introduction

1.1 Effects of Nitrogen Deposition on Ecosystems

Human activity in the last century has led to a significant increase in nitrogen (N) emissions and deposition (Galloway et al. 2003). Because of past, and, in some regions, continuing increases in emissions (Nilles and Conley 2001, Lehmann et al. 2005), N deposition has reached a level that has caused or is likely to cause alterations in many ecosystems across the United States. In some ecoregions, the impact of N deposition has been severe, driving altered N cycling and biodiversity. Indicators of altered N cycling include increased N mineralization, nitrification, and nitrate (NO_3^-) leaching rates, as well as elevated plant tissue N concentration. The eventual outcome of increases in these processes can be N saturation, the series of ecosystem changes that occur as available N exceeds plant and microbial demand (Aber et al. 1989, 1998).

As N availability increases there are progressive changes in biotic community structure and composition. For example, in the Mediterranean California ecoregion native plant species in some ecosystems have been replaced by invasive species more productive under elevated N deposition (Weiss 1999, Yoshida and Allen 2004, Fenn et al. 2010, Rao and Allen 2010, Rao et al. 2010). Such shifts in plant community composition and species richness can lead to overall losses in biodiversity and further impair particular threatened or endangered species (Stevens et al. 2004), as has occurred for the checkerspot butterfly (Weiss 1999).

1.2 Critical Loads Definition and Previous Uses

One method for evaluating potential impacts of air pollution on ecosystems is critical loads. The critical load is defined as *the deposition of a pollutant below which no detrimental ecological effect occurs over the long term according to present knowledge* (UBA 2004). Critical loads have been used broadly in Europe (Posch et al. 1995; Posch et al. 2001) as a tool in the process of negotiating decreases in air pollution. Critical loads have been more widely applied in Canada than in the United States; critical loads have been published for upland forests (Ouimet et al. 2006) and lakes (Dupont et al. 2005) in eastern Canada and included in European assessments (Hettelingh et al. 2008). In the United States (US), critical loads have been calculated for specific regions such as the Northeast (NEC/ECP 2003, Dupont et al. 2005), California (Fenn et al. 2003a, b, 2008), and Colorado (Williams and Tonnessen 2000, Baron 2006, Bowman et al. 2006), and, at a coarse scale, the conterminous United States (McNulty et al. 2007).

Despite relatively limited use in the US, the critical loads approach is being explored at Federal, state, and international levels as an ecosystem assessment tool with great potential to simplify complex scientific information and communicate effectively with the policy community and the public (Porter et al. 2005, Burns et al. 2008). The critical loads approach can provide a useful lens through which to assess the results of current policies and programs and to evaluate the potential ecosystem-protection value of proposed policy options. Critical loads are used by policymakers to inform the process of setting emissions standards, for assessing emissions control programs, and by natural resource managers as a tool to evaluate the potential impact of new pollution sources (Burns et al. 2008, Environment Canada 2008, Lovett et al. 2009, Porter et al. 2005, US EPA 2007, US EPA 2008). Policymakers and resource managers have used critical loads to establish benchmarks for resource protection and to communicate the impacts of deposition on natural resource conditions.

Critical loads have been determined most frequently in the United States for effects of acidity (NEG/ECP 2003, Sullivan et al. 2005), but are also being increasingly used in evaluating impacts of N deposition on ecosystems in terms of excess nutrient N availability, also known as eutrophication (Fenn et al. 2008, 2010). Empirical critical loads are determined from observations of detrimental responses of an ecosystem or ecosystem component to a given, observed N deposition input (Pardo 2010). This level of N deposition is set as the critical load and extrapolated to other similar ecosystems. Empirical critical loads for N are based on measurements from gradient studies, field experiments, or observations (Bobbink et al. 1992, 2003, 2010). Other approaches include steady-state mass balance modeling (UBA 2004) and dynamic modeling (de Vries et al. 2010, Slootweg et al. 2007). Steady-state mass balance modeling is based on estimating the net loss or accumulation of nitrogen inputs and outputs over the long term under the assumption that the ecosystem is at steady-state with respect to N inputs. Dynamic models also use a mass balance approach, but consider time-dependent processes and require detailed data sets for parameterization and testing (Belyazid et al. 2006, de Vries et al. 2007).

The empirical approach has the advantage that it is based on measurable physical evidence of ecosystem responses to N inputs; however, the method will overestimate the critical load (set it too high) if the system has not reached steady state, i.e., if a similar response would occur at a lower deposition level over a longer period because of cumulative dose effects. The only way to determine this empirically is to study the system over a longer time period. Steady-state mass balance approaches have the advantage over the empirical approach of being less likely to overestimate the critical load. In the United States, the uncertainty associated with steady-state mass balance approaches is high because data are not available to quantify the terms in the mass balance equations accurately. Indeed, our empirical critical loads synthesis may be useful in defining the acceptable critical thresholds for application in steady-state mass balance critical loads calculations.

Dynamic models for critical loads of N in the United States have been applied on a limited basis (Wu and Driscoll 2010). For dynamic modeling of nutrient N critical loads, empirical critical loads and other response data are essential: the current data for the United States on ecosystem N responses have not been sufficient to develop, parameterize, and test dynamic models that characterize the range of responses that nutrient N has on ecosystem structure and function (for example, changes in biodiversity). Dynamic models are necessary in order to depict the time-dependent response of ecosystems to different levels of N deposition, but the models are only as good as the data upon which they are based. Thus, empirical critical loads currently provide a uniquely valuable approach for assessing the risk of harm to ecosystems in the United States. This synthesis is a first step towards that end by indicating which data are available for key ecosystems and where dynamic modeling could most profitably be applied in the United States after further data collection.

1.3 Objectives

Our recent publication (Pardo et al. in press e) synthesized current research relating atmospheric N deposition to effects on terrestrial and freshwater ecosystems in the United States and quantified empirical critical loads for atmospheric N deposition, with one chapter devoted to each of twelve major ecoregions. Our objectives for this paper were to synthesize empirical critical loads for N reported for all the ecoregions of the United States, compare critical loads by life form or ecosystem compartment (mycorrhizal fungi, lichens, herbaceous species, and trees/forest ecosystems) across all ecoregions, discuss the abiotic and biotic factors that affect the critical loads, and compare critical loads in the United States to those for similar ecoregions/ecosystems in Europe. Finally, we discuss the significance of these findings, and the highest priorities for future research.

2. Approach

For this synthesis, we reviewed studies of responses to N inputs (Pardo et al. in press e) for U.S. ecoregions as defined by the Commission for Environmental Cooperation (CEC) Level I ecoregions map for North America (CEC 1997; Figure 1; Robin-Abbott and Pardo in press). We identified the receptor of concern (organism or ecosystem compartment), the response of concern, the critical threshold value for that response, and the criteria for setting the critical load and extrapolating the critical load to other sites or regions. These methods are described in detail in Pardo et al. (in press d).

The receptors evaluated included freshwater diatoms, mycorrhizal fungi and other soil microbes, lichenized fungi (henceforth lichens), bryophytes, herbaceous plants, shrubs, and trees. Ecosystem impacts included: (1) biogeochemical responses and (2) individual species, population, and community responses. Biogeochemical responses included increased N mineralization and nitrification (and N availability for plant and microbial uptake), increased gaseous N losses (ammonia volatilization, nitrous oxide from nitrification and denitrification), and increased N leaching. Individual species, population and community responses included increased tissue N concentration, physiological and nutrient imbalances, altered growth, altered root:shoot ratios, increased susceptibility to secondary stresses, altered fire regimes, changes in t species abundance, shifts in competitive interactions and community composition (including shifts within and across diatom, bacterial, fungal, or plant taxa groups), and changes in species richness and other measures of biodiversity and increases in invasive species.

We considered N addition, N deposition gradient, and long-term monitoring studies in order to evaluate ecosystem response to N deposition inputs. Most of these studies were not designed to quantify critical loads, which presented some challenges. We afforded greater weight to long-term fertilization studies (5-10 years) than to short-term studies, and single-dose forest fertilization studies exceeding 50 kg N ha^{-1} were generally not considered, although lower dose short-term studies were considered when other observations were limited. When studies were designed in order to determine critical loads, the addition levels generally depicted modest increases above ambient deposition; and were more likely to have smaller increments between the treatment levels; multiple (3+) treatment levels; and, ideally, treatments spanning the critical load. In such cases, estimates of the critical load are made with greater certainty than with other approaches. Nitrogen gradient studies implicitly include longer-term exposure to pollutants and therefore are more likely than N manipulation studies to depict conditions that are near steady-state with respect to ambient N inputs. Long-term monitoring studies sometimes offer the opportunity to observe changes over time in response to increasing or elevated N deposition inputs. We estimated critical loads based on data from >3200 sites (Figure 2).

In general, we determined the critical load based on the observed response pattern. In some cases, there was a clear dose-response relationship where the response changed above a certain threshold. A critical threshold is the value of a response parameter which represents an unacceptable condition. The critical threshold is also referred to as the critical limit (UBA 2004). In other cases, when response to increasing N was more linear, we estimated the “pristine” state of N deposition and the deposition that corresponded to a departure from that state. The criteria for setting critical loads are discussed in detail in Pardo et al. (in press d).

2.1 Deposition

Total N emissions have increased significantly since the 1950s (Galloway 1998, Galloway et al. 2003). As S deposition has declined in response to regulation, the rate of N deposition relative to S deposition has increased since the 1980s (Driscoll et al. 2003) followed by a general decrease in NO_x emissions from electric utilities since the early 2000s. More recently, the relative proportion of NH_x (NH_4^+ + NH_3) to NO_x (NO + NO_2) emissions has also increased for many areas of the United States (Kelly et al. 2005, Lehmann et al. 2005). Deposition at sites included in this analysis (Weathers and Lynch in press) was quantified by the Community Multiscale Air Quality (CMAQ) model v.4.3 (hereafter CMAQ 2001 model; which uses 2001 reported data) (Byun and Ching 1999, Byun and Schere 2006) simulations of wet + dry deposition of N species (Figure 2) and was used to calculate exceedance. Exceedance of the critical load is defined as the current deposition minus the critical load; when exceedance is greater than zero, the ecosystem is susceptible to harmful ecological effects. Exceedance is useful in communicating the extent of risk to ecosystems under current and future deposition scenarios.

We rarely had data to distinguish biotic or ecosystem response to reduced forms (NH_x) versus oxidized forms (NO_y) of N. There is some evidence that for some species, reduced forms of N may have more substantial impacts than oxidized N (Bobbink et al. 2003; Kleijn et al. 2008). This differential response may be due to direct toxicity of gaseous ammonia ($NH_{3;}$ Krupa 2003) or the toxicity to some plant species (or their mycorrhizal fungi) of high levels of ammonium (NH_4^+) in soil, but can also be a result of soil acidification which occurs when NH_4^+ is nitrified (van den Berg et al. 2005). Lichens in the California Central Valley (Jovan and McCune 2005) have been shown to be particularly sensitive to total reduced N (i.e. NH_x). Across

Europe, lichens responded particularly to NH_3 and to a lesser extent NH_4^+ (Cape et al. 2009a, Sutton et al. 2009). Much of the research on NH_3 effects evaluates the response to concentration of NH_3 in air, which would be used for determining the critical level of NH_3 rather than the critical load. This is an important distinction: the critical level is the atmospheric concentration above which adverse effects to sensitive vegetation may occur (UBA 2004). Differences in uptake rates and preference for NH_4^+ versus NO_3^- across different plant taxa (Falkengren-Grerup 1995, McKane et al. 2002, Miller and Bowman 2002, Nordin et al. 2006) lead to differences in sensitivity to NH_x (Krupa 2003) and NO_y . Importantly, not all species are more sensitive to NH_x than NO_y; these responses vary by species and functional type. Some species are more sensitive to increases in NO_y, as was demonstrated for boreal forests (Nordin et al. 2006).

In order to quantify the critical load, we generally used the deposition reported in the publication or, when that was not available, we used modeled deposition (e.g., CMAQ, ClimCalc (Ollinger et al. 1993), National Atmospheric Deposition Program (NADP; NADP 2009) maps). The different forms of N deposition included in this assessment were: wet, bulk, wet+dry, throughfall, and total (wet+dry+cloud/fog) inorganic N deposition. Total N deposition was considered the most appropriate value to use in evaluating ecosystem responses; however, in many studies this information is not available. Throughfall N is generally considered a good surrogate for total N deposition, because it typically does not underestimate total N inputs as much as wet or bulk deposition. However, because of the potential for canopy uptake of N, throughfall is usually considered as a lower-bound estimate of total N deposition. None of the studies included reported inputs of organic N, so this report focuses on responses to inputs of inorganic N.

The accuracy of the atmospheric N deposition influences the accuracy of the critical load and exceedance estimates. Several factors contribute to uncertainty in N deposition estimates, including the difficulty of quantifying dry deposition of nitrogenous gases and particles to complex surfaces, and sparse data, particularly for arid, highly heterogeneous terrain (e.g., mountains), sites with high snowfall or high cloudwater/fog deposition, where N deposition tends to be underestimated. Deposition models cannot account for these kinds of heterogeneity (e.g., Weathers et al. 2006) because the spatial scale (grid size) is typically too coarse to capture topographic and other local influences. These issues are discussed in detail elsewhere (Weathers et al. 2006, Fenn et al. 2008, Weathers and Lynch in press). When more accurate and precise N deposition estimates become available, the data presented in this study may be re-evaluated in order to refine the critical loads estimates.

3. Results and Discussion

The range of critical loads for nutrient N reported for the United States ecoregions, inland surface waters, and freshwater wetlands is 1-39 kg N ha^{-1} y^{-1} (Table 1). This broad range spans the range of N deposition observed over most of the country (see Weathers and Lynch in press). For coastal wetlands, critical loads are between 50-400 kg N ha^{-1} y^{-1} The number of locations for which ecosystem response data were available (Figure 2) for an ecoregion is variable, which impacts the level of certainty of the empirical critical loads estimates. The basis for the critical loads values (Tables 1, 2) is discussed in detail in Pardo et al. (in press e).

3.1 Comparison of Critical Load by Receptor across Ecoregions

Because N deposition varies considerably by region and the critical load varies both by region and receptor, we present the critical loads and likely risk of exceedance by receptor.

3.1.1 Mycorrhizal fungi

Background

Mycorrhizal fungi reside at the interface between host plants and soils, exchanging soil resources, especially nutrients, with host plants in exchange for photosynthates (carbon compound). Due to this important and unique ecological niche, mycorrhizal fungi are at particular risk due to changes in either the soil environment or host carbon allocation.

Response to N

Nitrogen deposition adversely affects mycorrhizal fungi (1) by causing decreased belowground C allocation by hosts and increased N uptake and associated metabolic costs (Wallander 1995) and (2) via soil chemical changes associated with eutrophication and acidification. There are two major groups of mycorrhizal fungi that are evolutionarily and ecologically distinct: arbuscular mycorrhizal fungi (AMF) and ectomycorrhizal fungi (EMF). Under sufficiently high N inputs, the progressive effect of elevated N is an early decline of sporocarp (reproductive structure) production for EMF and spore production for AMF, and subsequent decline in biological diversity and loss of taxa adapted to N-poor environments or sensitive to acidification (Lilleskov 2005). Sporocarp and spore production appears to be especially sensitive to N deposition, often declining before the communities on root tips have been substantially altered, presumably because sporocarps and spores are at the end of the carbon flux pathway from hosts.

Of the two plant-fungal symbioses examined here, mycorrhizal fungi appear to be less sensitive to N deposition than lichens (Tables 3 and 4), presumably because the soil environment buffers these soil fungi from some of the immediate impacts of N deposition, whereas lichens are directly exposed to atmospheric N pollution. Lichens have an advantage as indicators when compared with mycorrhizal fungi because they can be relatively easily inventoried. However, the critical role of mycorrhizal fungi as root symbionts central to plant nutrition and belowground production, as repositories of a large part of the eukaryote diversity in forests, as major components of forest food webs, and as non-timber forest products of high economic value (edible sporocarps) (Amaranthus 1998) provides sufficient impetus to improve our understanding of their response to N deposition.

Critical loads

We reviewed empirical studies on mycorrhizal fungal response to N inputs as the basis for determining empirical critical loads for the United States (Table 3, Figure 3.a). Despite the sparse data, it is clear that N deposition sufficient to elevate inorganic N, and especially NO_3^-, availability in soils can have measurable effects on mycorrhizal fungi. The data for EMF indicate that N deposition to N-limited conifer forests in the range of 5-10 kg ha^{-1} yr^{-1} can significantly alter community structure and composition and decrease species richness (Dighton et al. 2004, Lilleskov 1999, Lilleskov et al. 2001, 2002, 2008). Similarly, the data for AMF suggest N deposition levels of 7.8-12 kg ha^{-1} yr^{-1} can lead to community changes, declines in spore abundance and root colonization, and changes in community function, based on re-analysis of data from Egerton-Warburton et al. (2001) combined with N deposition data and decreases in fungal abundance (van Diepen et al. 2007, van Diepen et al. 2008) and declines in fungal activity (Egerton-Warburton, unpublished data). The actual threshold for N effects on AMF could be even lower, because high background deposition precludes consideration of sites receiving deposition at or near pre-industrial levels. Therefore, our provisional expert judgment is that critical loads for mycorrhizal diversity for sensitive ecosystem types are 5-10 kg ha^{-1} yr^{-1}. The uncertainty of this estimate is high, because few studies have been conducted at low N deposition to further refine the critical load. The critical load of N for mycorrhizal fungi, when community change occurs, is often on the order of current N deposition and thus is exceeded across most of the eastern and northern forests and in regions downwind of agricultural and urban emissions in the West (Figure 3.b). The uncertainty associated with the exceedance, like that for the CL, is high.

3.1.2 Lichens and Bryophytes

Background

Lichens and bryophytes make substantial contributions to biodiversity. About 4,100 lichens and 2,300 bryophytes are known from North America north of Mexico—approximately one forth of vascular plant diversity, which is about 26,600 species (USDA, NRCS 2009). Therefore, critical loads protective of the sensitive lichens and bryophytes help protect biological diversity.

Responses to N

Lichens and bryophytes are among the most sensitive bioindicators of N in terrestrial ecosystems (Blett et al. 2003, Bobbink et al. 2003, Fenn et al. 2003a, Glavich and Geiser 2008). Unlike vascular plants, lichens and bryophytes lack specialized tissues to mediate the entry or loss of water and gases (e.g., waxy epidermis, guard cells, root steele). Thus, they rapidly hydrate and absorb gases, water, and dissolved nutrients during high humidity or precipitation events. However, they dehydrate to a metabolically inactive state quickly as well, making them slow growing and vulnerable to contaminant accumulation. Consequently, the implementation of lichen or bryophyte-derived critical loads may prevent undesired impacts to much of the broader forest ecosystem (McCune et al. 2007). In some cases, alteration of lichen community composition may signal the beginning of a cascade of changes in ecosystem N cycling, which may dramatically alter the structure or function of the ecosystem as a whole. In many cases, changes in lichens may have implications beyond the lichen community. In other cases, alterations in the lichen community may have little impact on the overall structure and function of the ecosystem. It can be difficult to know, at the outset, whether the ultimate consequences of changes indicated by alterations to the lichen community will be large or small for the overall ecosystem over the long term.

Lichens and bryophytes can play important roles in ecosystems. Species of epiphytic lichens in wet and mesic forests that are most sensitive to N (i.e., the large pendant and foliose species) play important ecological roles that are not duplicated by the nitrophytic (i.e., nitrogen tolerant) species that may replace them. Dominant regional oligotrophs (e.g. *Alectoria*, *Bryoria*, *Lobaria*, *Ramalina*, *Usnea*) comprise the bulk of lichen biomass in old-growth forests, contribute to nutrient cycling through N_2 fixation, and are used for nesting material, essential winter forage for rodents and ungulates, and invertebrate habitat (McCune and Geiser, 2009). Storage of water and atmospheric nutrients by these lichen genera and epiphytic bryophytes moderates humidity and provides a slow release system of essential plant nutrients to the soil (Boonpragob et al. 1989, Cornelissen et al. 2007, Knops et al. 1991, Pypker 2004). In the tundra, lichens and bryophytes represent a significant portion of the biomass, and reindeer lichens are a vital link in the short arctic food chain (Kytöviita and Crittenden 2007). Mosses comprise the bulk of the biomass of the extensive boreal peatlands. In the desert, together with other microbiota, lichens and bryophytes form cryptogamic mats important to soil stabilization and fertility.

Critical loads

The critical loads estimated (Pardo et al. in press e) for lichens range from 1-9 kg N ha^{-1} yr^{-1} (Table 4, Figure 4.a). Although the reported range of critical loads is not as large as the ranges for forests or herbs, the certainty associated with these estimates varies considerably. This is partially because of differences in sampling scheme and intensity. For example in the Pacific Northwest, lichen communities were assessed intensively across wide environmental gradients spanning low to high N deposition on a fine grid over time, yielding highly reliable critical N load estimates (Geiser and Neitlich 2007, Jovan 2008) whereas assessments in the eastern United States are more problematic due to historical and contemporary S and acid deposition. In such cases, where historical information necessary to identify a “pristine” or “clean” state is lacking, it is more difficult to determine the critical load, and the resulting confidence associated with the critical load is low. The critical load of N for lichens, based on the shift in community composition when eutrophs dominate at the expense of oligotrophs, is on the order of current N deposition and thus is exceeded across most of the eastern and northern forests and in many areas downwind of agricultural and urban emissions or at high elevation in the West (Figure 4.b). The uncertainty associated with the exceedance, like that for the CL, is low for the Marine West Coast and Northwest Forested Mountains ecoregions, but high elsewhere.

Studies in the Pacific Northwest demonstrate that increasing precipitation allows lichens to tolerate higher N deposition (Geiser and Neitlich 2007, Jovan 2008, Geiser at al. 2010, Pardo et al. in press d). The importance of precipitation volume in the critical load for lichens is likely due to the direct influence of N concentration on lichens, that is, the concentrations of N compounds to which lichens are exposed are more important than total loading (Geiser et al. 2010). If such simple models could be tested and confirmed in other regions of the country, the confidence in the critical loads in those regions would improve.

3.1.3 Herbaceous Species and Shrubs

Background

Herbaceous species and shrubs (Table 5, Figure 5) are found in grasslands, shrublands, forests, deserts, and wetlands and comprise the majority of the roughly the 26,600 vascular plant species found in North America north of Mexico (USDA, NRCS 2009).

Response to N

Herbaceous species and some shrubs appear intermediate between cryptogram and tree species in their sensitivity to N deposition, due to specialized tissues that mediate the entry or loss of water and gases compared with cryptograms, and rapid growth rates, shallow rooting systems, and often shorter lifespan compared with trees. Thus, herbaceous species in a forest understory will likely respond more rapidly to changes in N deposition and to a greater degree than the trees that they coexist with. Herbaceous species in alpine or tundra environments will respond later and to a lesser degree than the cryptograms that they coexist with. Herbaceous plants clearly play an important role in those ecosystems in which they are the dominant primary producers (e.g., grasslands, shrublands). In forests, however, the role of the herbaceous community in ecosystem function has a significance that is disproportionate to its low relative biomass. For example, although they represent only ~0.2 percent of standing above-ground biomass, herbaceous understory species produce >15 percent of forest litter biomass and comprise up to 90 percent of forest plant biodiversity, including endangered or threatened species (Gilliam 2007).

Critical loads

The range of critical loads for N for herbaceous species and shrubs across all ecoregions is 3-33 kg N ha^{-1} yr^{-1} (Table 5, Figure 5). Although this range is broader than those for lichens or mycorrhizal fungi, many of the critical loads for herbaceous species fall into the range of 5-15 kg N ha^{-1} yr^{-1}. The uncertainty of these estimates is moderate. The shorter lifespan of some herbaceous species results in a more rapid response to N addition. This is especially relevant for perennials with little N storage or annuals. In grasslands, for example, elevated N deposition often leads to a rapid (1-10 years) increase in herbaceous production and a shift in biomass allocation towards more aboveground tissue. This often decreases light levels at ground surface and decreases the numbers of plant species, primarily of perennials, legumes, and natives (Clark and Tilman 2008, Suding et al. 2004, Tilman 1993). Experimental studies of moderate to long duration (3-10 years) allow determination of the critical load with reasonable certainty. Longer studies (>10 years) would decrease the uncertainty further. In some cases, it can be difficult to determine whether the condition in reference plots or at the low end of a deposition gradient represents a “pristine” condition or whether a site has already been altered by N deposition prior to or at the time of the study. For example, the Watershed Acidification Study at Fernow Experimental Forest, West Virginia (Adams et al. 2006) added 35 kg N ha^{-1} yr^{-1} via aerial application in addition to ambient deposition of 15-20 kg N ha^{-1} yr^{-1}, which has led to changes in understory species composition. Recently, similar changes in understory species composition have occurred on the adjacent reference watershed receiving only ambient atmospheric deposition (Gilliam unpublished data, Gilliam et al. 1996). This pattern suggests that the deposition to the reference watershed currently exceeds the critical load. It is difficult to determine the empirical critical load at sites where ambient deposition exceeds the critical load. Where deposition rates exceed the critical load, empirical measurement of the rate of change of an ecological metric (e.g. plant abundance, diversity, or community composition) over a range of N inputs provides an approach to estimate the N level at which that metric just begins to change (the exceeded critical load) (Bowman et al. 2006).

The critical load of N for herbaceous species and herbs, when community change occurs (in some cases with invasives replacing native species), is exceeded across much of the Great Plains and in portions of the Southwest and high elevation and high deposition areas of the other ecoregions (Figure 5.b). The uncertainty associated with the exceedance, like that for the CL, varies.

3.1.4 Trees/Forest Ecosystems

Background

In this section we discuss the responses of trees and the overall biogeochemical responses of forest ecosystems to N inputs (Table 6), excluding the specific responses of mycorrhizal fungi, lichens, or understory herbaceous plants. Forest ecosystems represent about a third of landcover in the United States (FIA 2001) and are significant in many of the ecoregions: Northern, Eastern, Tropical Wet, and Marine West Coast Forests, Northwestern Forest Mountains, and Mediterranean California.

Response to N

In northeastern forests, gradient studies demonstrate that N deposition enhances growth in some fast-growing tree species, including the hardwoods studied with arbuscular mycorrhizal associations, whereas it slows growth in some species (red spruce, red maple), and has no detectable effect on still other species (Thomas et al. 2010). Similarly, N deposition enhances survivorship in a few species (black cherry, red maple, paper birch) and decreases survivorship in others (Thomas et al. 2010). Survivorship under chronic N deposition, and possibly other co-occurring pollutants such as ozone, is often dependent on interactions with other stressors such as pests, pathogens, climate change, or drought (Grulke et al. 2009, McNulty and Boggs 2010). Over the long-term, these differential effects of N deposition on tree growth and survivorship are likely to shift species composition, possibly to more nitrophilic species, similar to patterns seen for organisms with shorter lifespans.

We have few data that show a major structural or functional shift in forest ecosystems because of the long response time of trees and forest soils to changes in N inputs and N availability (Table 6). The relatively large pools of organic N in the forest floor, mineral soil, tree biomass, and detritus contribute to the relatively long lag-time in forest ecosystem response to N inputs. Because of the long lag-time in response to N treatments, it can be difficult to determine the actual critical N load for forest ecosystems based on short-term fertilization studies. If a response is observed over a relatively short period of time (i.e. years), it is nearly certain that the critical load is below the total N input at the treatment site and it can be difficult to further constrain the critical load.

It is expected that the more complex and interconnected processes in forests will result in a higher critical load, in part because large N storage pools give forest ecosystems a greater capacity to buffer N inputs. In herbaceous plants, too, responses in individual species tend to be observed at lower N inputs than changes in community composition, which are more complex and interconnected (Bowman et al. 2006).

Critical loads

The range of critical loads reported for forest ecosystems is 4-39 kg N ha^{-1} yr^{-1} (Table 6, Figure 6.a). The threshold N deposition value which caused increased NO_3^- leaching from forest ecosystems into surface water was 8-17 kg N ha^{-1} yr^{-1}; the lower end of the range representing Northern and Eastern Forests, the upper end representing Mediterranean California mixed conifers (Table 6, Figure 7.a). At 4 kg N ha^{-1} yr^{-}1 in the Colorado Rockies, increasing $[NO_3^-]$ was reported in the organic horizon, which suggests incipient N saturation (Rueth and Baron 2002).The highest critical loads were reported for Mediterranean California mixed conifer forests for forest sustainability and for soil acidification caused by increased N deposition. These sites experience some of the highest N deposition reported in the United States, up to approximately 70 kg N ha^{-1} yr^{-1} (Fenn et al. 2008).

The critical load is exceeded across much of the eastern forests (Eastern and Northern Forest Ecoregions). The lower end of the critical load range is exceeded for the remaining portions of the eastern forests, as well as portions of the Marine West Coast, Northwest Forested Mountains, and Tropical and Sub-tropical Humid Forest Ecoregions (Figure 6.b).

3.1.5 Freshwater and wetland ecosystems

Background

Freshwater lakes and streams, and wetlands (freshwater and estuarine intertidal) are both ecosystem types that occur in most ecoregions in North America. In freshwater lakes and streams, phytoplankton, or algae that live in the water column, are sensitive to the chemical environment in which they reside, and many species can be used as indicators of the levels of nutrients or acidity because of individual species’ preference for specific chemical conditions. Diatoms, unicellular plants that form the base of freshwater food webs, are used in this discussion because there has been more work published on these algae than others, but other types of algae also respond to N deposition (Lafrancois et al. 2004, Michel et al. 2006). Of the wetlands which occur in the conterminous United States, 95 percent are freshwater wetlands and 5 percent are estuarine or marine wetlands (USDI FWS 2005). The species composition tends to differ between freshwater and intertidal wetlands, although together they support more than 4200 native plant species. Despite the high biodiversity, the effects of N loading are studied in just a few plant species.

Response to N

For the analysis of nutrient N effects to freshwater lakes and streams, we relied on papers and studies that linked aquatic biological and ecological response to atmospheric deposition, but the results are consistent with laboratory or *in situ* dose-response studies and even land use change studies. The productivity of minimally disturbed aquatic ecosystems is often limited by the availability of N, and slight increases in available N trigger a rapid biological response that increases productivity and rearranges algal species assemblages (Nydick et al. 2004, Saros et al. 2005). The mechanism for change is alteration of N:P ratios, which can increase productivity of some species at the expense of others (Elser et al. 2009). As with the terrestrial systems described above, the nutrient responses of lakes and streams are most evident where land use change and acidic deposition have been limited, thus most evidence of exceedance of critical loads comes from the western United States (Baron et al. in press). As with terrestrial plants, some diatoms respond rapidly to an increase in available N. An example that has been observed from a number of different lakes of the Rocky Mountains is dominance of two diatoms (*Asterionella formosa* and *Fragilaria crotonensis*) in lakes with higher N, in contrast with the flora of lakes with lower N deposition where there is a more even distribution, thus high biodiversity, of diatoms. Higher trophic levels (zooplankton, macroinvertebrates) may be secondarily affected by N, but further increases in primary, or autotrophic, production will be limited by other nutrients such as P or silica (Si).

Both freshwater and estuarine intertidal wetlands tend to be N-limited ecosystems (LeBauer and Tresseder 2008, U.S. EPA 1993). Known responses to N enrichment are generally derived from nutrient-addition studies in the field and observations along gradients of N deposition. A variety of ecological endpoints are evaluated, such as altered soil biogeochemistry, increased peat accumulation, elevated primary production, changes in plant morphology, changes in plant population dynamics, and altered plant species composition (U.S. EPA 2008). In general, the sensitivity of wetland ecosystems to nitrogen is related to the fraction of rainfall (a proxy for atmospheric N deposition) in its total water budget. Most freshwater wetlands, such as bogs, fens, marshes and swamps, have relatively closed water and N cycles, thus are more sensitive to N deposition than intertidal wetlands, such as salt marshes and eelgrass beds (Greaver et al. in press).

Critical loads

In general, critical loads for freshwater lakes and streams tend to be low, because the target organisms are unicellular algae that respond rapidly to changes in their chemical environment. The range of critical loads for eutrophication and acidity is 2-9 kg N ha^{-1} y^{-1} (Baron et al. in press); the range reported for terrestrial ecosystems is much broader (Table 1). Critical loads for NO_3^- leaching from terrestrial ecosystems ranged from 4-17 kg N ha^{-1} y^{-1} (Figure 7a)**,** but many sensitive freshwaters at high altitudes are found above the tree-line where few watershed buffering mechanisms exist due to little vegetation, poorly developed soils, short hydraulic residence time, and steep topography. Numerous hydrological factors including hydraulic residence time, N pool size, and conditions of water saturation affect N loss. These factors influence how rapidly a system exhibits elevated N leaching in response to increased N deposition, and how this increased N availability subsequently influences biota. In general, lakes have relatively rapid N turnover times compared to soil N pools and are at least seasonally well-mixed. They would, thus, be expected to have lower critical loads. Turnover times for N in mineral soil pools can be very long, slowing or buffering changes in soil solution that would affect terrestrial plants. Thus responses by terrestrial plants would not be expected to be as rapid as those of freshwater organisms. The critical load for nitrate leaching is exceeded in portions of the Mediterranean California and the lower end of the critical load range is exceeded for most eastern forest and part of the Great Plains (Figure 7.b).

Generally the most sensitive type of wetland to N deposition are freshwater wetlands, with critical loads that range from 2.7-14 kg N ha^{-1} y^{-1} (Greaver et al. in press). The non-vascular plant genus Sphagnum and the carnivorous pitcher plant are the two species most commonly studied. The critical loads reported for freshwater wetlands (Greaver et al. in press) fall between those reported for inland surface waters (Baron et al. in press) and those reported for terrestrial ecosystems (Pardo et al. in press b). This may be related to the rate of N released by soils/sediment to the ecosystem. The critical load tends to be higher for intertidal wetlands than other types of ecosystems because they have open nutrient cycles which are often strongly affected by N loading sources other than atmospheric deposition. Based on field observations of N loading to plant growth and species composition on salt marsh and eel grass habitat, the critical load ranges between 50-400 kg N ha^{-1} y^{-1}.

3.2 Overview of critical loads across U.S. Ecoregions/summary text

Empirical critical loads for N tend to increase in the following sequence for different life forms: diatoms, lichens and bryophytes, mycorrhizal fungi, herbaceous plants and shrubs, and trees. Low-biomass ecosystems (e.g., grasslands, coastal sage scrub, desert) are more sensitive to N-enhanced growth of invasive species (if invasive pressure occurs), leading to vegetation type change. These low-biomass ecosystem types sometimes occur because of warm and dry climatic conditions. Because warmer temperatures often correspond to greater metabolic rates, longer periods of biological activity, greater biomass, and more rapid N cycling, one might expect that the critical load would increase with increasing temperature as has been suggested in Europe (Bobbink et al. 2003). We do not observe such a pattern across U.S. ecoregions in the critical loads reported in this synthesis, but Europe does not have warm and dry deserts with low critical loads as in the U.S. Note, however, that the uncertainty of the critical load estimates varies and is often fairly high, which may make it difficult to discern patterns in critical load values across regions. Moreover, a temperature pattern may be confounded by gradients in deposition quality and quantity, moisture and elevation. Critical loads vary more by receptor and response type than by region. For the same response of a given receptor, the western U.S. has generally similar critical load values to the eastern U.S., with the apparent exception that the critical load for NO_3^- leaching is approximately twice as high in Mediterranean California mixed conifers compared to northeastern forests (Figure 7). In contrast, the critical load for NO_3^- leaching in high elevation catchments in the Colorado Front Range are lowest in the United States, likely attributable to low biological N retention and storage capacity in these steep, rocky catchments (Baron et al. 2000, Williams and Tonnessen 2000, Sickman et al. 2002, Fenn et al. 2003a).

In setting critical loads, ideally one would identify an indicator that would allow prediction of future deterioration in ecosystem structure or function before it occurs—an early indicator of ecosystem change. We are not yet able to definitively determine which early responses to N deposition are the best indicators. In some cases, early responses may lead to a cascade of alterations in the N cycle that ultimately affect the function or structure of the ecosystem (Galloway et al. 2003). For example, elevated N inputs may lead to plant nutrient imbalances, which then increase plant susceptibility to inciting stressors such as cold, drought, or pests (Bobbink et al. 1998, Schaberg et al. 2002). This series of responses was observed in a southern Vermont montane red spruce stand, where increased foliar N concentration was associated with decreases in foliar membrane-associated calcium and decreased cold tolerance, which resulted in increased winter injury (Schaberg et al. 2002). Another example of the N cascade (Galloway et al. 2003) is increased soil NO_3^- leaching, which can result in episodic acidification of surface waters, harming fish species (Baker et al. 1996).

The magnitude or type of ecosystem change that is unacceptable may vary according to resource management goals or ecosystem services that are valued by a particular stake holder. In a conservation area, for example, any alteration in N cycling may be considered unacceptable, whereas for other land areas, changes of a certain magnitude or scope may be considered acceptable or desirable based on resource use (such as timber harvesting) or other factors. For example, some responses to low levels of elevated N deposition, such as increased plant growth and increased C-sequestration by trees (Thomas et al. 2010) may be considered beneficial where forests are managed for tree growth. Land and resources may be valued for a wide range of purposes, including biodiversity, food and wood production, water quality and quantity, and recreation. Quantification and then valuation of these ecosystem services for each land area of interest is required to fully account for impacts of N deposition.

There are several sources of uncertainty in our assessment of empirical critical loads, beyond those associated with atmospheric deposition (see section 2.1). In general, there is a dearth of observations on ecosystem response to inputs near the critical load. We suggest priorities for future research to address these data gaps below. A single study or very few studies have been conducted in some ecoregions. Without extensive, spatially stratified observations, it is not possible to know whether a study site is more or less sensitive than other sites in the ecoregion. The threshold value is best defined by a large number of studies which demonstrate the range of responses observed.

Other sources of uncertainty include time lags in the response to N deposition and the effects of multiple stressors, both of which are artifacts of the empirical approach, and, as such, are difficult to address. Because ecosystems do not respond instantaneously to changes in N inputs, there is a time lag associated especially with N addition studies; the magnitude of the time lag is a function of the N residence time and the organisms considered. This time lag increases with lifespan and size of organism; a tree will respond more slowly than an herbaceous annual, for example. Time lags are also a function of the rate of N input, with lower rates of input typically leading to longer time lags before an initial response (Clark and Tilman 2008). Some species adapted to low nutrient supply also tend to respond slowly to N additions (Theodose and Bowman 1997). (Note that, although the time lag may be longer for these low-N-adapted species, they may still be amongst the most sensitive to small N additions).

Heterogeneity of responses among species within the same ecosystem may be large, with many species being relatively unresponsive and a few opportunistic species transforming community structure and function. For N gradient studies, it can also be difficult to sort out the impact of other factors which may also vary along the deposition gradient, such as climate, interannual variation in weather, soils, vegetation, disturbances, and other pollutants. On the other hand, because these represent “real-world” conditions—in most locations, multiple stressors co-occur—the critical loads estimated in the presence of these stressors may better protect the ecosystems under the current conditions (Fenn et al. 2008).

One would anticipate that as an ecosystem approaches N saturation, smaller increments of additional N might result in reaching a “tipping point”. However, it is important not to confuse *proximity to N saturation* with the actual level of deposition; an ecosystem may be near N saturation when the ambient N deposition is low or when it is high. Thus, while prior exposure to elevated N deposition does push an ecosystem towards N saturation, high ambient deposition does not indicate the ecosystems most sensitive to further inputs—that status is a function of the ecosystem characteristics and the receptor.

Another source of uncertainty in empirical relationships is that they are simply field observations of responses to N inputs; often mechanistic explanations are lacking. Empirical observations reflect only research done to date, and, with the exception of N addition studies, only conditions observed to date. Because these factors affect the accuracy of the critical load, it is important to consider the level of uncertainty associated with our estimates of critical loads (Pardo et al. in press d). With more long-term studies and more data on the response of ecosystems to changes in N deposition, confidence in empirical loads will improve, as has occurred in Europe (Bobbink et al. 1992, 2010). In addition, over time, empirical observations will continue to inform dynamic models and improved dynamic models will facilitate understanding of the mechanisms behind field observations.

3.3 Factors that affect the Critical Load

One of the objectives of this assessment was to lay the groundwork for further refining and improving estimates of critical loads. To that end, in this section, we discuss some of the factors that affect where the value of the critical load falls within the reported range (Table 2). Abiotic factors which may affect the critical load include elevation, latitude, topographic location, climate (temperature, precipitation, extent and rate of climate change), catchment size, soil type, soil age, soil depth extent of soil cover in high elevation systems, parent material, and hydrologic flowpaths and processes. Disturbance may also play a substantial role, for example, N removal by fire or forest cutting may increase the critical load for nutrient N . A sub-region within an ecoregion may be more sensitive (e.g., the high-elevation Rockies are more sensitive to NO_3^- leaching than high elevation catchments in the Sierra Nevada of California). Biological factors likely to contribute to lower N critical loads include particularly sensitive species (diatoms, lichens, mycorrhizal fungi, certain plants), single species versus community responses, low biomass and low productivity ecosystems, short lifespan of receptor of concern, presence of invasive grasses, and presence of ozone-sensitive species.

The factors discussed above provide general guidance in applying critical loads. In order to set a critical load for a given site, the first step would be to determine whether the site of concern is similar to the site/or sites on which the critical load for that ecosystem type is based. Details on the estimation of critical loads are described for Tundra (Nadelhoffer and Geiser, in press), Taiga (Geiser and Nadelhoffer in press), Northern Forests (Pardo et al. in press c), Northwestern Forested Mountains (Bowman et al. in press), Marine West Coast Forests (Perakis et al. in press), Eastern Forests (Gilliam et al. in press), Great Plains (Clark in press), North American

Deserts (Allen and Geiser in press), Mediterranean California (Fenn et al. in press), Southern Semi-Arid Highlands (Fenn and Allen in press), Temperate Sierra (Fenn and Geiser in press), Tropical and Subtropical Humid Forests (Hall in press), Wetlands (Greaver at al. in press), Inland surface waters (Baron et al. in press). If the site differs from the sites upon which the critical load is based, Table 2 lists ecoregion-specific factors affecting the critical load that can be useful in adjusting the estimated critical load for a given site.

The more we are able to identify and quantify the factors that affect the critical load, the more we move towards a mechanistic understanding of the responses, and the better we are able to extrapolate observations across ecoregions or across different ecosystems within an ecoregion. In some cases, it may be possible to develop simple empirical relationships as a function of one or several variables that allow us to refine our critical loads estimates. For example, for lichens, Geiser et al. (2010) developed simple regression relationships which included precipitation that explain much of the variability in lichen community composition in response to N deposition. These regression models can be used to estimate critical loads in other regions and also can provide an estimate of the uncertainty associated with the critical load. Such models, strongly tied to empirical observations, will prove invaluable in the development of dynamic models for nutrient N critical loads.

3.4 Comparison to Critical Loads in Europe

The critical loads for N deposition we report are consistently lower than those reported for Europe, with a few exceptions (Pardo et al. b in press). It is difficult to make the comparison between the United States and Europe because the ecosystem classification systems used are not parallel and critical loads are often at different resolution or detail of vegetation classification.

Furthermore, the response variables and thresholds values of those variables are not always the same.

There are several reasons that critical loads for Europe may be higher than for the United States. One explanation for this pattern is that because of high historic deposition levels, many European systems lack pristine baseline ecosystems as a reference to compare those experiencing elevated N deposition. If the baseline reference sites are already altered by N deposition, then there is no means of estimating critical loads below the altered baseline. This is even more likely to have occurred in regions of Europe where deposition has been very high. For example, European critical loads for lichens were influenced by study sites in Scotland experiencing a deposition gradient from 10-22 kg N ha^{-1} y^{-1} from which critical loads were set at 11-18 kg N ha^{-1} y^{-1} (Mitchell et al. 2005). However, no oligotrophic species were observed, presumably because they were eliminated following initial increases in N deposition earlier in the 20th century. Not surprisingly, this European critical load is higher than any N critical loads for lichens in the United States. In addition, NH_4^+ inputs tend to be higher and represent a greater proportion of total N inputs in Europe, particularly in past decades. Note that when dry deposition is underestimated in the United States, the critical loads will also be underestimated which would contribute to them being lower than those in Europe (where throughfall is often used to set critical loads). Finally, since a greater proportion of the landscape in Europe, especially forested land, is managed (harvested and planted), this may contribute to European critical loads being higher as N removal by harvesting results in greater N demand and storage during re-establishment of the forest stand.

Another possible explanation for the fact that European critical loads are often higher than those reported here is that the response thresholds utilized in Europe are sometimes higher. A key example is lichen community response: when a shift in community composition is considered the threshold of change, the critical loads will be low. Some earlier work in Europe, in contrast, used a different biological threshold--the near extirpation of lichen species—leading to a higher critical load (Bobbink et al. 2003). Another example of higher response thresholds used for setting critical loads in Europe relates to responses at the forest ecosystem level. Using a more sensitive endpoint, such as initial changes in N biogeochemistry interpreted as incipient responses of N saturation, led to a critical load < 4 kg N ha^{-1} y^{-1} in the Colorado Front Range (Rueth et al. 2003). This is a subtle initial N enrichment response when compared to the magnitude of change (a later stage of N saturation) for the critical loads thresholds in Europe (10-15 kg/ha/yr). Note that critical loads in China are even higher than those in Europe (Duan 2009).

4. Conclusions

Because most terrestrial and many freshwater ecosystems are N limited under unpolluted conditions, increases in N input to ecosystems are likely to have an impact. Increased N deposition can cause a shift in the processing and fluxes of N along with an array of biological responses caused by N enrichment (function) and can cause significant changes to the physical composition (structure) of ecosystems. The resources most threatened by elevated N deposition include diatoms, lichens, bryophytes, and herbaceous plants. The most significant changes that we are currently observing in the United States in response to elevated N deposition are changes in species composition: losses of N-sensitive species, shifts in dominance, and losses of native species in favor of exotic, invasive species. Shifts in diatom and lichen community composition away from N-intolerant (oligotrophic) species are observed across the country. Alterations in herbaceous species are broadly observed, but are not always clearly documentable because of the long-term pollution inputs and other disturbances (including land-use change) that caused changes prior to the initiation of careful observations.

Numerous examples illustrate the significance of these species- and community-level effects. In serpentine grasslands in California, it was clearly demonstrated that unless N inputs are decreased or N is removed in biomass, a larval host plant and numerous nectar source plants utilized by a threatened and endangered butterfly will decrease to levels unable to sustain the butterfly population (Weiss 1999, Fenn et al. 2010). In Joshua Tree National Park in southern California, N deposition favors the production of sufficient invasive grass biomass to sustain fires that threaten the survival of the namesake species (Fenn et al. 2010, Rao et al. 2010). Other sensitive ecosystems include alpine meadows, where relatively low levels of N deposition have already changed species composition (Bowman et al. 2006). Changes in historical diatom community composition from N-limited to N-tolerant species have been observed in lake sediment cores at many locations in the western United States, providing early evidence of freshwater ecosystem eutrophication (Wolfe et al. 2001, 2003).

Changes in ecosystem structure are linked to changes in ecosystem function. For example, extirpation of lichens can alter food webs by reducing the availability of nesting material for birds, invertebrate habitat, and critical winter forage for mammals, and can also affect nutrient cycling (Cornelissen et al. 2007). In California, where elevated N deposition occurs in arid low-biomass ecosystems (e.g., coastal sage scrub, grassland, desert), N-enhanced growth of invasive species results in major alterations of plant communities, conversion of vegetation type, and increased fire risk, even in areas where fire is normally infrequent (Allen at al. 2009, Rao et al. 2010, Fenn et al. 2010).

There is also evidence of N deposition contributing to multiple stress complexes, resulting in reduced forest sustainability in California (Grulke et al. 2009) and North Carolina (McNulty and Boggs 2010). In North Carolina, elevated N deposition predisposed a pine ecosystem to a pest outbreak following a drought (McNulty and Boggs 2010). Another example of N deposition interactions with other forest stressors is the observation that increased NO_3^- leaching and nitrification contribute to soil acidification and depletion of available nutrient cations, which have negative effects on tree growth, vigor, and cold tolerance in some forests (Driscoll et al. 2001). These types of complex interactions may be difficult to predict, but may intensify the impact of elevated N deposition in concert with other stressors, including climate change. (Wu and Driscoll 2010). Further examples of changes in ecosystem structure and function are observed in coastal areas, where increased N export has led to toxic algal blooms (Rabalais 2002). As an example of N deposition effects on trace gas chemistry and climate change, N loading to ecosystems results in increased emissions of N trace gases, such as NO (nitric oxide, an ozone precursor), N_2O (nitrous oxide, a long-lived and powerful greenhouse gas); as well as declines in soil uptake of CH_4 (methane, another long lived and powerful greenhouse gas) (e.g., Liu and Greaver 2009).

This synthesis demonstrates that elevated N deposition has altered ecosystem structure and function across the United States. Empirical critical loads for N provide a valuable approach for evaluating the risk of harm to ecosystems. This approach has been used broadly in Europe (Bobbink et al. 2003, UBA 2004) and has the advantage of being scientifically based on observed responses. This link to actual ecosystem responses is especially beneficial in resource management and policy contexts.

Pardo et al. (in press e) provides the first comprehensive assessment of empirical critical loads of N for ecoregions across the United States. It represents an important step toward providing policymakers and resource managers with a tool for ecosystem protection, as was suggested by the National Research Council (NRC 2004).

5. Future Research Priorities

The principal knowledge gaps that limit our understanding of N impacts on ecosystems include poor quantification of total N deposition (especially in deposition hotspots), the paucity of long-term, low N fertilization studies and adequate N deposition gradient studies. A higher density of long-term, low N fertilization studies and long-term and larger scale gradient studies across a greater diversity of ecosystem types and extending to regions of low N deposition are necessary in order to develop the dose response curves that would better define the critical load and the associated uncertainty. These studies should examine all of the key receptors defined above, to explicitly test their relative sensitivity to N deposition and suitability as indicators of changes in other system properties. Future research should be directed at evaluating environmental and ecological factors that influence critical loads for ecoregions and quantifying how the critical load varies as key factors change across ecoregions. In the United States, the sparsest datasets are in the tundra, taiga, and desert ecoregions. Other important issues include:

- the differential response to reduced (NH_x) versus oxidized (NO_x) N inputs. Because some plants are particularly sensitive to NH_x inputs (Krupa 2003) while others are more sensitive to NO_y (Nordin et al. 2006), assembling more comprehensive data about these species-specific responses would allow more accurate assessment of potential risks to ecosystems in relation to the major N emissions sources.

- impacts on plant biodiversity have not been well described, in part, because of the difficulty of assessing such changes in ecosystems with longer-lived organisms, and, in part, because in many of these ecosystems, the herbaceous plants have been altered by historical N deposition, other pollutants, or habitat alteration.
- effects of N deposition on forest growth and sustainability. Insufficient data are available to determine critical loads for the effects of increasing N inputs on pest outbreaks, drought, cold tolerance, tree vigor, and multiple stress complexes in general.
- identification of mechanisms that control plant and ecosystem responses to N deposition. This is a necessary step in refining critical loads estimates, improving their reliability, and laying the groundwork for more complex dynamic models, which are necessary for broad scale assessments, including detailed national maps of empirical critical loads for N.

Better integration of improved atmospheric deposition models, empirical and dynamic critical load models, and vegetation cover data layers. From this critical load and critical load exceedance maps should be developed at scales useful for regulatory, policy making, land management, and resource protection purposes.

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Table 1 – Summary of critical loads of nutrient N for North American ecoregions

reliable; # fairly reliable; (#) expert judgment

Ecoregion	Ecosystem Component	CL for N deposition *kg N ha^{-1} yr^{-1}*	Reliability	Response	Comments	Study
Tundra	Prostrate dwraf shrubs	1-3	##	Changes in CO$_2$ exchange, cover, foliar N, and community composition of vascular plants	N addition study, Greenland high arctic, P enhanced N effects.	Arens et al. 2008[a]
Tundra	Lichens	1-3	(#)	Changes in lichen pigment production and ultrastructure, changes in lichen and bryophyte cover	N addition studies, high and low arctic, P enhanced or moderated N effects.	Arens et al. 2008[a], Hyvärinen et al. 2003[b], Makonen et al. 2007 [b]
Taiga	Forest	1-3	#	Changes in alga, bryophyte, and lichen community composition, cover, tissue N or growth rates.		Berryman et al. 2004 [c], Berryman and Straker 2008 [c], Geiser et al. 2010, Moore et al. 2004[c], Poikolainen et al. 1998 [b], Strengbom et al. 2003 [d], Vitt et al. 2003 [c],
Taiga	Spruce forests	5-7	(#)	Ectomycorrhizal fungi, change in community structure	Expert judgment extrapolated from Marine West coast spruce and northern spruce-fir forest	Lilleskov 1999; Lilleskov et al. 2001, 2002, 2008

Taiga	Shrublands	6	##	Shrub and grass cover, increased parasitism of shrubs	Long term, low N addition study: shrub cover decreased, grass cover increased	Nordin et al. 2005 [d], Strengbom et al. 2003 [d]
Northern Forests	Hardwood and Coniferous Forests	>3	#	Tree growth and mortality	Decreased growth of red pine, and decreased survivorship of yellow birch, scarlet and chestnut oak, quaking aspen, and basswood	Thomas et al. 2010
Northern Forests	Lichens	4-6	(#)	Epiphytic lichen community change	Loss of oligotrophic species. Synergistic/confounding effects of acidic deposition not considered; assumes response threshold similar to Marine West Coast Forest	Geiser et al 2010.
Northern Forests	Ectomycorhizzal fungi	5-7	#	Change in fungal community structure		Lilleskov et al. 2008
Northern Forests	Herbaceous cover species	>7 and <21	#	Loss of prominent species	Response observed in low-level fertilization experiment	Hurd et al. 1998
Northern Forests	Hardwood and Coniferous Forests	8	##	Increased surface water NO_3^- leaching		Aber et al. 2003
Northern Forests	Old-growth montane red spruce	>10 and <26	#	Decreased growth and/or induced mortality	Response observed in low-level fertilization experiment	McNulty et al. 2005

Northern Forests	Arbuscular mycorrhizal fungi	<12	(#)	biomass decline and community composition change		van Diepen 2008, van Diepen et al. 2007
Northwest Forested Mountains	Alpine lakes	1.5	##	Diatom assemblages	As wet deposition only	Baron 2006
Northwest Forested Mountains	Lichens	1.2-3.7	(#)	Epiphytic lichen community change in mixed-conifer forests, Alaska	Application of western Oregon and Washington model	Geiser et al. 2010
Northwest Forested Mountains	Lichens	2.5-7.1	##	Epiphytic lichen community change, thallus N enrichment in mixed-conifer forests, non-Alaska		Fenn et al. 2008, Geiser et al. 2010
Northwest Forested Mountains	Sub-alpine forest	4	##	Increase in organic horizon N, foliar N, potential net N mineralization, and soil solution N, initial increases in N leaching below the organic layer		Rueth and Baron 2002, Baron et al. 1994
Northwest Forested Mountains	Alpine lakes	4.0	#	Episodic freshwater acidification		Williams and Tonnesson 2000
Northwest Forested Mountains	Alpine grassland	4-10	##	Plant species composition		Bowman et al. 2006
Northwest Forested Mountains	Ectomycorrhizal fungi	5-10	(#)	Ectomycorrhizal fungi community structure in white, black, and Engelmann spruce forests	Expert judgment extrapolated from Marine West Coast spruce and northern spruce-fir forest	Lilleskov 1999; Lilleskov et al. 2001, 2002, 2008

Northwest Forested Mountains	Mixed conifer forest	17	##	NO_3^- leaching, reduced fine root biomass		Fenn et al. 2008
Marine West Coast Forest	Western OR and WA forests	2.7-9.2	##	Epiphytic lichen community change	Loss of oligotrophic species, enhancement of eutrophic species. CL increases with regional range in mean annual precipitation from 45-450 cm	Geiser et al. 2010
Marine West Coast Forest	SE Alaska forests	5	(#)	Fungal community change; declines in ectomycorrhizal fungal diversity		Lilleskov 1999; Lilleskov et al. 2001, 2002 ; Whytemare et al. 1997
Eastern Temperate Forest	Eastern Hardwood Forest	>3	#	Decreased growth of red pine, and decreased survivorship of yellow birch, scarlet and chestnut oak, quaking aspen, and basswood		Thomas et al. 2010
Eastern Temperate Forest	Lichens	4-8	(#)	Epiphytic lichen community change	Loss of oligotrophic species. Synergistic/ confounding effects of acidic deposition not considered; based on application of model and estimated response threshold	Geiser et al. 2010
Eastern Temperate Forest	Southeast Coastal Plain	5-10	(#)	Ectomycorrhizal fungi community response		Dighton et al. 2004; Lilleskov et al. 2001, 2002, 2008

Eastern Temperate Forest	Eastern Hardwood Forests	8	##	Increased surface water loading of NO_3^-		Aber et al. 2003
Eastern Temperate Forest	Michigan deposition gradient	<12	(#)	Arbuscular mycorrhizal fungal biomass decline and community composition change		van Diepen 2008, van Diepen et al. 2007
Eastern Temperate Forest	Herbaceous species	<17.5	(#)	Increases in nitrophilic species, declines in species-rich genera (e.g., *Viola*)		Gilliam 2006, 2007; Gilliam et al. 2006
Great Plains	Tall-grass prairie	5-15	#	Biogeochemical N cycling, plant and insect community shifts		Clark et al. 2009, Clark and Tilman 2008; Tilman 1993, 1987; Wedin and Tilman 1996
Great Plains	Mixed-grass prairie	10-25	#	Soil NO_3^- pools, leaching, plant community shifts		Clark et al. 2003, 2005; Jorgenson et al. 2005
Great Plains	Short-grass prairie	10-25	(#)		Inferred from mixed grass	Epstein 2001, Barret and Burke 2002
Great Plains	Mycorrhizal fungi	12	(#)	Decline in arbuscular mycorrhizal fungal activity		Egerton-Warburton
North American Desert	lichens	3	(#)	Lichen community shifts, thallus N concentration	Uncertainty regarding modeled estimates	Geiser et al. 2008, Porter et al. 2007
North American Desert	shrubland, woodland, desert grassland	3-8.4	#	Vegetation response, vascular plant community change		Allen et al. 2009; Baez et al. 2007; Inouye 2006; Rao et al. 2009, 2010

Mediterranean California	Coastal Sage Scrub	7.8-10	#	Invasive grass cover, native forb richness, arbuscular mycorrhizal fungi richness	Modeled and inferential N deposition estimates and published data for mycorrhizae, unpublished data for vegetation survey.	Fenn et al. in press, Egerton-Warburton and Allen 2000, Tonnesen et al. 2007
Mediterranean California	Chaparral; Lichens	3-6	#	Epiphytic lichen community change	Lichen critical load is from modeled N deposition data and published data for lichens.	Geiser et al. 2010; Jovan 2008; Jovan and McCune 2005;
Mediterranean California	Chaparral, Oak Woodlands, Central Valley	10-14	#	NO_3^- leaching; stimulated N cycling	Critical load for NO_3^- leaching of 10 kg N ha^{-1} yr^{-1} is based on one year of throughfall data in Chamise Creek and an additional year of throughfall data from adjacent Ash Mountain, both in Sequoia National Park.	Fenn et al. 2003a, b, c; Fenn and Poth 1999; Meixner and Fenn 2004
Mediterranean California	Mixed conifer forest; Lichens	3.1-5.2	##	Lichen chemistry and community changes	The lowest critical load is based on lichen tissue chemistry above the clean site threshold.	Fenn et al. 2008
Mediterranean California	Mixed conifer forest; plant physiology	17	#	Reduced fine root biomass		Fenn et al. 2008; Grulke et al. 1998
Mediterranean California	Mixed conifer forest; soil processes	17-25.9	#	NO_3^- leaching; soil acidification		Breiner et al. 2007, Fenn et al. 2008

Mediterranean California	Mixed conifer forest; forest sustainability	24-39	(#)	Understory biodiversity; forest sustainability	N deposition from Fenn et al. 2008	Allen et al. 2007; Grulke and Balduman 1999; Grulke et al. 1998, 2009; Jones et al. 2004
Mediterranean California	Serpentine grassland	6	##	Annual grass invasion, replacing native herbs	Critical load based on a local roadside gradient; Serpentine grassland site is actually west of the Central Valley.	Weiss 1999; Fenn et al. 2010
Temperate Sierras	Lichens	4-7	(#)	Epiphytic lichen community change	Increase in proportion of eutrophic species. Estimated from MWCF model, response threshold allows ~60% eutrophs due to dry, hot climate, hardwood influence	Geiser et al. 2010
Temperate Sierras	Las Cruces and Chichinautzin Ranges S/SW of Mexico City	15	#	Elevated NO_3^- in stream and spring waters	Data are from *Pinus hartwegii* sites in the Desierto de los Leones National Park and Ajusco	Fenn et al. 1999, 2002
Tropical and Subtropical humid orests	N-rich forests	<5-10	(#)	NO_3^- leaching, N trace gas emissions	CL for N-rich forests should be lower than for N-poor forests based on possibility of N losses.	ND
Tropical and Subtropical Humid Forests	N-poor forests	5-10	(#)	Changes in community composition; NO_3^- leaching, N trace gas emissions	CL for N-poor forests based on estimates for Southeastern Coastal Plain forests.	ND

Wetlands	Freshwater wetlands	2.7-13	#	Peat accumulation and NPP	CL for a wetlands in the northeastern U.S. and southeastern Canada	Aldous 2002[c], Moore et al. 2004[c], Rochefort and Vitt 1990[c], Vitt et al 2003[c]
Wetlands	Freshwater wetlands	6.8-14	(#)	Pitcher plant community change	CL based on northeastern populations	Gotelli and Ellison 2002, 2006
Wetlands	Intertidal wetlands	50-100	##	Loss of eelgrass		Latimer and Rego 2010
Wetlands	Intertidal salt marshes	63-400	(#)	Salt marsh community structure, microbial activity and biogeochemistry		Caffrey et al. 2007, Wigand et al. 2003
Aquatic	Western Lakes	2	##	Freshwater eutrophication		Baron 2006
Aquatic	Eastern Lakes	8	#	NO_3^- leaching		Aber et al. 2003

a– based on data from Greenland; b – based on data from Finland; c – based on data from Canada; d – based on data from Sweden

Table 2 – Assessment and interpretation of empirical critical loads of nutrient N for North American ecoregions

Ecoregion	Factors affecting the range of CL[a]	Comparison within Ecoregion[b]
Tundra	1) moisture 2) competition between vascular plants and cryptogams 3) P-limitation 4) temperature 5) pH	The critical load is higher in wet and P-limited tundra; acidic tundra may be more sensitive to N deposition than non-acidic tundra. Increased N deposition may be more detrimental to lichens in the presence of graminoids and shrubs in the low and mid arctic than to lichens with less competition in the high arctic. Response time increases with latitude due to colder temperatures, less light, and poorer N and P mobilization.
Taiga	1) soil depth 2) vegetation type and species composition 3) latitude	Morphological damage to lichens has been observed at a lower deposition in forests and woodlands than in shrublands or bogs and fens; cryptogam dominated mats on thin soils become N saturated faster than forest islands.
Northern Forest	1) receptor 2) tree species 3) stand age 4) site history 5) pre-existing N status	CLs for lichen are generally lowest, followed by CLs for ectomycorrhizal fungi and NO_3^- leaching. CLs for herbaceous species and forests are generally higher than for other responses.
Northwest Forested Mountains	1) biotic receptor 2) accumulated load of N 3) ecosystem 4) region	In alpine regions, diatom changes in lakes are seen at lowest the CL. Changes in individual plants are seen next, followed by vegetation community change, then soil responses. In subalpine forests, the CL of 4 kg ha^{-1} yr^{-1} for foliar and soil chemistry changes is similar to the lichen CL of 3.1 – 5.2 for lichen community change.
Marine West Coast Forest	1) background N status 2) soil type 3) species composition 4) fire history 5) climate	The midrange of responses reported for lichens (2.7 – 9.2 kg ha^{-1} yr^{-1}) is broadly comparable to that for plant, soil, and mycorrhizal responses (5 kg ha^{-1} yr^{-1}), despite limited studies for non-lichen responses.

Eastern Forests	1) precipitation 2) soil cation fertility and weathering 3) biotic receptors	The CL for NO_3^- leaching, lichen community change, and ectomycorrhizal fungal response are within the same range. Arbuscular mycorrhizal fungal and herbaceous CLs are higher.
Great Plains	1) N status 2) receptor 3) precipitation	CLs are lower in the tall grass prairie than in the mixed- and short-grass prairies. CL in tall- and mixed-grass prairie is lower on N poor sites and sites with very N responsive plant species. CL in the short-grass prairie is likely lower in wet years than in dry years.
North American Deserts	1) receptor 2) interaction of annual grasses with native forb cover 2) precipitation	The lichen CL is lowest, at 3 kg N ha^{-1} yr^{-1}; vegetation CL varies from 3-20 kg N ha^{-1} yr^{-1}
Medi-terranean California	1) Presence of invasive exotic annual grasses interacting with a highly diverse native forb community 2) N-sensitivity of mycorrhizal fungi 3) N-sensitivity of lichens 4) N retention capacity of catchments, catchment size 5) co-occurence of ozone and ozone-sensitive tree species.	The lowest CLs in Mediterranean California are for sensitive lichen in chaparral and oak woodlands and mixed conifer forests. The CL for plant and mycorrhizal fungal community change in coastal sage scrub is higher, at 7.8 to 10 kg ha^{-1} yr^{-1}. CL for NO_3^- leaching is lower in chaparral and oak woodlands (10 -14 kg ha^{-1} yr^{-1}) than in mixed conifer forests (17 kg ha^{-1} yr^{-1}). CLs are highest for mixed conifer forest plant community change and sustainability.
Wetlands	1) vegetation species 2) the fraction of rainfall in the total water budget 3) the degree of openness of N cycling	CL is much higher for intertidal wetlands (50-400 kg ha^{-1} y^{-1}) than for freshwater wetlands (2.7-14 kg ha^{-1} y^{-1}), which have relatively close water and N cycles.

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[a] - This explains what factors cause the critical load (CL) to be at the low or high end of the range reported.

[b] - Comparison of values and causes for differences if multiple critical loads are reported for an ecoregion.

Table 3 – Empirical critical loads of nutrient N for mycorrhizal fungi in U.S. ecoregions

reliable; # fairly reliable; (#) expert judgment

Ecoregion	Ecosystem (Site)	CL for N deposition *kg ha^{-1} yr^{-1}*	Reliability	Response of	Comments	Study
Taiga	Spruce forests	5-7	(#)	Ectomycorrhizal fungi, change in community structure	Expert judgment extrapolated from Marine West coast spruce and northern spruce-fir forest	Lilleskov 1999; Lilleskov et al. 2001, 2002, 2008
Northern Forests	Spruce-fir forest (Northeastern U.S. deposition gradient)	5-7	#	Ectomycorrhizal fungi, change in morphotype community structure	Wet deposition estimated from Ollinger et al (1993) model	Lilleskov et al. 2008
Northern Forests	Northern hardwood forests; Sugar maple dominated (Michigan gradient)	<12	(#)	Arbuscular mycorrhizal fungi, decrease in abundance in roots, soil, community change	N fertilization experiment	Van Diepen et al. 2007 van Diepen 2008
Northwest Forested Mountains	Engelmann spruce forests	5-10	(#)	Ectomycorrhizal fungi, change in community structure	Expert judgment extrapolated from Marine West coast spruce and northern spruce-fir forest	Lilleskov 1999; Lilleskov et al. 2001, 2002, 2008
Marine West Coast	White spruce forest (Kenai Peninsula, Alaska)	5	(#)	Ectomycorrhizal fungi, change in community structure, decrease in species richness	Bulk deposition. Historic N deposition was higher but unquantified. CL estimated from regression	Lilleskov 1999, Lilleskov et al. 2001, 2002, Whytemare et al. 1997
Eastern Temperate Forests	Southeast Coastal Plain	5-10	(#)	Ectomycorrhizal fungi, change in community structure	From one study in pine barrens plus extrapolation from other oligotrophic conifer forests	Dighton et al. 2004; Lilleskov et al. 2001, 2002, 2008
Eastern Temperate	Pine Barrens (New Jersey;	<8	(#)	Ectomycorrhizal fungal morphotype	Bulk deposition. Gradient study	Dighton et al. 2004

Ecoregion	Ecosystem (Site)	CL for N deposition *kg ha^{-1} yr^{-1}*	Reliability	Response of	Comments	Study
Forests	Southeast Coastal Plain)			community change	with three sample points	
Eastern Temperate Forests	Eastern Hardwoods; sugar maple dominated (Michigan gradient)	<12	(#)	Arbuscular mycorrhizal fungi; decrease in abundance in roots, soil, community change	Long term (12 yr) N fertilization experiment in sugar maple	Van Diepen et al. 2007, van Diepen 2008
Great Plains	Chicago Grassland	12		Arbuscular mycorrhizal fungi; decrease in % colonization, spore density	CL estimated from logarithmic curve of soil N vs. AMF activity. No low N baseline, so CL may be lower.	Egerton-Warburton
Mediterranean California	Coastal sage scrub (southern California)	7.8-9.2	#	Arbuscular mycorrhizal fungi, decrease in % colonization, spore density, spore richness	CL estimated from logarithmic curve fitted to data from this study compared to modeled and inferential N deposition data	Egerton-Warburton and Allen 2000, Tonnesen et al. 2007

Table 4 – Empirical critical loads of nutrient N for lichens in U.S. ecoregions

reliable; # fairly reliable; (#) expert judgment

Ecoregion	**Ecosystem (Site)**	**CL for N deposition** *kg ha^{-1} yr^{-1}*	**Reli-ability**	**Response of**	**Comments**	**Study**
Tundra	Tundra	1-3	(#)	Changes in lichen pigment production and ultrastructure, changes in lichen and bryophyte cover	N addition studies, high and low arctic, P enhanced or moderated N effects.	Arens et al. 2008 [a], Hyvärinen et al. 2003[b], Makkonen et al. 2007 [b]
Taiga	Taiga	1-3	#	Changes in alga, bryophyte, and lichen community composition, cover, tissue N or growth rates.		Berryman et al. 2004 [c], Berryman and Straker 2008 [c], Geiser et al. 2010, Moore et al. 2004[c], Poikolainen et al. 1998 [b], Strengbom et al. 2003 [d], Vitt et al. 2003 [c]
Northern Forests	Northern Forests	4-6	(#)	Changes in lichen physiology and community structure	CL proposed based on values in the Taiga and Northwest Forested Mountains.	Geiser et al. 2010
Northwest Forested Mountains	Coniferous forests, Alaska	1.2-3.7	(#)	Lichen community composition	Application of western Oregon and Washington model	Geiser et al. 2010
Northwest Forested Mountains	Coniferous Forests, non- Alaska	2.5-7.1	##	Lichen community composition	Application of western Oregon and Washington model	Geiser et al. 2010
Northwest Forested Mountains	Central Southern Sierras	3.1-5.2	##	Shifts in epiphytic lichen communities favoring eutrophs	CL based on exceedance of a N concentration threshold in the	Fenn et al. 2008

Ecoregion	Ecosystem (Site)	CL for N deposition *kg ha^{-1} yr^{-1}*	Reli-ability	Response of	Comments	Study
					lichen *Letharia vulpina*	
Marine West Coast Forests	Western OR and WA forests	2.7-9.2	##	Shifts in epiphytic lichen communities favoring eutrophs	CL increases with increasing mean annual precipitation from 40 to 240 cm.	Geiser et al. 2010
Eastern Forests	Eastern hardwoods and Southeast Coastal Plain	4-8 4-6	(#) (#)	Shifts in epiphytic lichen communities favoring eutrophs		Geiser et al. 2010
North American Deserts	Cold desert (Hells Canyon National Resource Area)	3	(#)	Increased cover and abundance of nitrophilous lichens on tall shrubs, increased parasitism of lichens.	CL estimated from overlay of course grid (36 km) CMAQ N; local N deposition from NH_3 was likely higher.	Geiser et al. 2008, Porter et al. 2007
Mediterranean California	Oak woodlands and chaparral (Central Valley: Sacramento Valley, Coast Ranges and Sierra foothills)	3-6	#	Shifts in epiphytic lichen communities favoring eutrophs	FHM lichen survey of 118 forested sites. Eutrophs dominated communities when CMAQ 4 km N dep estimates were >5.5 kg ha^{-1} yr^{-1}	Geiser et al. 2010, Jovan 2008, Jovan and McCune 2005
Mediterranean California	Mixed Conifer forest (Sierra Nevada)	3.1-5.2	##	Shifts in epiphytic lichen communities favoring eutrophs	Extrapolated from Northwestern Forested Mountains Sierra Nevada study.	Fenn et al. 2008
Temperate Sierras	Lichens	4-7	(#)	Shifts in epiphytic lichen communities favoring eutrophs	Increase in proportion of eutrophic species.	Geiser et al. 2010

a– based on data from Greenland; b – based on data from Finland; c – based on data from Canada; d – based on data from Sweden

Table 5 – Empirical critical loads of nutrient N for herbaceous plants and shrubs in U.S. ecoregions

reliable; # fairly reliable; (#) expert judgment

Ecoregion	**Ecosystem (Site)**	**CL for N** *kg ha^{-1} yr^{-1}*	**Reli-ability**	**Response**	**Comments**	**Study**
Tundra	Prostrate dwarf shrub	1-3	##	Changes in CO_2 exchange, cover, foliar N, and community composition of vascular plants	N addition study, Greenland high arctic, P enhanced N effects.	Arens et al. 2008[a]
Taiga	Shrublands	6	##	Change in shrub and grass cover, increased parasitism of shrubs	Long term, low N addition study: shrub cover decreased, grass cover increased	Nordin et al. 2005[b], Strengbom et al 2003[b]
Northern forests	Northern hardwood forests (Adirondacks)	> 7 and <21	#	Alteration of herbaceous understory		Hurd et al. 1998
Northwestern Forested Mountains	Alpine grasslands	4-10	##	Plant species composition change	Based on long-term experiment	Bowman et al. 2006
Eastern Forests	Eastern hardwood forests (Fernow Experimental Forest, WV)	<17.5	(#)	Increases in nitrophilic species, declines in species-rich genera (e.g., *Viola*)		Gilliam 2006, Gilliam 2007, Gilliam et al. 2006
Great Plains	Tall-grass prairie	5-15	#	Biogeochemical N cycling, plant and insect community shifts	Long-term, low N addition study that also added other nutrients.	Clark et al. 2009; Clark and Tilman 2008; Tilman 1993, 1987; Wedin and Tilman 1996
Great Plains	Mixed-grass prairie	10-25	#	Soil NO_3^- pools, leaching, plant community shifts	Short-term, low N addition study.	Jorgenson et al. 2005, Clark et al 2003, 2005
Great Plains	Short-grass prairie	10-25	(#)		Inferred from mixed grass.	Epstein 2001, Barrett and Burke 2002
North American Desert	Warm desert (Joshua Tree National Park, Mojave Desert)	3-8.4	#	Increased biomass of invasive grasses; decrease of native forbs		Allen et al. 2009, Rao et al. 2009, 2010

Ecoregion	Ecosystem (Site)	CL for N $kg\ ha^{-1}\ yr^{-1}$	Reli-ability	Response	Comments	Study
Mediterranean California	Serpentine grassland	6	##	Annual grass invasion, replacing native herbs	Critical load based on a local roadside gradient; Serpentine grassland site is actually west of the Central Valley.	Weiss 1999; Fenn et al. 2010
Mediterranean California	Coastal Sage Scrub	7.8-10	#	Invasive grass cover, native forb richness	Modeled and inferential N deposition estimates and unpublished data for vegetation survey.	Fenn et al. in press, Egerton-Warburton et al. 2001, Tonnesen et al. 2007
Mediterranean California	Mixed conifer forests (San Bernardino mountains)	24-33	(#)	Biodiversity of understory: percent cover and no. of species/3 ha	Based on plant surveys in 1970s and 2003.	Allen et al. 2007 N deposition data: Fenn, unpublished data ; Fenn et al. 2008
Wetlands	Freshwater wetlands	6.8-14	(#)	Pitcher plant community change	CL based on northeastern populations	Gotelli and Ellison 2002, 2006
Wetlands	Intertidal wetlands	50-100	##	Loss of eelgrass		Latimer and Rego 2010
Wetlands	Intertidal salt marsh	63-400	(#)	Salt marsh community structure, microbial activity and biogeochemistry		Caffrey et al. 2007, Wigand et al. 2003

9 a - based on data from Greenland; b – based on data from Sweden

10

Table 6 – Empirical critical loads of nutrient N for forest ecosystems in U.S. ecoregions

reliable; # fairly reliable; (#) expert judgment

Ecoregion	**Ecosystem (Site)**	**CL for N** *kg ha^{-1} yr^{-1}*	**Reli-ability**	**Response**	**Comments**	**Study**
Northern forests	Northeastern gradient	>3	#	Decline in survivorship of sensitive species	Based on study of gradient of N deposition from 3-11 kg N ha^{-1} yr^{-1}	Thomas et al. 2010
Northern Forests	Hardwood and coniferous forests	8	##	Increased surface water and NO_3^- leaching		Aber et al. 2003
Northern forests	Montane spruce fir (Mt. Ascutney, VT)	>10 and <26	#	Declines in growth and increased mortality		McNulty et al. 2005
Northwestern Forested Mountains	sub-alpine forest	4	##	soil organic horizon and foliar N enrichment and higher potential net N mineralization rates		Baron et al. 1994, Rueth and Baron 2002
Northwestern Forested Mountains	Mixed conifer forest	17	##	NO_3^- leaching, reduced fine root biomass		Fenn et al. 2008
Marine West Coast Forests	Coastal white spruce forest (South-Central Alaska)	5	(#)	declines in tree health; changes in understory composition; foliar nutritional imbalances; elevated NO_3^- in forest floor and mineral soil		Lilleskov 1999, Lilleskov et al. 2001, 2002; Whytemare et al. 1997
Eastern Forests	Eastern hardwood forests	>3	#	Decline in survivorship of sensitive species	Based on study of gradient of N deposition from 3-11 kg N ha^{-1} yr^{-1}	Thomas et al. 2010
Eastern Forests	Eastern Hardwood Forests	8	##	Increased surface water loading of NO_3^-		Aber et al. 2003

Ecoregion	Ecosystem (Site)	CL for N *kg ha^{-1} yr^{-1}*	Reli-ability	Response	Comments	Study
Mediterranean California	mixed conifer forests (San Bernardino mountains and southern Sierra Nevada range)	17	##	Streamwater [NO_3^-] > 14 µM	Based on regression of throughfall vs. peak streamwater NO_3^- concentrations. Daycent simulations gave similar results.	Fenn et al. 2008
Mediterranean California	Mixed conifer forests (San Bernardino mountains)	17	#	Reduced fine root biomass	Based on regression of throughfall N deposition and fine root biomass in ponderosa pine.	Fenn et al. 2008; Grulke et al., 1998
Mediterranean California	Mixed conifer forests (San Bernardino mountains)	25.9	#	Soil acidification; pH </= 4.6	Based on regression of throughfall N deposition and mineral soil H+.	Breiner et al. 2007
Mediterranean California	Mixed conifer forests (San Bernardino mountains)	39	(#)	Forest sustainability	Based on shifts in plant phenology and C allocation. Caused by combined effects of ozone and N deposition. Leads to increased bark beetle mortality and wildfire risk.	Grulke and Balduman 1999; Grulke et al. 1998, 2009; Jones et al. 2004 N deposition data from Fenn et al. 2008.
Tropical and Subtropical Humid Forests	N-poor tropical and subtropical forests	5-10	(#)	ND	CL for N-poor forests based on estimates for Southeastern Coastal Plain forests.	ND
Tropical and Subtropical Humid Forests	N-rich tropical and subtropical forests	<5-10	(#)	ND	CL for N-rich forests should be lower than for N-poor forests based on possibility of N losses.	ND

Figure legends

Figure 1-- Ecological Regions of North America, Level I

From the Commission for Environmental Cooperation (1997)

Figure 2 -- Estimates of wet + dry nitrogen (N) deposition in kg ha^{-1} yr^{-1} (includes wet ammonium and nitrate, dry nitric acid, particulate nitrate and ammonium, and gaseous ammonia, but not organic forms) generated by the CMAQ 2001 model for the more than 3200 locations for which we report ecological responses to N deposition.

Figure 3 – Map of (a) critical loads and (b) exceedances for mycorrhizal fungi by ecoregion in the United States

The range of critical loads reported for mycorrhizal fungi is shown for each ecoregion. The hatch marks indicate increasing level of uncertainty: no hatch marks for the most certain "reliable" category, single hatching for the "fairly reliable" category, and double hatching for the “expert judgment” category. The color sequence moves from red toward blue and violet as the critical load increases. As the range of the critical load gets broader, the saturation of the color decreases.

Exceedance (critical load – deposition) is shown for several categories: (1) No exceedance (Below CL), when deposition is lower than the CL range, (2) At CL, when deposition is within +/-1 of the CL range, (3) Above CL_{min}, when deposition is above the lower end of the CL range, but lower than the upper end of the range, (4) Above CL_{max}, when deposition is above the upper end of the CL range. CMAQ deposition data were not available for Alaska, so we were not able to calculate exceedance for Alaska.

Figure 4 - Map of (a) critical loads and (b) exceedances for lichens by ecoregion in the United States

The range of critical loads reported for lichens is shown for each ecoregion. The hatch marks indicate increasing level of uncertainty: no hatch marks for the most certain "reliable” category, single hatching for the "fairly reliable" category, and double hatching for the “expert judgment” category. The color sequence moves from red toward blue and violet as the critical load increases. As the range of the critical load gets broader, the saturation of the color decreases.

Exceedance (critical load – deposition) is shown for several categories: (1) No exceedance (Below CL), when deposition is lower than the CL range, (2) At CL, when deposition is within +/-1 of the CL range, (3) Above CL_{min}, when deposition is above the lower end of the CL range, but lower than the upper end of the range, (4) Above CL_{max}, when deposition is above the upper end of the CL range. CMAQ deposition data were not available for Alaska, so we were not able to calculate exceedance for Alaska.

Figure 5 – Map of (a) critical loads and (b) exceedances for herbaceous plants and shrubs by ecoregion in the United States.

The range of critical loads reported for herbaceous plants and shrubs is shown for each ecoregion. The hatch marks indicate increasing level of uncertainty: no hatch marks for the most certain "reliable” category, single hatching for the "fairly reliable" category, and double hatching for the “expert judgment” category. The color sequence moves from red toward blue and violet as the critical load increases. As the range of the critical load gets broader, the saturation of the color decreases.

Exceedance (critical load – deposition) is shown for several categories: (1) No exceedance (Below CL), when deposition is lower than the CL range, (2) At CL, when deposition is within +/-1 of the CL range, (3) Above CL_{min}, when deposition is above the lower end of the CL range, but lower than the upper end of the range, (4) Above CL_{max}, when deposition is above the upper end of the CL range. CMAQ deposition data were not available for Alaska, so we were not able to calculate exceedance for Alaska.

Figure 6 – Map of (a) critical loads and (b) exceedances for forest ecosystems by ecoregion in the United States.

The range of critical loads reported for forest ecosystems is shown for each ecoregion; this map does not include the responses of mycorrhizal fungi, lichens, or understory herbaceous plants already represented. The hatch marks indicate increasing level of uncertainty: no hatch marks for the most certain "reliable" category, single hatching for the "fairly reliable" category, and double hatching for the “expert judgment” category. The color sequence moves from red toward blue and violet as the critical load increases. As the range of the critical load gets broader, the saturation of the color decreases.

Exceedance (critical load – deposition) is shown for several categories: (1) No exceedance (Below CL), when deposition is lower than the CL range, (2) At CL, when deposition is within +/-1 of the CL range, (3) Above CL_{min}, when deposition is above the lower end of the CL range, but lower than the upper end of the range, (4) Above CL_{max}, when deposition is above the upper end of the CL range. CMAQ deposition data were not available for Alaska, so we were not able to calculate exceedance for Alaska.

Figure 7 – Map of (a) critical loads and (b) exceedances based on increased nitrate leaching by ecoregion in the United States.

The range of critical loads based on increased nitrate leaching for each ecoregion. The hatch marks indicate increasing level of uncertainty: no hatch marks for the most certain "reliable” category, single hatching for the "fairly reliable" category, and double hatching for the “expert judgment” category. The color sequence moves from red toward blue and violet as the critical load increases. As the range of the critical load gets broader, the saturation of the color decreases.

Exceedance (critical load – deposition) is shown for several categories: (1) No exceedance (Below CL), when deposition is lower than the CL range, (2) At CL, when deposition is within +/-1 of the CL range, (3) Above CL_{min}, when deposition is above the lower end of the CL range, but lower than the upper end of the range, (4) Above CL_{max}, when deposition is above the upper end of the CL range. CMAQ deposition data were not available for Alaska, so we were not able to calculate exceedance for Alaska.

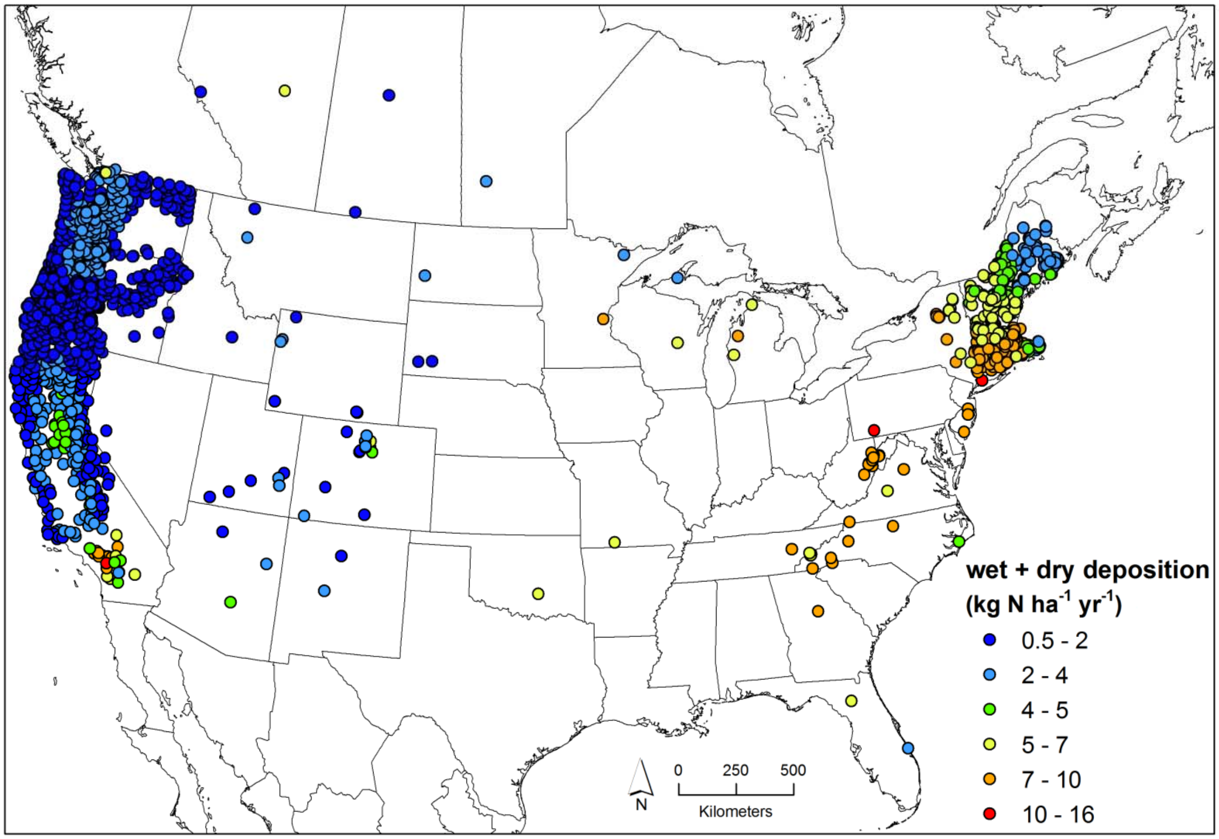

wet + dry deposition
(kg N ha^{-1} yr^{-1})
● 0.5 - 2
● 2 - 4
● 4 - 5
● 5 - 7
● 7 - 10
● 10 - 16
N
0
250
500
Kilometers

Figure 1

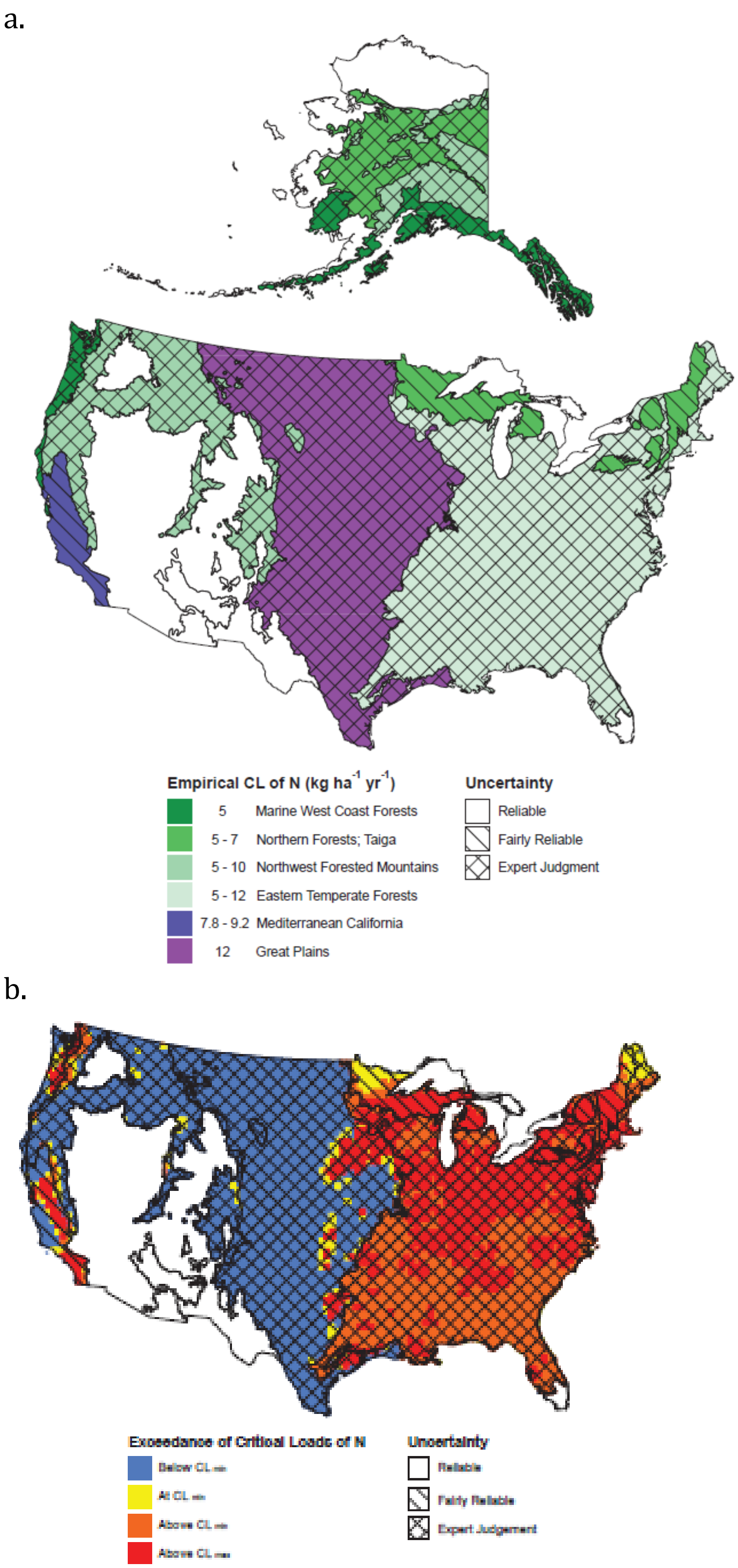
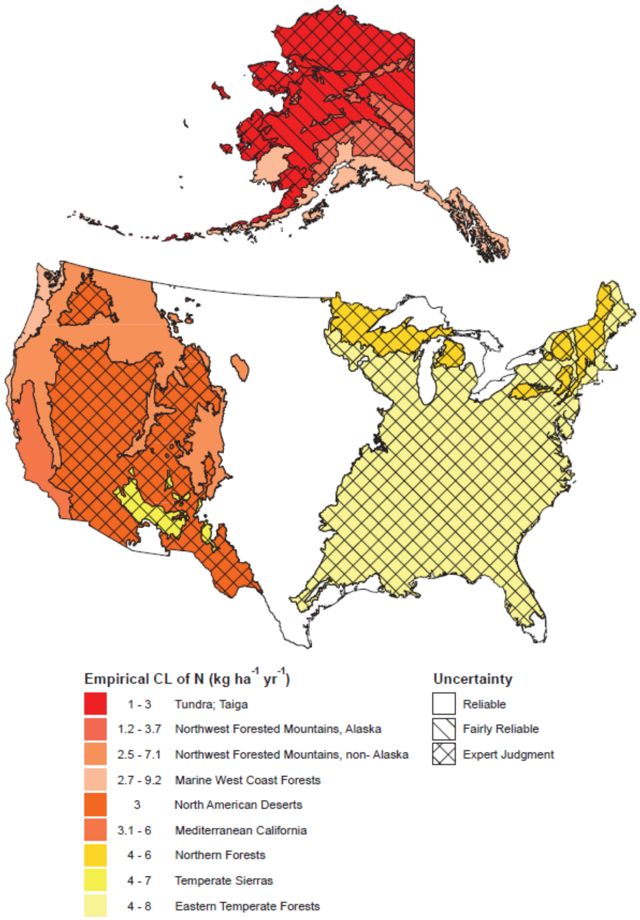

a.
Empirical CL of N (kg ha^{-1} yr^{-1})
5 Marine West Coast Forests
5 - 7 Northern Forests; Taiga
5 - 10 Northwest Forested Mountains
5 - 12 Eastern Temperate Forests
7.8 - 9.2 Mediterranean California
12 Great Plains
Uncertainty
Reliable
Fairly Reliable
Expert Judgment
b.
Exceedance of Critical Loads of N
Below CL$_{min}$
At CL$_{min}$
Above CL$_{min}$
Above CL$_{max}$
Uncertainty
Reliable
Fairly Reliable
Expert Judgement

Figure 2

a.


Empirical CL of N (kg ha^{-1} yr^{-1})
1 - 3 Tundra; Taiga
1.2 - 3.7 Northwest Forested Mountains, Alaska
2.5 - 7.1 Northwest Forested Mountains, non- Alaska
2.7 - 9.2 Marine West Coast Forests
3 North American Deserts
3.1 - 6 Mediterranean California
4 - 6 Northern Forests
4 - 7 Temperate Sierras
4 - 8 Eastern Temperate Forests
Uncertainty
Reliable
Fairly Reliable
Expert Judgment

b.

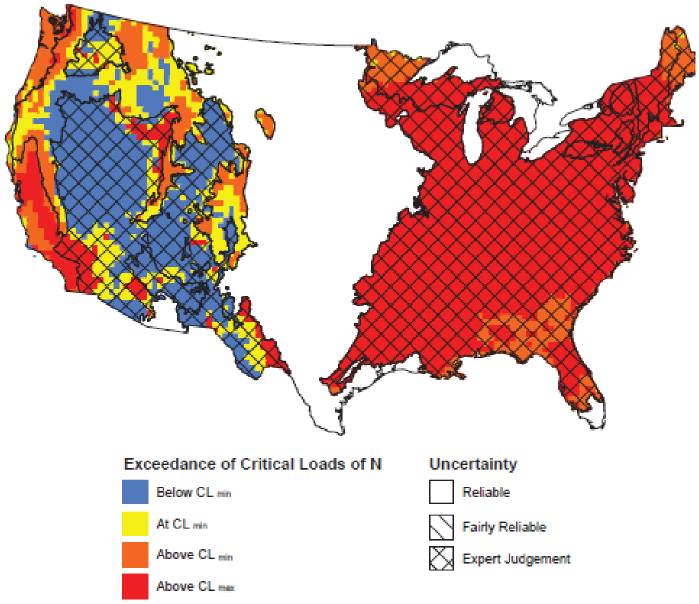

Exceedance of Critical Loads of N
Below CL$_{min}$
At CL$_{min}$
Above CL$_{min}$
Above CL$_{max}$
Uncertainty
Reliable
Fairly Reliable
Expert Judgement

Figure 3

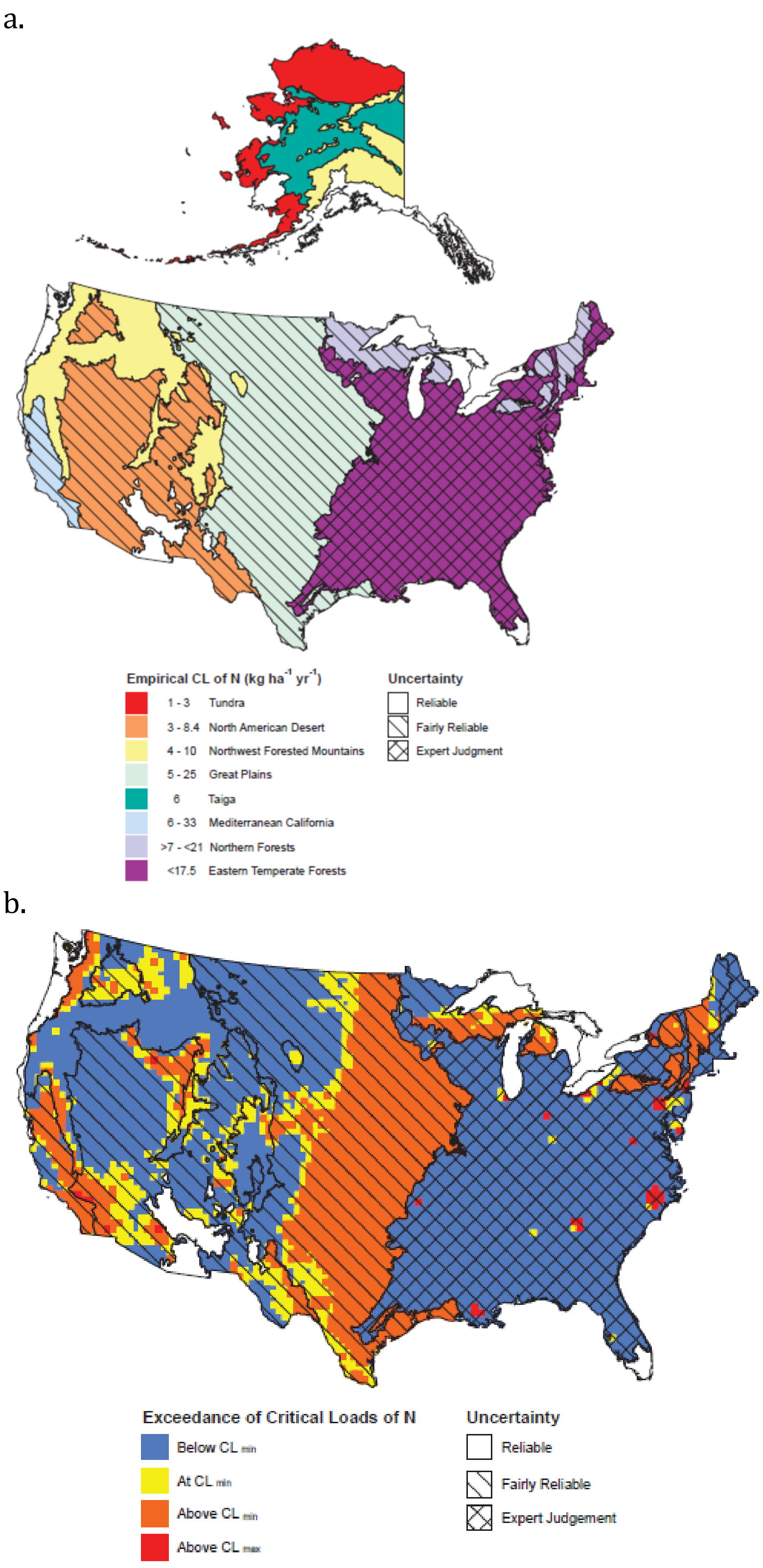

a.
Empirical CL of N (kg ha^{-1} yr^{-1})
1 - 3 Tundra
3 - 8.4 North American Desert
4 - 10 Northwest Forested Mountains
5 - 25 Great Plains
6 Taiga
6 - 33 Mediterranean California
>7 - <21 Northern Forests
<17.5 Eastern Temperate Forests
Uncertainty
Reliable
Fairly Reliable
Expert Judgment
b.
Exceedance of Critical Loads of N
Below CL min
At CL min
Above CL min
Above CL max
Uncertainty
Reliable
Fairly Reliable
Expert Judgement

Figure 4

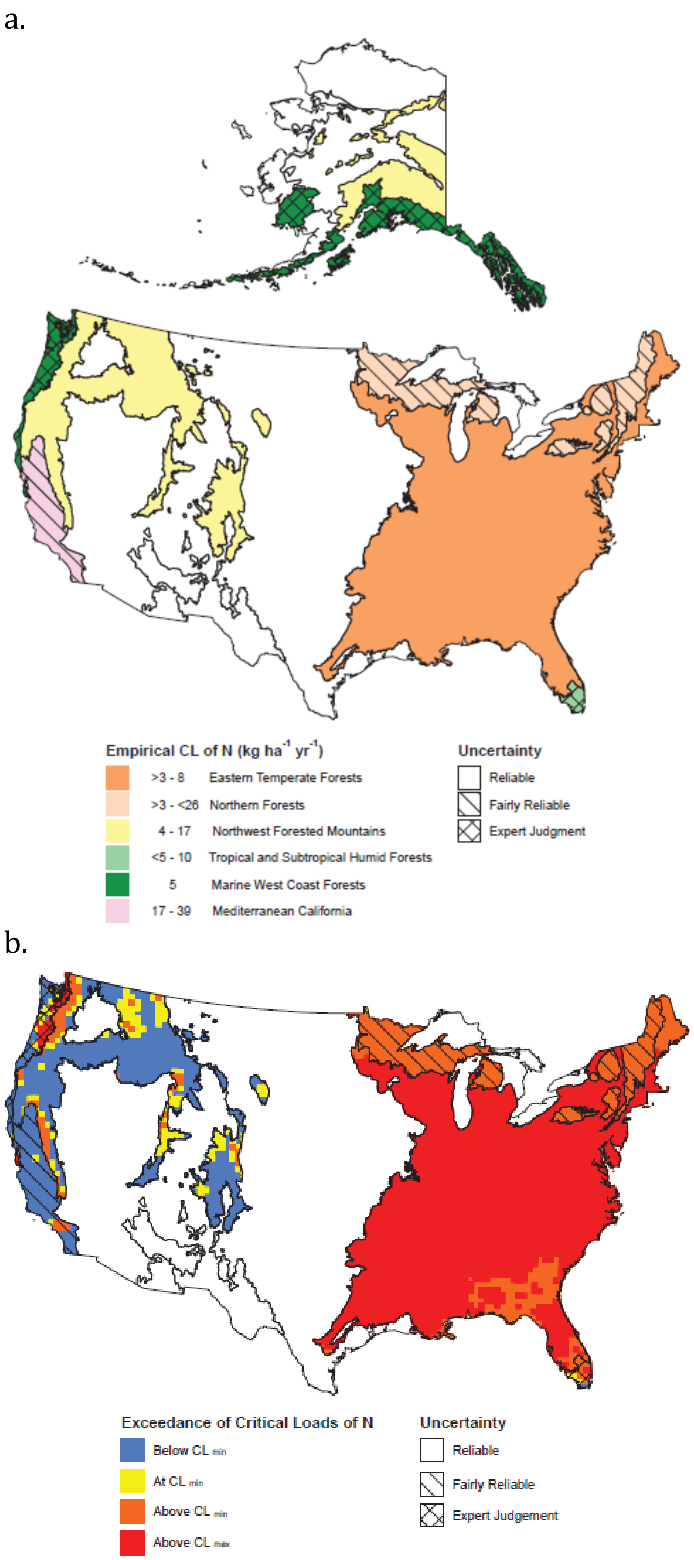

a.
Empirical CL of N (kg ha-1 yr-1)
>3 - 8 Eastern Temperate Forests
>3 - <26 Northern Forests
4 - 17 Northwest Forested Mountains
<5 - 10 Tropical and Subtropical Humid Forests
5 Marine West Coast Forests
17 - 39 Mediterranean California
Uncertainty
Reliable
Fairly Reliable
Expert Judgment
b.
Exceedance of Critical Loads of N
Below CL min
At CL min
Above CL min
Above CL max
Uncertainty
Reliable
Fairly Reliable
Expert Judgement

Figure 5

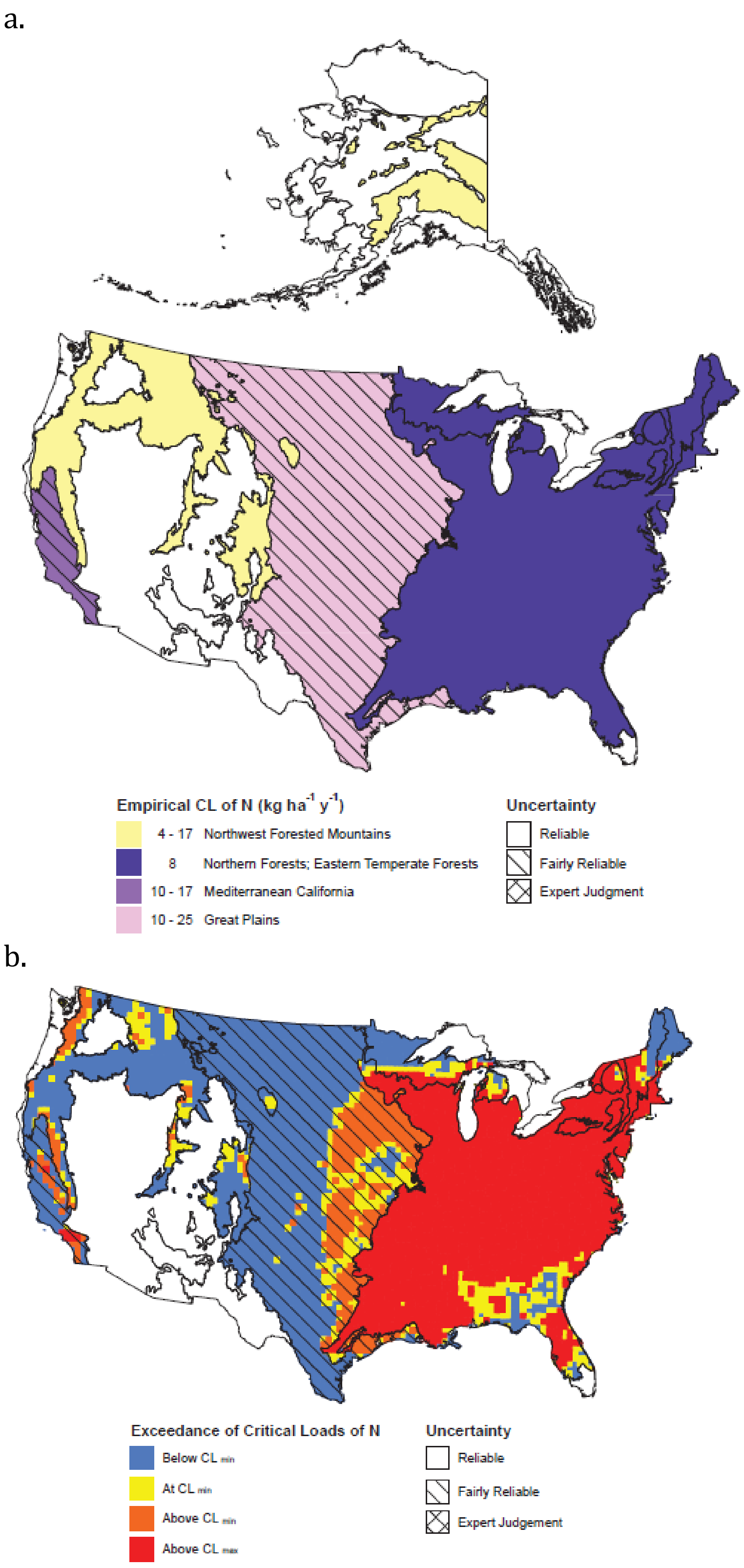

a.
Empirical CL of N (kg ha^{-1} y^{-1})
4 - 17 Northwest Forested Mountains
8 Northern Forests; Eastern Temperate Forests
10 - 17 Mediterranean California
10 - 25 Great Plains
Uncertainty
Reliable
Fairly Reliable
Expert Judgment
b.
Exceedance of Critical Loads of N
Below CL min
At CL min
Above CL min
Above CL max
Uncertainty
Reliable
Fairly Reliable
Expert Judgement

Figure 6