

Tree species at risk from nitrogen deposition in the northeastern United States: A geospatial analysis of effects of multiple stressors using exceedance of critical loads

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ABSTRACT

A recently developed online GIS tool, Nitrogen Critical Loads Assessment by Site (N-CLAS), was used to assess the effects of nitrogen (N) deposition and climate change on 23 tree species of management concern in the northeastern United States. The N-CLAS tool calculates and maps critical loads, target loads, and exceedances across the landscape by linking information on the relationships between N deposition, tree growth and environmental conditions with high resolution geospatial data for species composition and abiotic modifying factors (topography, climate, and soils). Outputs can be customized to capture specific species, locations or applications of interest to land managers.

The summary analyses presented here show that most forests in the northeastern United States are at risk of detrimental effects from N deposition, although the extent and magnitude of the risk varies spatially. Eighty-six percent of the forested area in the region (98 M acres) is in exceedance of the critical load. The magnitude of this exceedance is highest ($6\text{--}8\text{ kg N ha}^{-1}\text{ yr}^{-1}$) in the southwestern part of the study region where N deposition is highest (e.g. North Central Hardwood Forests, Erie Drift Plain, Driftless Area, and Southern Michigan/Northern Indiana Drift Plains ecoregions). The magnitude of exceedance is lowest ($1\text{--}2\text{ kg N ha}^{-1}\text{ yr}^{-1}$) in the northeastern and northwestern part of the study area where N deposition is lowest (e.g. Acadian Plains and Hills and the Northern Minnesota Wetland ecoregions). White pine (*Pinus strobus*), quaking aspen (*Populus tremuloides*), yellow birch (*Betula alleghaniensis*), northern red oak (*Quercus rubra*) and bigtooth aspen (*Populus grandidentata*) are in exceedance of the critical load across large portions of the study area—between 31 and 56 million acres are in exceedance for each species. Red pine (*Pinus resinosa*), pitch pine (*Pinus rigida*), and chestnut oak (*Quercus montana*), which occur over a small geographic extent, are in exceedance of the critical load over 89 to 100 percent of their range.

N-CLAS provides land managers easy access to a tool with significant refinement in determining empirical critical loads at a spatial resolution applicable to forest management. This represents an important step towards improving our understanding of the potential risk to forests in the northeastern U.S and linking current state of the science to decision making processes on the ground.

1. Introduction

Nitrogen deposition, climate change and pest outbreaks are among the most significant stressors to forest ecosystems in the United States and have the potential to alter the structure and function of forest stands (Lovett et al., 2006). N is often limiting in terrestrial ecosystems. However, elevated N inputs can lead to detrimental effects on ecosystems (Nihlgård, 1985), including soil and surface water acidification, plant nutrient imbalances, declines in plant health, changes in species composition, increases in invasive species, increased susceptibility to secondary stresses such as freezing, drought, and insect outbreaks, as

well as eutrophication of fresh and coastal waters (Aber et al., 1989, 1998; Galloway et al., 2003; Pardo et al., 2011a). Decreased species richness has also been documented in ecosystems with increasing N deposition (Stevens et al., 2004; Payne et al., 2013; Simkin et al., 2016). There is, however, little information about how N deposition interacts with other stressors to affect forest ecosystems across the landscape.

In recent years, an approach for assessing the impacts of air pollution on ecosystems has been gaining acceptance and is becoming widely used in the United States. This approach uses the critical load of a pollutant—the level below which detrimental ecological effects do not occur, according to present knowledge (Nilsson and Grennfelt,

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1988)—to quantify the potential harm to forests. Exceedance of the critical load (actual deposition-critical load) is a useful metric for communicating the risk of harmful effects from air pollution on ecosystems to resource managers, policy makers, and the public. In the United States, critical loads are currently set for sulfur (S) and nitrogen (N) deposition (Burns et al., 2008). (Critical loads may also be set for other pollutants, e.g., heavy metals (UBA, 2004).) In this assessment, we focus on the impacts of N deposition, as N deposition has become increasingly important relative to S deposition, due both to the success of the Clean Air Act amendments in reducing SO_x emissions and to the fact that ammonia (NH₃) and ammonium (NH₄) emissions are not regulated (except as a fraction of PM_{2.5}) and are increasing in many areas (Li et al., 2016; National Atmospheric Deposition Program, n.d.).

Critical loads are increasingly used in U.S. federal agencies. For example, critical loads are used by the National Park Service, Bureau of Land Management, and Forest Service in assessing impacts of pollution sources. Critical loads must be considered by the Forest Service in the Forest Planning process. And most significantly, critical loads are used by the U.S. Environmental Protection Agency (2018) in their review of secondary ambient air quality standards for N and S oxides, which protect public welfare (including protection against damage to vegetation). Resource managers and policy makers may also set target loads to meet management or policy goals, often within a given time frame. Target loads may be set higher than critical loads in accordance with specific management goals (Porter et al., 2005).

Previously reported critical loads for northeastern forests (Pardo et al., 2011b) provided a single range of critical load values, which encompassed all observed types of detrimental effects for forests across an entire ecoregion. However, the response to N deposition, and thus the critical load, may vary within an ecoregion based on site conditions as well as species present; trees will respond to increasing N loads based on their inherent nutrient requirements, functional traits, and abiotic site conditions (Leyton, 1957). Thus, the same factors that affect forest growth and species characteristics—i.e., climate, soil characteristics, topographic position, competition, and other biotic interactions—should also affect the critical load. Recognizing the significance of abiotic factors in affecting forest response to atmospheric deposition, an approach was proposed in Europe in the early 2000s to modify critical loads based on site factors (e.g., Achermann and Bobbink, 2003). However, it was not implemented at that time due to the challenges in determining the direction of impact for each factor, as well as the interactions of multiple factors across diverse climatic and site conditions in Europe. The approach was later used on a smaller scale in the United Kingdom (Hall and Wadsworth, 2010).

As the use of critical loads has increased in the United States, it has become apparent that resource managers need this information at the same spatial scale as the forests they manage, with detail on individual species (as opposed to broad ecoregions), and with consideration of the specific, potentially modifying site conditions at the forests they manage. In order to address these needs, we developed an online geographic information system (GIS) tool called Nitrogen Critical Loads Assessment by Site (N-CLAS; <http://nadp.slh.wisc.edu/committees/clad/links.aspx>). N-CLAS uses species-specific critical loads (Robin-Abbott and Pardo, 2017) in combination with an extensive assessment of how climatic conditions, site, and soil characteristics affect tree growth (Robin-Abbott and Pardo, 2017; Climate Change Atlas (U.S. Forest Service, n.d)). N-CLAS incorporates the potential influence of site, stand and environmental conditions on tolerance to N deposition into an online GIS tool to quantify critical loads and exceedance across a heterogeneous landscape (Fig. 1). It provides maps and summary statistics for individual tree species as well as for all species present within the user-defined area of interest—with outputs that allow quantitative assessment of the spatial extent of the area at risk and the magnitude of the impact from N deposition. N-CLAS also provides easy access to the abiotic data layers used in the assessments.

In this analysis, we used this newly developed N-CLAS tool to assess

critical loads and exceedance across the northeastern United States. Specifically, our objectives were to quantify the overall area and magnitude of exceedance, assess differences between species, examine spatial patterns across the landscape, and predict levels of N deposition that would protect sensitive species and ecoregions.

2. Methods

Our study area consists of the twelve level III ecoregions – areas with similar ecosystems and environmental conditions (U.S. Environmental Protection Agency, n.d.) that are bounded by three contiguous level II ecoregions: Atlantic Highlands, Mixed Wood Plains, and Mixed Wood Shield (Fig. 2). These are part of the broader Northern Forest and Eastern Temperate Forests level I ecoregions.

N-CLAS calculates the adjusted critical load for every 30 m pixel across the landscape for each species present (Fig. 1). The figures and tables generated by the N-CLAS tool quantify and summarize critical load and exceedance by user-selected area and/or species, thus facilitating evaluation of the severity and extent of risk from N deposition across the heterogeneous landscape.

N-CLAS uses geospatial data for abiotic modifying factors (topographic, climatic, and soil parameters) to predict whether growth in each 30 m × 30 m pixel is likely to be optimal or suboptimal for each species (Table 1). This is based on the foundational concept that for each abiotic parameter, a range of values for optimal growth exists for each species (Jenny, 1994); for values above or below that range, growth is not optimized (Fig. 1). At sites where growth conditions are optimal, plant nutrient demands will be higher, and more of the plant-available N will be incorporated into terrestrial biomass (Hyvönen et al., 2007; Schimel et al., 1997).

Thus, we expect that optimal growth conditions for a species will generally push the critical load to the upper half of the species' critical load range, indicating higher potential tolerance of deposition. At sites with suboptimal growth conditions, plant nutrient demands should be lower, and less plant-available N would be incorporated into the terrestrial biomass. The critical load for a species growing in suboptimal conditions is expected to be in the bottom half of the species' critical load range, indicating the potential for increased susceptibility to N deposition.

N-CLAS uses the combined effect of abiotic modifying factors on growth to determine whether the critical load for a species will be in the bottom half or upper half of the species' reported critical load range (Robin-Abbott and Pardo, 2017). The process by which N-CLAS calculates the adjusted critical load for each pixel includes:

- (1) identifying the species present;
- (2) evaluating whether the effect of each abiotic modifying factor is more likely to lead to optimal or suboptimal conditions for growth for each species present;
- (3) weighing the strength of evidence (weight of evidence) for the response of each abiotic factor;
- (4) incorporating the relative ecological significance (weight of influence) of each abiotic factor; and
- (5) adjusting the previously reported critical load value for each species based on the combined effect of all abiotic modifying factors.

Species present in each pixel (1) were determined using LANDFIRE geospatial data (www.landfire.gov), which provides SAF (Society of American Foresters) forest cover type for existing vegetation. Optimal growth ranges (2) were based on species importance values (used to indicate the relative importance of a species within a plot), and distribution data from the Climate Change Atlas (U.S. Forest Service, n.d.) and information from other sources, including the Forest Service silvics manual, "Silvics of North America" (Burns and Honkala, 1990); the USDA PLANTS database (NRCS, 2014); peer-reviewed literature; and consultation with experts on individual tree species (Fig. S1-1). Because

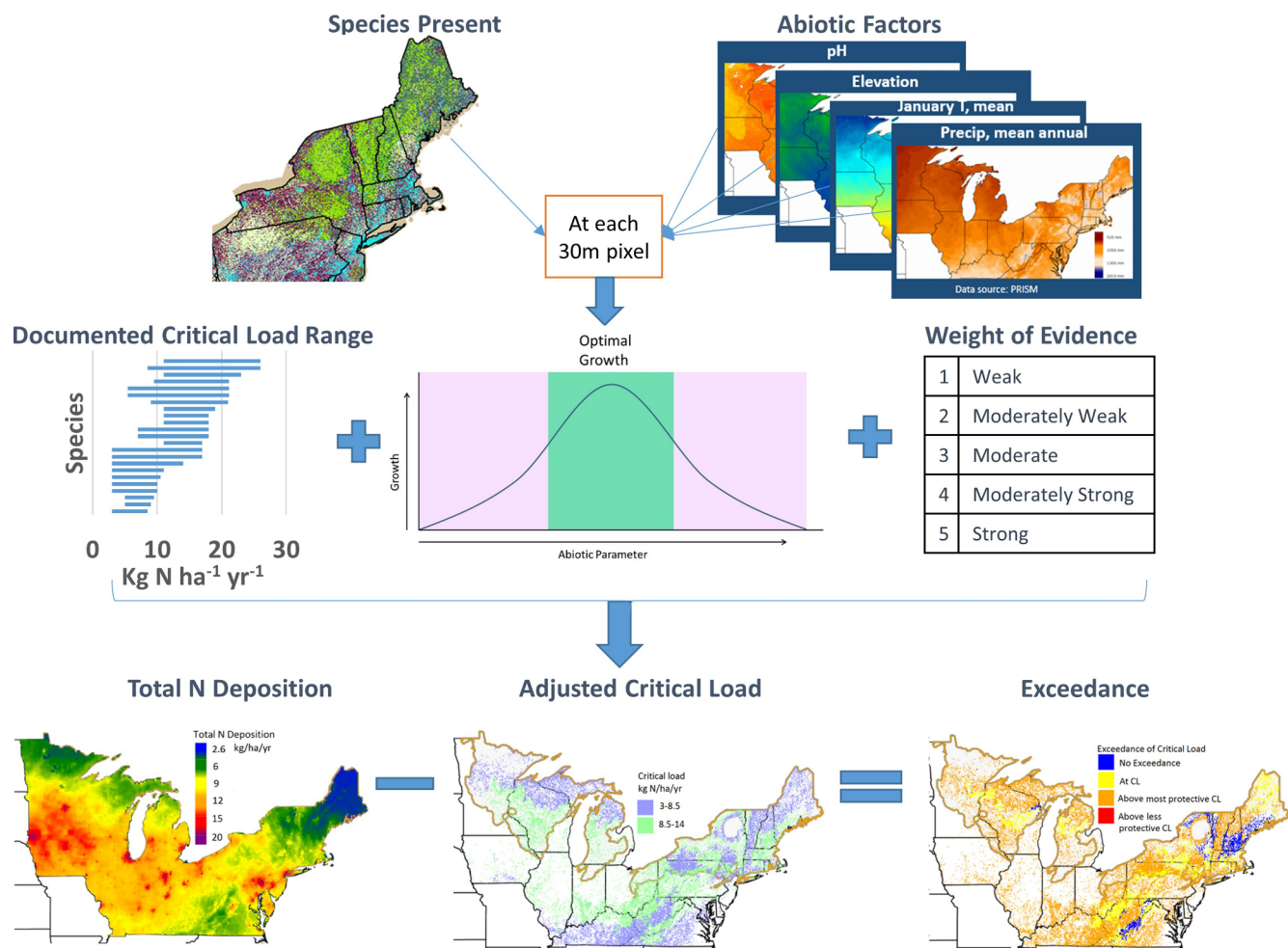


Fig. 1. Approach for determining adjusted CL of N and exceedance using the N-CLAS GIS tool.

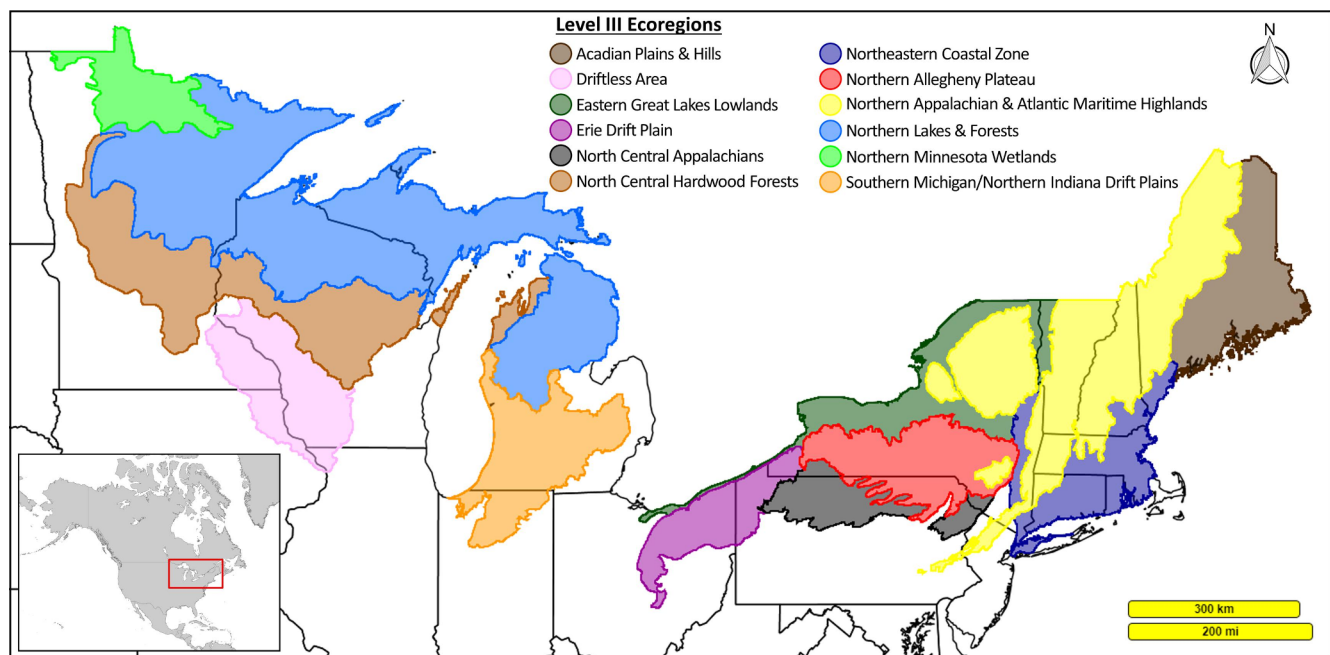


Fig. 2. Level III ecoregions included in the study region. The N-CLAS tool includes all level III ecoregions in the northeastern United States within the Atlantic Highlands, Mixed Wood Plains, and Mixed Wood Shield level II ecoregions.

Table 1
Data sources for data layers used in N-CLAS.

Data layer	Units	Resolution	Data source	Web site
Landfire vegetation		30 m		www.landfire.gov
Species range map		12 km		https://esp.cr.usgs.gov/data/little/
Elevation, northeastern U.S.	m	30 m	USGS ^a	http://ned.usgs.gov
Aspect		30 m	USGS	http://ned.usgs.gov
Slope Gradient	%	30 m	USGS	http://ned.usgs.gov
N deposition		4,134 m	TDEP	https://www.epa.gov/castnet
January temperature average	°C	800 m	PRISM ^b	http://www.prism.oregonstate.edu/normals/
July temperature average	°C	800 m	PRISM ^b	http://www.prism.oregonstate.edu/normals/
May to September temperature average	°C	800 m	PRISM ^b	http://www.prism.oregonstate.edu/normals/
Precipitation, annual	mm	800 m	PRISM ^b	http://www.prism.oregonstate.edu/normals/
Precipitation, May to September	mm	800 m	PRISM ^b	http://www.prism.oregonstate.edu/normals/
Soil pH		30 m	SSURGO ^c	http://sdmdataaccess.nrcs.usda.gov/
Soil clay	%	30 m	SSURGO ^c	http://sdmdataaccess.nrcs.usda.gov/
Soil coarse sand	%	30 m	SSURGO ^c	http://sdmdataaccess.nrcs.usda.gov/
Soil permeability	cm hr ⁻¹	30 m	SSURGO ^c	http://sdmdataaccess.nrcs.usda.gov/
Soil depth to bedrock	m	30 m	SSURGO ^c	http://sdmdataaccess.nrcs.usda.gov/

^a USGS = U.S. Geological Survey.

^b PRISM spatial climate data sets (PRISM Climate Group 2014).

^c Soil Survey Staff (accessed 2016). When SSURGO data were not available, data from the Conterminous United States Multilayer Soil Characteristics Dataset (Miller and White 1998), based on STATSGO data, were used. Soil data used were a weighted averaged of the first 60 cm of mineral soil.

data were evaluated in an ecosystem context – i.e., they are based on plot data that include many species and individual stems - optimal ranges are for tree growth with competition from other trees. See Robin-Abbott and Pardo (2017) and the Supplemental Material for further details. N-CLAS weights the impact of individual modifying factors on the site critical load by the weight of evidence (3) for each factor; a measure of the certainty of the effect of the modifying factor on the critical load (Robin-Abbott and Pardo, 2017). N-CLAS incorporates the weight of influence (4) of each factor on tree growth based on how sensitive each species is to that factor. For example, for one species, one factor (e.g. temperature) may be far more significant than all others; for another species, several factors may be equally important. In the current version of N-CLAS, climate factors are given the highest weight of influence. If any climate factor for a species in a pixel is suboptimal, growth is assumed to be suboptimal. The combined impact of all abiotic modifying factors (5) determines whether the adjusted critical load is in the bottom or upper half of the previously reported critical loads range (Robin-Abbott and Pardo, 2017; Fig. S1-2).

N-CLAS currently includes 23 tree species of management concern for commercial and wildlife uses, and rare and dominant species; the species vary in their sensitivity to N deposition. Each pixel in N-CLAS contains data for multiple species; each species has a minimum and maximum critical load. The adjusted critical loads can be reported for individual species or aggregated for all the species present in a given pixel. This allows users of this tool to select different levels of protection for the forest as a whole. Four different thresholds for all species combined are calculated for each pixel (Fig. 3):

CL = critical load for the most sensitive species: the most protective critical load for the most N sensitive species

TL_{LOW} = target load at which at least one species is severely at risk: based on the least protective critical load for the most N sensitive species

TL_{MID} = target load that protects the least sensitive species: based on the most protective critical load for the least N sensitive species

TL_{HIGH} = target load at which all species are severely at risk: based on the least protective critical load for the least N sensitive species

More details on N-CLAS model function can be found in the Supplemental Material and on the N-CLAS website (<http://nadp.slh.wisc.edu/committees/clad/links.aspx>).

3. Results

All of the critical loads and exceedances presented here are predicted values based on N-CLAS calculations that adjust previously reported, species-specific critical loads to the upper or bottom half of the critical loads range as described above. The critical load presented represents the minimum value (most protective) in the critical loads range.

3.1. Critical loads

The critical loads for our study area across the northeastern United States range from 3 to 18 kg N ha⁻¹ yr⁻¹ (Fig. 4a); with the majority of this area falling between 3 and 7 kg N ha⁻¹ yr⁻¹. Only the Driftless Area and Southern Michigan/Northern Indiana Drift Plains have a sizeable percentage of area with a critical load higher than 7 kg ha⁻¹ yr⁻¹. For target loads (deposition thresholds) that are less stringent, the TL_{LOW}, at which point all individuals of the most sensitive species are severely at risk, ranged from 6 to 12 kg N ha⁻¹ yr⁻¹ for most of the area (Fig. 4b). The target load (TL_{MID}) which is the most protective for the least sensitive species ranged from 7 to 18 kg N ha⁻¹ yr⁻¹ for the majority of the study area (Fig. 4c).

3.2. Exceedance: area

Eighty-six percent of the forested area in the region (98 M acres) is in exceedance of the predicted critical load (Fig. 4a). Within level III ecoregions, the extent of exceedance of the critical load ranges from 64% to greater than 99% (Fig. 5; Table 2a). Thirty-six percent of the region is in exceedance of TL_{LOW}, with the extent of exceedance ranging from 4 to 91% across the level III ecoregions (Fig. 4b; Table 2b). Only 4% of the region is in exceedance of TL_{MID}; the extent of exceedance is less than 1% in any given level III ecoregion (Fig. 4c; Table 2c). There was no exceedance of TL_{HIGH} (Table 2d).

3.3. Exceedance: magnitude

While there is exceedance of the critical load across the region, the magnitude of the exceedance varies from 1 to 12 kg N ha⁻¹ yr⁻¹. The magnitude of exceedance of the critical load is highest, 6–8 kg N ha⁻¹ yr⁻¹, in high N deposition areas of the upper Midwest: North Central Hardwood Forests (deposition 5.3–19.0 kg N ha⁻¹ yr⁻¹), the Erie Drift Plain (deposition 8.3–15.5 kg N ha⁻¹ yr⁻¹), the Driftless

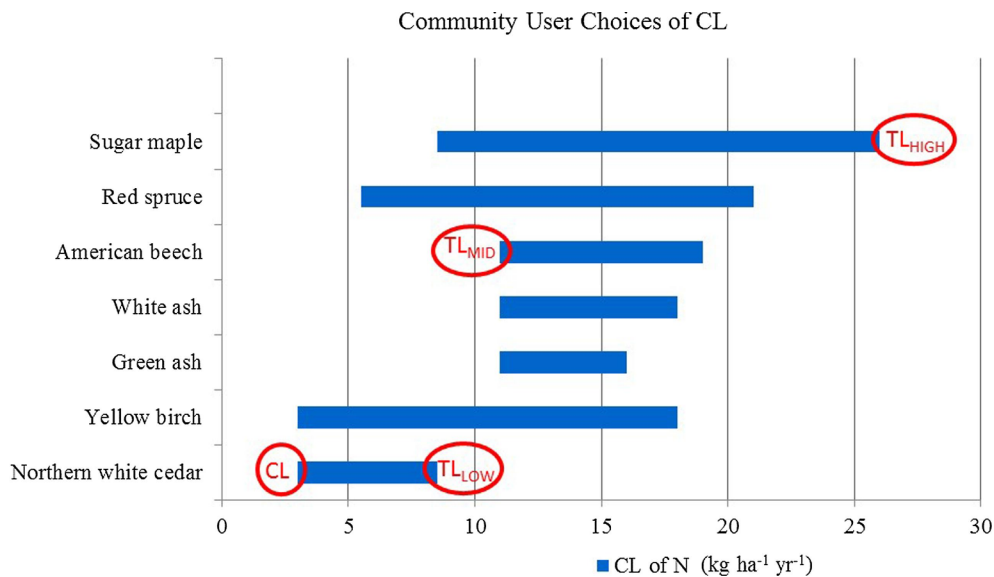


Fig. 3. Identifying critical load endpoints for multiple species in a pixel: CL = CL for most sensitive species; TL_{LOW} = least protective CL for most sensitive species (one species is severely at risk) TL_{MID} = most protective CL for least sensitive species; TL_{HIGH} = least protective CL for least sensitive species (all species severely at risk).

Area (deposition 9.0–15.0 kg N ha⁻¹ yr⁻¹), and Southern Michigan/Northern Indiana Drift Plains (deposition 7.9–16.3 kg N ha⁻¹ yr⁻¹). The level of exceedance is lowest (1–2 kg N ha⁻¹ yr⁻¹) in lower N deposition areas, most notably the ecoregions in the northernmost part of the study area: the Acadian Plains and Hills ecoregion in Maine (where N deposition ranges from 2.6 to 7.7 kg N ha⁻¹ yr⁻¹) and the Northern Minnesota Wetlands (where N deposition ranges from 4.2 to 8.2 kg N ha⁻¹ yr⁻¹). The Acadian Plains and Hills is the only ecoregion where N deposition ever falls below 3 kg N ha⁻¹ yr⁻¹, which is lower than the lowest critical load reported. The areas with the highest magnitude of exceedance fall along the western part of southern boundary of the study region, while the areas with the lowest exceedance occur in the north, both on the western and eastern extremities of the study region. These spatial patterns in magnitude of exceedance correspond generally with deposition patterns across the regions (Fig. 6).

3.4. Species patterns

3.4.1. Which species have the most exceedance

The species with the greatest area in exceedance of the most protective critical load (between 31 and 56 million acres for each species) include yellow birch (*Betula alleghaniensis*), eastern white pine (*Pinus strobus*), quaking aspen (*Populus tremuloides*), and northern red oak (*Quercus rubra*) (Fig. 7). Several species with narrower critical load ranges (Table 3) have a high percentage (> 80%) of their geographic area in exceedance, including red pine (*Pinus resinosa*), pitch pine (*Pinus rigida*), bigtooth aspen (*Populus grandidentata*), and chestnut oak (*Quercus montana*) (Fig. 7).

3.4.2. Broad spatial patterns

The species with the greatest area in exceedance of the critical load vary by ecoregion (Table S2-1). For the four species with the greatest area in exceedance across the whole region, only the northeastern part of the Northern Appalachian and Atlantic Maritime Highlands and the northern part of the Acadian Plains and Hills had little or no exceedance for three of these species: yellow birch, quaking aspen, and white pine (Maps S2-2, S2-5, and S2-4). In addition, for quaking aspen, the northernmost portion of the western Northern Minnesota Wetlands also had no exceedance. For white pine, the area not in exceedance extended further south in the Northern Appalachian and Atlantic Maritime Highlands. For the fourth species, northern red oak, the pattern was quite different: the area with no exceedance was found in central and

coastal New England (Map S2-5).

3.4.3. Which species set the critical load

Several species with suboptimal growing conditions across large portions of multiple ecoregions also have a low minimum critical load (3 to 7 kg N ha⁻¹ yr⁻¹, Fig. S1-2). For these species, yellow birch, butternut (*Juglans cinerea*), eastern white pine, bigtooth aspen, quaking aspen, northern red oak, and American elm (*Ulmus Americana*), the critical loads are adjusted to the bottom half of the critical load range, resulting in low adjusted critical loads and extensive exceedance. These species are instrumental in setting the critical load for the combined species assessment in multiple level III ecoregions.

3.5. What level of deposition will protect the region

Using N-CLAS, it is possible to assess the consequences of different levels of N deposition. If deposition is less than 2 kg N ha⁻¹ yr⁻¹, there would be no exceedance of the critical load anywhere across the region (Fig. 8). When deposition is greater than 3 kg N ha⁻¹ yr⁻¹, more than 80% of the region has exceedance of the critical load; when deposition reaches 12 kg N ha⁻¹ yr⁻¹, the entire region has exceedance of the critical load (Fig. 8). For the most protective target load, TL_{LOW}, more than 80% of the region would not have exceedance if deposition remains lower than 7 kg N ha⁻¹ yr⁻¹ (Fig. 8). When we compare target loads TL_{MID} and TL_{HIGH} to the deposition map (Fig. 6), it is clear that these target loads will rarely be exceeded, since the deposition is rarely over 9 kg N ha⁻¹ yr⁻¹ and never greater than 16 kg N ha⁻¹ yr⁻¹.

3.6. What level of deposition will protect level III ecoregions

N-CLAS also allows us to evaluate the potential impact of N deposition on the level III ecoregions. If deposition is greater than 3 kg N ha⁻¹ yr⁻¹, there would be exceedance of the critical load for most of the area within ten of the twelve level III ecoregions (Fig. 9). The remaining two (the Driftless Area of Wisconsin, Minnesota, and Iowa and the Southern Michigan/Northern Indiana Drift Plains in the upper Midwest) have notably different responses to deposition. If deposition remains below 5–6 kg N ha⁻¹ yr⁻¹, the majority of the ecoregion (~60%) is not in exceedance of the critical load (Fig. 9). The risk of detrimental impacts of N deposition varies considerably by species. For example, in these two ecoregions (Tables 4a and 4b), from four to six species are at risk if the deposition remains below 5–6 kg N ha⁻¹ yr⁻¹.

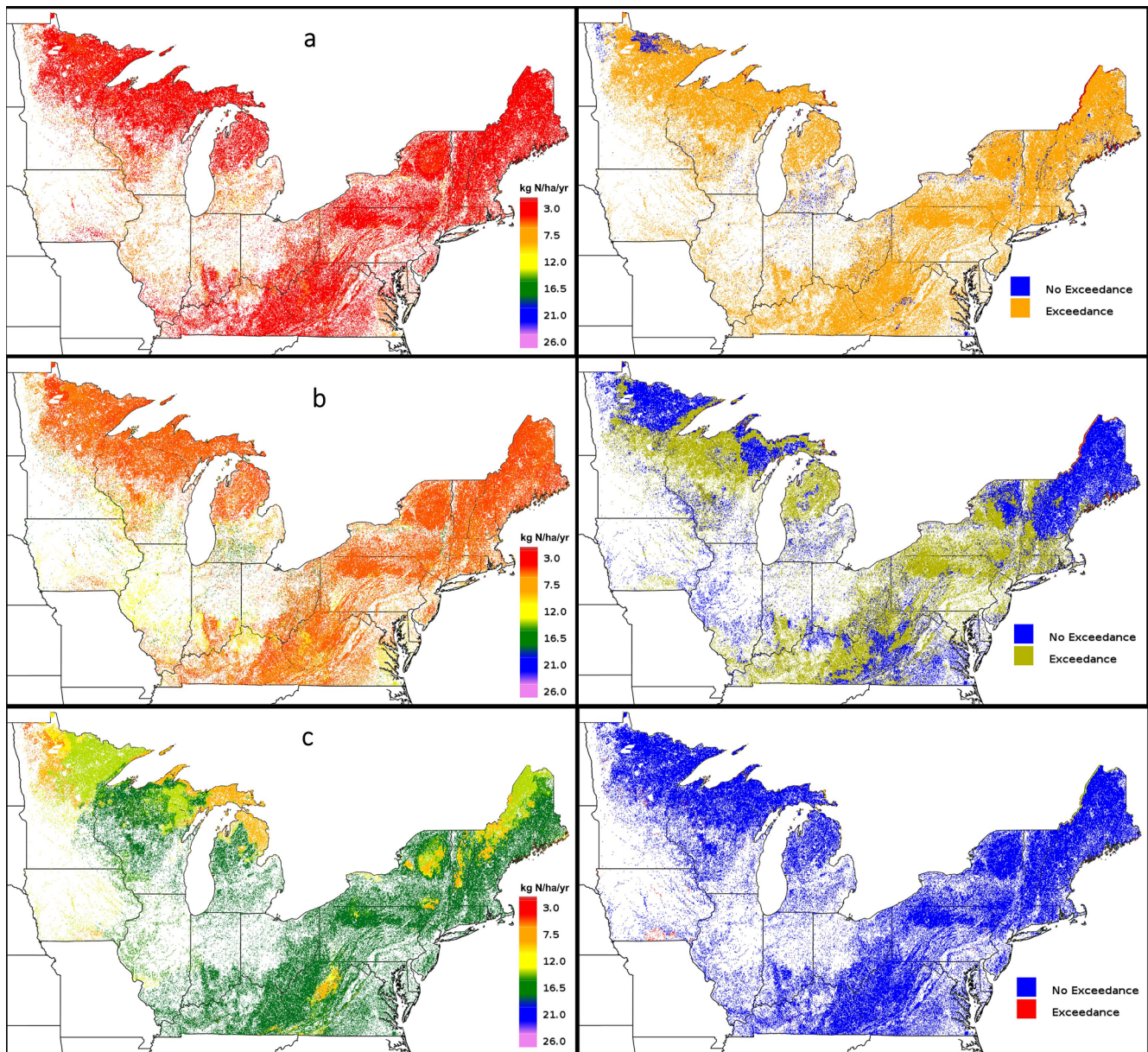


Fig. 4. Critical loads, target loads, and exceedance of N in the northeastern United States (a) CL ($\text{kg ha}^{-1} \text{yr}^{-1}$) and exceedance. (b) TL_{LOW} ($\text{kg ha}^{-1} \text{yr}^{-1}$) and exceedance of TL_{LOW} , where at least one species is severely at risk (c) TL_{MID} ($\text{kg ha}^{-1} \text{yr}^{-1}$) and exceedance of TL_{MID} , which protects the least sensitive species.

4. Discussion

The primary objective in the development of the N-CLAS tool was to allow assessment of critical loads at a finer spatial resolution, at the species level, and taking into account the influence of climatic conditions, site and soil characteristics on tree growth and, hence, on the critical load. The widespread exceedance we observed across the region based on this adjusted critical load (Fig. 3) gives us information about where there is at least one species at risk of detrimental effects of N deposition. In the only prior assessment of empirical critical loads for forest ecosystems in this region, Pardo et al. (2011a,b) report a critical load range of $3\text{--}8 \text{ kg N ha}^{-1} \text{yr}^{-1}$ for the Eastern Temperate Forest ecoregion and from 3 to $< 26 \text{ kg N ha}^{-1} \text{yr}^{-1}$ for the Northern Forest ecoregion. In general, the adjusted critical loads for *all species combined* tend to fall at the low end of the range previously reported for forest ecosystems in this region; the adjusted critical loads for *individual species* span the range, with many grouped at the lower end of previously reported ranges. This indicates that previous coarser assessments of

critical loads (Pardo et al., 2011a,b) may have overestimated the ability of many forests in the northeastern United States, especially in the Northern Forest ecoregion, to tolerate N deposition.

Based on previous studies of forest decline, we expected that red spruce (*Picea rubens*; Schaberg et al., 2002; Engel et al., 2016), balsam fir (*Abies balsamea*; Boyce et al., 2013), paper birch (*Betula papyrifera*; Halman et al., 2011), and sugar maple (*Acer saccharum*; Sullivan et al., 2013) would be most susceptible to N deposition across the region. However, our results indicate that none of these species showed a significant area of exceedance within the study region. The unexpected absence of red spruce exceedance in the current analysis may reflect shifts in N and S deposition rates, and an interaction between changing climate regimes, within the range of this species, and its susceptibility to N deposition. In particular, recovery of red spruce growth in recent decades has been attributed to declines in acidic deposition inputs, as well as increased winter temperatures, which may limit the extent of winter injury events historically linked to excessive N deposition in high elevation sites (Kosiba et al., 2018).

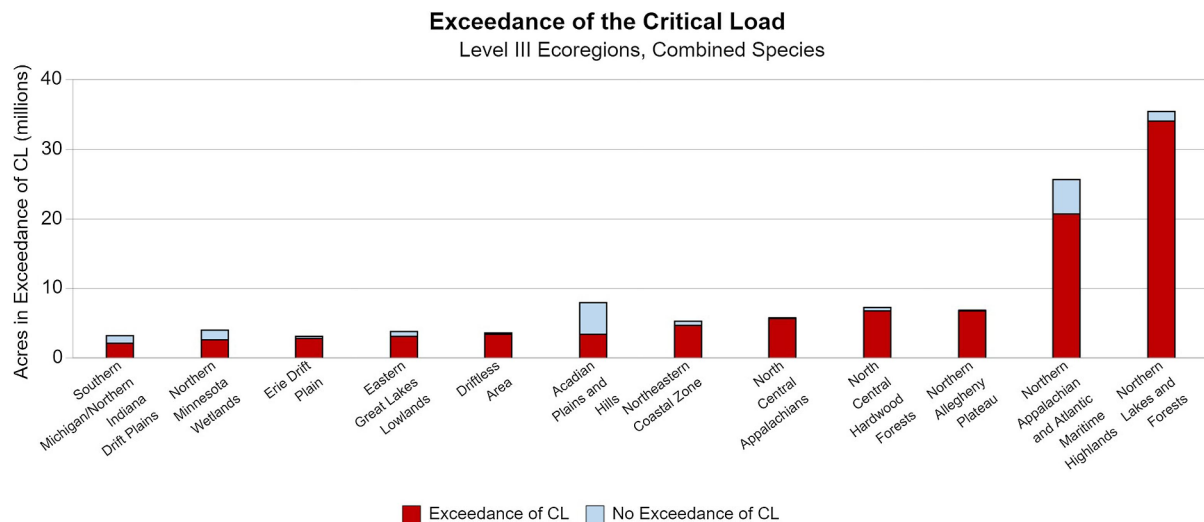


Fig. 5. Acres in exceedance of the CL of N for all level III ecoregions in the study region.

Eight species had extensive exceedance of the critical load across their range in the study area; these were white pine, quaking aspen, yellow birch, northern red oak, bigtooth aspen, red pine, pitch pine, and chestnut oak (discussed in order from highest to lowest acres in exceedance). For each of the eight species with the broadest exceedance (by acres in exceedance or by percent of species range in exceedance), we review their ecological significance and ecosystem services, evaluate the primary abiotic factors that render them susceptible to N deposition, and describe how projected future changes in climate appear most likely to impact them, which may have implications for forest management. We used histograms of the distribution of each abiotic factor within each ecoregion that were generated by N-CLAS (Supplemental Material Histograms S2-1 to S2-5) for this assessment.

What makes N-CLAS most useful for resource management is that it provides information about the potential species responses to N deposition and spatial patterns of critical load and exceedance across the region—at a scale relevant for forest management. N-CLAS distills information from the large analysis of Forest Inventory and Analysis (FIA) data in the Climate Change Atlas (U.S. Forest Service, n.d.), facilitates analysis of the data layers it utilizes (Table 1) for interpreting the patterns of abiotic conditions and biotic responses, and allows us to consider which of the abiotic factors are implicated in making forests more susceptible to detrimental effects from N deposition (adjusting critical loads based on sub-optimal growth conditions). For example, January temperature might be very important to one species (such as red spruce, which tolerates a fairly narrow temperature range), while growing season (May–September) temperature might be most important for another species. In locations where growth is sub-optimal because of environmental conditions, trees are less likely to tolerate secondary stressors and therefore more susceptible to detrimental effects from N deposition (Holdaway, 1990).

4.1. White pine

Eastern white pine is both widespread across the region (~90 million acres) and a valued timber resource. The abundance of this species has increased in the past two centuries in the eastern ecoregions, observed by establishment on abandoned agricultural fields (Thompson et al., 2013), but has been greatly reduced in the upper Great Lakes region following extensive timber harvesting and associated slash fires in the 19th century (Schulte et al., 2007).

NCLAS reports white pine in exceedance across 56 million acres (approximately 60% of its total area). While white pine decline is more commonly linked to pests and pathogens (Wendel and Smith, 1990;

Costanza et al., 2018), acid deposition has also been historically linked to reduced growth rates and exceedance was significantly negatively correlated with white pine growth on Forest Inventory and Analysis (FIA) plots across the region (Duarte et al., 2013).

Temperature was the abiotic factor with sub-optimal conditions most frequently adjusting the critical load for white pine into the lower end of its reported critical load range (more susceptible to detrimental effects of N deposition). Across many of the twelve level III ecoregions, temperature tended to fall below the optimal range for white pine growth, especially in the western part of the region where more than half of the area was outside the optimal range. The distributions of temperature for the ecoregions are shown in supplemental histograms S2-3, S2-4, and S2-5. The optimal temperature range for white pine growth is based in values in Robin-Abbott and Pardo (2017; https://www.fs.fed.us/nrs/pubs/download/gtr_nrs172_appendix2.pdf). Other studies have demonstrated connections between cold hardness and growth potential in white pine (Lu et al., 2003), indicating that low temperatures may impact growth conditions and tolerance to N deposition across much of the study area. Climate projections indicate an increase in temperatures across the region (Wuebbles et al., 2017), but extreme cold events resulting in winter injury and sub-optimal growth are still likely to occur.

Annual precipitation tended to be substantially lower than the optimal range in the western portion of the region, most significantly for the North Central Hardwoods, Northern Lakes and Forests, and Northern Minnesota Wetlands. May–September precipitation was also lower than the optimal range for minor portions of these ecoregions as well as the Eastern Great Lakes. For most of the mountainous ecoregions (North Central Appalachians, Northern Allegheny Plateau, and Northern Appalachian and Atlantic Maritime Highlands), and for smaller fractions of the Erie Drift Plain and Northern Lakes and Forests, elevation was higher than optimal.

As eastern white pine is sensitive to drought (Janowiak et al., 2018; Kipfmüller et al., 2010; Livingston and Kenefic, 2018), projected shifts toward lower growing season precipitation in the western portion of the region (USGCRP, 2018) are likely to increase the portion of the region outside of the optimal range, especially in the North Central Hardwoods, Northern Lakes and Forests, Northern Minnesota Wetlands, and Southern Michigan/Northern Indiana Drift Plains. Less concerning, since white pine is more sensitive to dry conditions, are increases in precipitation in the northeastern ecoregions projected by many climate change scenarios (Horton et al., 2014; Lynch et al., 2016), which would increase the portion of these areas above the optimal range. In addition, in many projections, increased precipitation occurs during the spring

Table 2
Area in Exceedance by Ecoregion.

2.a CL for most sensitive species					
Level III ecoregion	Ecoregion Area (million acres)	N Deposition (kg ha ⁻¹ yr ⁻¹)	Forested Area (million acres)	Forested Area in Exceedance of CL (million acres)	% of Forested Area in Exceedance of CL
Southern Michigan/Northern Indiana Drift Plains	13.1	7.9–16.3	3.3	2.1	64.2%
Northern Minnesota Wetlands	5.6	4.2–8.2	4.0	2.6	66.3%
Erie Drift Plain	7.7	8.3–15.5	3.1	2.9	91.9%
Eastern Great Lakes Lowlands	10.0	4.1–15.5	3.8	3.2	83.9%
Driftless Area	11.7	9.1–15.0	3.7	3.4	92.9%
Acadian Plains and Hills	11.2	2.6–7.7	8.0	3.4	42.8%
Northeastern Coastal Zone	10.4	4.1–19.9	5.3	4.7	89.5%
North Central Appalachians	6.6	7.3–11.4	5.8	5.7	99.6%
North Central Hardwood Forests	22.0	5.3–19.0	7.2	6.8	93.2%
Northern Allegheny Plateau	11.5	6.8–12.5	6.9	6.8	98.1%
Northern Appalachian and Atlantic Maritime Highlands	30.7	2.8–15.7	25.7	20.7	80.8%
Northern Lakes and Forests	47.4	3.9–12.4	35.5	34.1	96.3%
Level II ecoregion					
Atlantic Highlands	37.3	2.8–15.7	31.4	26.5	84.3%
Mixed Wood Plains	97.5	2.6–19.9	41.3	33.2	80.5%
Mixed Wood Shield	53.1	3.9–12.4	39.4	36.8	93.3%
Ecoregions combined					
All Ecoregions	187.8	2.6–19.9	112.2	96.5	86.0%
2.b TL_{LOW} = target load at which at least one species is severely at risk					
Level III ecoregion	Ecoregion Area (million acres)	N Deposition (kg ha ⁻¹ yr ⁻¹)	Forested Area (million acres)	Forested Area in Exceedance of TL _{LOW} (million acres)	% of Forested Area in Exceedance of TL _{LOW}
Acadian Plains and Hills	11.2	2.6–7.7	8.0	0.0	0.3%
Northern Minnesota Wetlands	5.6	4.2–8.2	4.0	0.1	3.6%
Southern Michigan/Northern Indiana Drift Plains	13.1	7.9–16.3	3.3	1.4	42.4%
Eastern Great Lakes Lowlands	10.0	4.1–15.5	3.8	1.5	39.7%
Driftless Area	11.7	9.1–15.0	3.7	1.6	43.8%
Northeastern Coastal Zone	10.4	4.1–19.9	5.3	2.4	44.8%
Erie Drift Plain	7.7	8.3–15.5	3.1	2.5	81.1%
Northern Appalachian and Atlantic Maritime Highlands	30.7	2.8–15.7	25.7	3.8	15.0%
North Central Hardwood Forests	22.0	5.3–19.0	7.2	4.4	60.8%
Northern Allegheny Plateau	11.5	6.8–12.5	6.9	5.0	72.1%
North Central Appalachians	6.6	7.3–11.4	5.8	5.2	90.8%
Northern Lakes and Forests	47.4	3.9–12.4	35.5	12.2	34.5%
Level II ecoregion					
Atlantic Highlands	37.3	2.8–15.7	31.4	9.1	28.9%
Mixed Wood Shield	53.1	3.9–12.4	39.4	12.4	31.4%
Mixed Wood Plains	97.5	2.6–19.9	41.3	18.8	45.5%
Ecoregions combined					
All Ecoregions	187.8	2.6–19.9	112.2	40.3	35.9%
2.c TL_{MID} = target load that protects the least sensitive species					
Level III ecoregion	Ecoregion Area (million acres)	N Deposition (kg ha ⁻¹ yr ⁻¹)	Forested Area (million acres)	Forested Area in Exceedance of TL _{MID} (thousand acres)	% of Forested Area in Exceedance of TL _{MID}
Erie Drift Plain	7.7	8.3–15.5	3.1	0.01	0.0%
North Central Appalachians	6.6	7.3–11.4	5.8	0.05	0.0%
Northern Allegheny Plateau	11.5	6.8–12.5	6.9	0.09	0.0%
Northern Appalachian and Atlantic Maritime Highlands	30.7	2.8–15.7	25.7	1.19	0.0%
Northeastern Coastal Zone	10.4	4.1–19.9	5.3	1.74	0.0%
Northern Minnesota Wetlands	5.6	4.2–8.2	4.0	2.33	0.1%
Driftless Area	11.7	9.1–15.0	3.7	6.14	0.2%
Southern Michigan/Northern Indiana Drift Plains	13.1	7.9–16.3	3.3	8.27	0.3%
Eastern Great Lakes Lowlands	10.0	4.1–15.5	3.8	9.66	0.3%
Acadian Plains and Hills	11.2	2.6–7.7	8.0	13.27	0.2%
North Central Hardwood Forests	22.0	5.3–19.0	7.2	37.69	0.5%
Northern Lakes and Forests	47.4	3.9–12.4	35.5	51.88	0.1%
Level II ecoregion					
Atlantic Highlands	37.3	2.8–15.7	31.4	1.23	0.0%
Mixed Wood Shield	53.1	3.9–12.4	39.4	54.21	0.1%

(continued on next page)

Table 2 (continued)

2.a CL for most sensitive species					
Level III ecoregion	Ecoregion Area (million acres)	N Deposition (kg ha ⁻¹ yr ⁻¹)	Forested Area (million acres)	Forested Area in Exceedance of CL (million acres)	% of Forested Area in Exceedance of CL
Mixed Wood Plains	97.5	2.6–19.9	41.3	76.86	0.2%
Ecoregions combined					
All Ecoregions	187.8	2.6–19.9	112.2	4985	4.4%
2.d TL _{HIGH} = target load at which all species are severely at risk					
Level III ecoregion	Ecoregion Area (million acres)	N Deposition (kg ha ⁻¹ yr ⁻¹)	Forested Area (million acres)	Forested Area in Exceedance of TL _{HIGH} (thousand acres)	% of Forested Area in Exceedance of TL _{HIGH}
Northern Minnesota Wetlands	5.6	4.2–8.2	4.0	0.00	0.0%
Acadian Plains and Hills	11.2	2.6–7.7	8.0	0.00	0.0%
Northern Appalachian and Atlantic Maritime Highlands	30.7	2.8–15.7	25.7	0.00	0.0%
Driftless Area	11.7	9.1–15.0	3.7	0.00	0.0%
Erie Drift Plain	7.7	8.3–15.5	3.1	0.01	0.0%
North Central Appalachians	6.6	7.3–11.4	5.8	0.02	0.0%
Northern Allegheny Plateau	11.5	6.8–12.5	6.9	0.04	0.0%
Northeastern Coastal Zone	10.4	4.1–19.9	5.3	0.11	0.0%
Eastern Great Lakes Lowlands	10.0	4.1–15.5	3.8	0.56	0.0%
Northern Lakes and Forests	47.4	3.9–12.4	35.5	2.03	0.0%
Southern Michigan/Northern Indiana Drift Plains	13.1	7.9–16.3	3.3	2.95	0.1%
North Central Hardwood Forests	22.0	5.3–19.0	7.2	5.58	0.1%
Level II ecoregion					
Atlantic Highlands	37.3	2.8–15.7	31.4	0.02	0.0%
Mixed Wood Shield	53.1	3.9–12.4	39.4	2.03	0.0%
Mixed Wood Plains	97.5	2.6–19.9	41.3	9.26	0.0%
Ecoregions combined					
All Ecoregions	187.8	2.6–19.9	112.2	11.30	0.0%

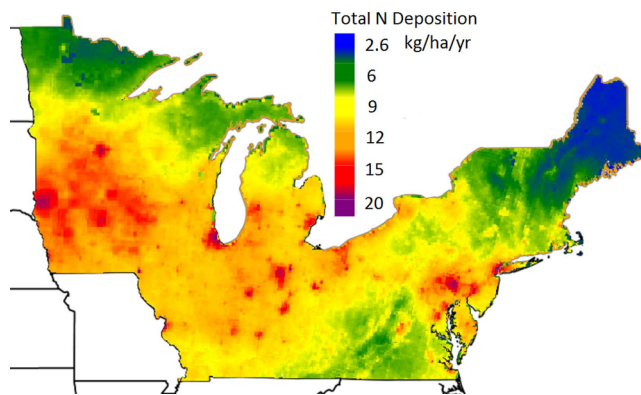


Fig. 6. Average total N deposition (kg ha⁻¹ yr⁻¹) for the northeastern United States for 2013–2015 (TDEP from CASTNET; <https://www.epa.gov/castnet>).

and fall, rather than the growing season (Lynch et al., 2016). Nevertheless, increases in early growing season precipitation have been recently linked to widespread needlecasts and declining growth, highlighting potential need to monitor interactions between critical load exceedance and changing pathogen dynamics (Wyka et al., 2017).

4.2. Quaking aspen

Quaking aspen is an important timber species in the United States, especially used for particle board and for pulp (Clark et al., in press). The extent of this species increased significantly in the upper Lake States region following extensive logging, such that it now represents the dominant forest type across large portions of this region (Schulte et al., 2007). Quaking aspen is also used for site reclamation. Quaking aspen has many wildlife uses - as a food source, important especially in fall and winter, and for habitat, particularly for ruffed grouse. The

species range for quaking aspen extends beyond the study range to the north and south.

Of the 90 million acres quaking aspen covers in the study area, over 50 million acres are classified in exceedance (59% of its extent). In experimental studies, Ca deficiency was the primary cause of growth reduction in quaking aspen (Lu and Sucoff, 2001), an element readily leached from soils in areas of high acid deposition (Johnson and Lindberg, 1992). Other studies have also documented direct impacts of acid deposition on quaking aspen such as leaching of base cations from canopy foliage (Jung and Chang, 2013).

Temperature was the abiotic factor with sub-optimal conditions most frequently adjusting the critical load for quaking aspen into the lower end of its reported critical load range (more susceptible to detrimental effects of N deposition). January and/or growing season temperatures were above the optimal range along most of the southern border of the region (Driftless Area, Erie Drift Plain, North Central Appalachians, Northeastern Coastal Zone, Northern Allegheny Plateau, Southern Michigan/Northern Indiana Drift Plains). This study area occupies the southern end of the native range for quaking aspen, near the high end of its natural temperature tolerance roughly delineated by the 24 °C (75 °F) mean July temperature isotherm in the eastern US (Burns and Honkala, 1990). Given the projections of increasing temperature (Horton et al., 2014), the proportion of these areas with temperature above the optimal range (and the amount above the optimal range) would increase. Modeling areas of suitable habitat also indicate diminishing suitable habitat area for quaking aspen across the region (Iverson et al., 2008).

Precipitation was also above the optimal range for most of the area of all the ecoregions except the three northernmost ecoregions along the western boundary of the study region. Increases in precipitation in the northeastern ecoregions projected by many climate change scenarios (Horton et al., 2014; Lynch et al., 2016) would increase the portion of these areas above the optimal range. While quaking aspen

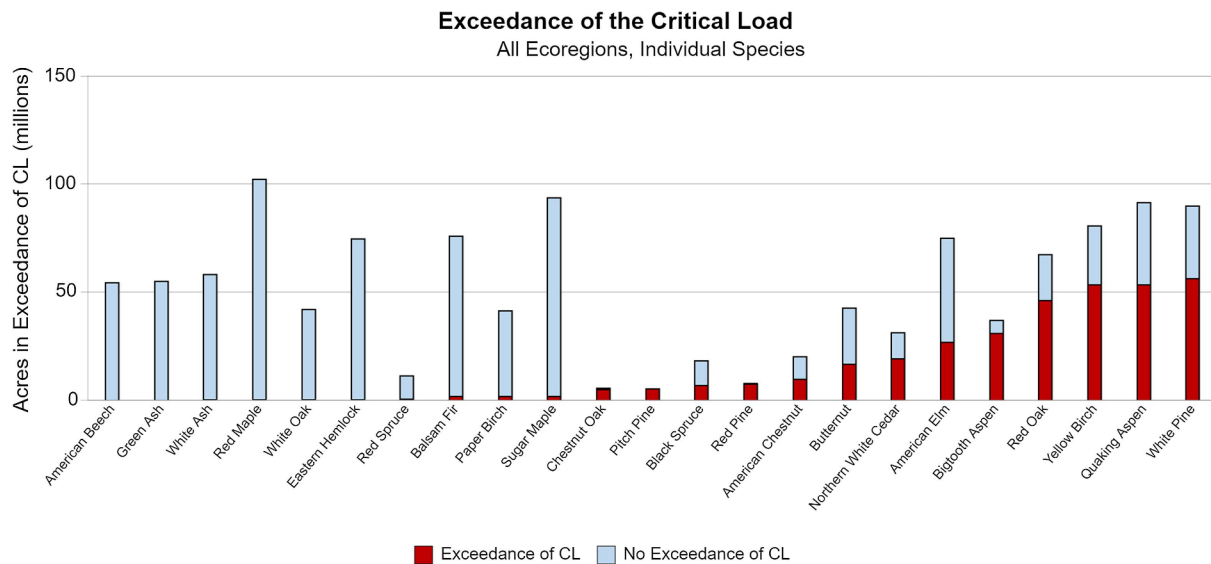


Fig. 7. Acres in exceedance of the CL of N for 23 tree species in level III ecoregions in the study region.

tolerates a broad range of precipitation across its native range, growth is limited on shallow water tables (Burns and Honkala, 1990). However, regional declines in quaking aspen health in the western boundary of the study area are more commonly linked with drought and outbreaks of defoliating insects (Worrall et al., 2013), suggesting that, in the future, such interactions between forest stress and pest outbreaks could be expected.

4.3. Yellow birch

Yellow birch is a long-lived species with moderate growth that can be found on well-drained mountain ravines and upland soils, often as an associate with more shade-tolerant species such as sugar maple, American beech, eastern hemlock, and red spruce. As such, its recruitment in these systems largely relies on mesoscale disturbances that create the light and microsite conditions it needs for establishment (Hanson and Lorimer, 2007). Although it can grow on a variety of soil

types, yellow birch does not compete well with other hardwoods and forbs. Due to its shallow root system and low leaf litter, yellow birch does not tolerate drought. A variety of birds and mammals consume yellow birch seedlings, seeds, bark, sap, and leaves (Clark et al., in press). Yellow birch grows across southeastern Canada and in the northeastern and northcentral United States down through the Appalachian Mountains.

Of the 80 million acres it occupies within the study area, 53 million are classified in exceedance by NCLAS (66% of its extent, Table 3). While yellow birch has experienced historical decline (e.g. widespread birch dieback), declines have been primarily attributed to adverse climate conditions in combination with secondary stress agents (Burns and Honkala, 1990; Hepting, 1971), with little evidence for direct impacts of acid deposition. However, exposure to acid mist has demonstrated significant amino acid leaching from yellow birch foliage (Scherbatskoy and Klein, 1983) and in analyses of FIA plots, yellow birch growth was significantly negatively correlated with exceedance

Table 3

Area in Exceedance of the Critical Load by Species.

Species Latin name	Species common name	Species Area (million acres)	Area in Exceedance (million acres)	% Area in Exceedance
<i>Fagus grandifolia</i>	American beech	54.6	0.0	0.04
<i>Fraxinus pennsylvanica</i>	Green ash	55.2	0.1	0.24
<i>Fraxinus americana</i>	White ash	58.2	0.2	0.41
<i>Acer rubrum</i>	Red maple	102.4	0.3	0.25
<i>Quercus alba</i>	White oak	42.2	0.4	0.97
<i>Tsuga canadensis</i>	Eastern hemlock	74.7	0.5	0.60
<i>Picea rubens</i>	Red spruce	11.3	0.8	6.9
<i>Abies balsamea</i>	Balsam fir	76.1	1.8	2.3
<i>Betula papyrifera</i>	Paper birch	41.5	2.0	4.7
<i>Acer saccharum</i>	Sugar maple	93.9	2.0	2.1
<i>Quercus montana</i>	Chestnut oak	5.6	5.0	89
<i>Pinus rigida</i>	Pitch pine	5.3	5.3	100
<i>Picea mariana</i>	Black spruce	18.3	7.1	39
<i>Pinus resinosa</i>	Red pine	8.0	7.7	96
<i>Castanea dentata</i>	American chestnut	20.2	9.8	48
<i>Juglans cinerea</i>	Butternut	42.7	16.6	39
<i>Thuja occidentalis</i>	Northern white cedar	31.2	19.3	62
<i>Ulmus americana</i>	American elm	75.0	26.8	36
<i>Populus grandidentata</i>	Bigtooth aspen	37.2	31.1	84
<i>Quercus rubra</i>	Red oak	67.5	46.1	68
<i>Betula alleghaniensis</i>	Yellow birch	80.8	53.6	66
<i>Populus tremuloides</i>	Quaking aspen	91.5	53.6	59
<i>Pinus strobus</i>	Eastern white pine	89.9	56.4	63

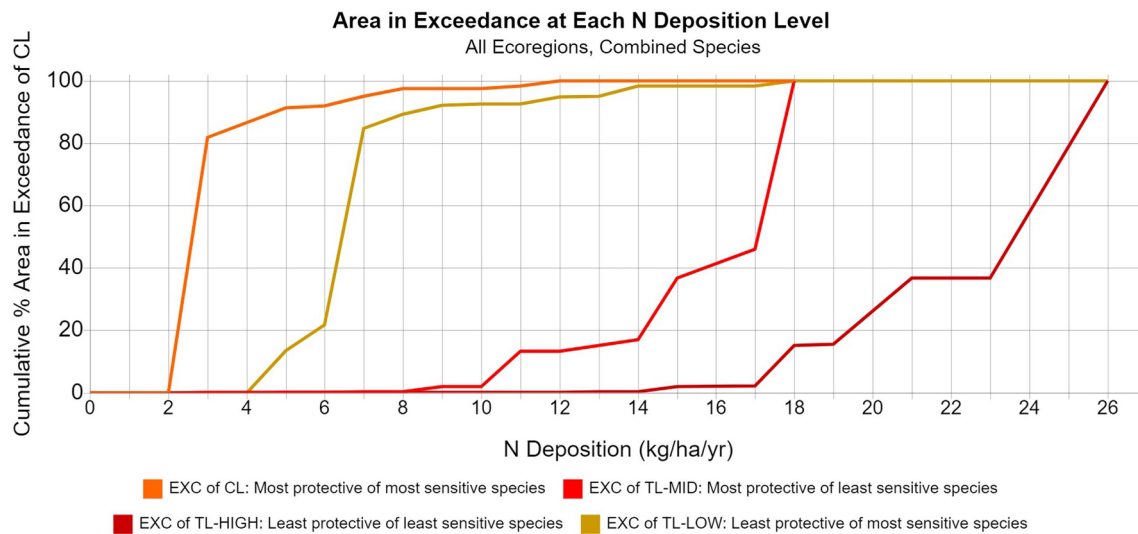


Fig. 8. Cumulative % area in exceedance of CL of N for level III ecoregions with increasing N deposition. CL = most protective CL for most sensitive species; TL_{LOW} = least protective CL for most sensitive species (one species is severely at risk); TL_{MID} = most protective CL for least sensitive species; TL_{HIGH} = least protective CL for least sensitive species (all species severely at risk). This figure shows the area that would be exceeded as N deposition increases; it does not reflect actual deposition values.

(Duarte et al., 2013).

Temperatures across the study area are generally above the optimal range for yellow birch; May to September temperatures are above optimal across the majority of the study area. January temperatures are primarily within the optimal range or below optimal in northern ecoregions: Acadian Plains and Hills, Northern Appalachian and Atlantic Maritime highlands, Northern Lakes and Forests, and Northern Minnesota Wetlands.

Historic decline episodes for this species have been linked to freeze-thaw events, which reflects the sensitivity of the shallow-rooted species to changes in winter precipitation and associated root injury (Bourque et al., 2005). Its shallow root system and low leaf litter also make yellow birch drought sensitive. However, precipitation was only below optimal in large portions of Midwestern ecoregions. Predicted decreases in growing season precipitation and increases in temperature in these regions (Horton et al., 2014) will result in a decrease in optimal conditions for yellow birch, especially in the southern and Midwestern

parts of its range.

4.4. Northern red oak

Northern red oak can be found on a variety of soil types in north-eastern forests, but grows best on deep, fertile, well drained soils. Red oak is an important source of food and habitat for a wide variety of insects, birds, and mammals. The hard, strong wood has many uses, including flooring and cabinetry (Clark et al., in press). Northern red oak grows across the much of the eastern United States.

Of the 67 million acres it occupies within the study area, 46 million acres are classified as in exceedance by NCLAS (68% of its extent). Several studies have demonstrated impacts of acid deposition on red oak, including: significant reduction in mycorrhiza in acid treated seedlings (e.g. Reich et al., 1985) and nutrient imbalances and deficiencies that result from atmospheric deposition (Hallett and Hornbeck, 1997). Across FIA plots, red oak growth was significantly negatively

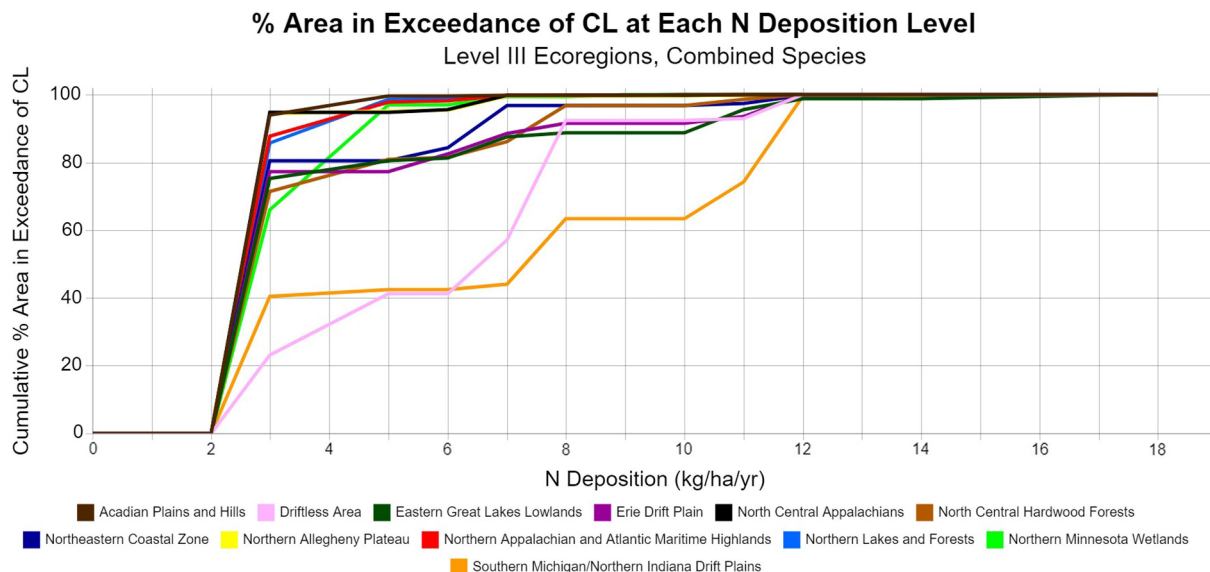


Fig. 9. Cumulative % areas in exceedance of the CL of N for individual level III ecoregions with increasing N deposition. This figure shows the area that would be exceeded as N deposition increases; it does not reflect actual deposition values.

Table 4a

Percent area in exceedance of the CL of N for the Driftless Area ecoregion for varying levels of N deposition. This table shows the area that would be exceeded at each N deposition level and does not reflect actual deposition values.

% Area in Exceedance of the CL at Each N Deposition Level

Area: Level III ecoregion
 Site: Driftless Area
 Size (ac): 11,709,382
 N Deposition (kg/ha/yr): 9.1 to 15.0

	N Deposition (kg ha ⁻¹ yr ⁻¹)																			
	0	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19
Balsam fir	0	0	0	0	0	0	0	0	0	100	100	100	100	100	100	100	100	100	100	100
Red maple	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Sugar maple	0	0	0	0	0	0	0	0	0	1	1	1	1	1	1	1	1	1	1	100
Yellow birch	0	0	0	100	100	100	100	100	100	100	100	100	100	100	100	100	100	100	100	100
Paper birch	0	0	0	0	0	0	0	0	0	85	85	85	85	85	85	85	100	100	100	100
White ash	0	0	0	0	0	0	0	0	0	0	23	23	23	23	23	100	100	100	100	100
Green ash	0	0	0	0	0	0	0	0	0	0	3	3	3	3	3	100	100	100	100	100
Butternut	0	0	0	0	0	0	0	37	37	37	37	37	37	37	100	100	100	100	100	100
Black spruce	0	0	0	0	0	0	100	100	100	100	100	100	100	100	100	100	100	100	100	100
Red pine	0	0	0	99	99	99	99	100	100	100	100	100	100	100	100	100	100	100	100	100
Eastern white pine	0	0	0	0	0	8	8	8	100	100	100	100	100	100	100	100	100	100	100	100
Bigtooth aspen	0	0	0	100	100	100	100	100	100	100	100	100	100	100	100	100	100	100	100	100
Quaking aspen	0	0	0	0	0	100	100	100	100	100	100	100	100	100	100	100	100	100	100	100
White oak	0	0	0	0	0	0	0	0	0	0	0	24	24	24	24	100	100	100	100	100
Red oak	0	0	0	1	1	1	1	1	1	100	100	100	100	100	100	100	100	100	100	100
Northern white cedar	0	0	0	100	100	100	100	100	100	100	100	100	100	100	100	100	100	100	100	100
Eastern hemlock	0	0	0	0	0	0	0	0	0	0	0	5	5	5	5	5	5	100	100	100
American elm	0	0	0	0	0	0	0	4	4	4	4	4	4	4	100	100	100	100	100	100

Table 4b

Percent area in exceedance of the CL of N for the Southern Michigan/Northern Indiana Drift Plains ecoregion for varying levels of N deposition. This table shows the area that would be exceeded at each N deposition level and does not reflect actual deposition values.

% Area in Exceedance of the CL at Each N Deposition Level

Area: Level III ecoregion
 Site: Southern Michigan/Northern Indiana Drift Plains
 Size (ac): 13,051,228
 N Deposition (kg/ha/yr): 7.9 to 16.3

	N Deposition (kg ha ⁻¹ yr ⁻¹)																			
	0	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19
Balsam fir	0	0	0	0	0	0	0	0	0	0	0	2	2	2	2	2	2	2	2	100
Red maple	0	0	0	0	0	0	0	0	0	1	1	1	1	1	1	1	1	1	100	100
Sugar maple	0	0	0	100	100	100	100	100	100	100	100	100	100	100	100	100	100	100	100	100
Yellow birch	0	0	0	0	0	0	0	0	0	0	100	100	100	100	100	100	100	100	100	100
Yellow birch	0	0	0	0	0	0	0	0	0	0	0	38	38	38	100	100	100	100	100	100
White ash	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	100	100	100	100
Green ash	0	0	0	0	0	0	0	0	0	0	0	6	6	6	6	100	100	100	100	100
Butternut	0	0	0	0	0	0	0	30	30	30	30	30	30	100	100	100	100	100	100	100
Black spruce	0	0	0	0	0	0	100	100	100	100	100	100	100	100	100	100	100	100	100	100
Red pine	0	0	0	95	95	95	95	100	100	100	100	100	100	100	100	100	100	100	100	100
Eastern white pine	0	0	0	0	0	7	7	7	100	100	100	100	100	100	100	100	100	100	100	100
Bigtooth aspen	0	0	0	76	76	76	76	100	100	100	100	100	100	100	100	100	100	100	100	100
Quaking aspen	0	0	0	0	0	100	100	100	100	100	100	100	100	100	100	100	100	100	100	100
White oak	0	0	0	0	0	0	0	0	0	0	0	36	36	36	36	100	100	100	100	100
Chestnut oak	0	0	0	100	100	100	100	100	100	100	100	100	100	100	100	100	100	100	100	100
Red oak	0	0	0	1	1	1	1	1	1	1	100	100	100	100	100	100	100	100	100	100
Northern white cedar	0	0	0	100	100	100	100	100	100	100	100	100	100	100	100	100	100	100	100	100
Eastern hemlock	0	0	0	0	0	0	0	0	0	0	0	30	30	30	30	30	30	100	100	100
American elm	0	0	0	0	0	0	0	7	7	7	7	7	7	100	100	100	100	100	100	100

correlated with exceedance (Duarte et al., 2013). Other studies indicate a geographic pattern in red oak sensitivity to acid deposition, with little threat to red oak growth in the southern portion of its range and higher sensitivity in the Northeast (Joslin and Wolfe, 1989).

Temperatures are optimal for red oak in many of the southern ecoregions in the study area, but are currently almost entirely below optimal in the Northern Minnesota Wetlands, much of the Acadian Plains and Hills, Northern Appalachian and Atlantic Maritime highlands, and Northern Lakes and Forests. These sub-optimal conditions are expected as much of the study area occurs near the northern extent of the native range for red oak (Burns and Honkala, 1990). Predicted increases in temperature (Horton et al., 2014) may result in some of the southern ecoregions in the study area becoming less optimal for red oak, while northern ecoregions may become more optimal.

The majority of the study area is within the optimal precipitation range, although about 40% of the North Central Appalachians has above optimal May to September precipitation, while almost all of the Northern Minnesota Wetlands have below optimal annual precipitation. The vast majority of red oak decline has been attributed to a range of pest and pathogen agents (Wargo et al., 1983), but has also been linked to drought (Tainter et al., 1990) and lower than normal winter temperatures (Tainter et al., 1984). While an increased frequency of drought may increase red oak vulnerability, projections of future habitat suitability for red oak also suggest an increasing level of suitability for northern regions over the next century (Wang et al., 2017).

4.5. Bigtooth aspen

Bigtooth aspen grows in the northeastern and north central United States and southeastern Canada. Aspen is a relatively fast-growing pioneer species that is eventually replaced by other hardwood and coniferous species on fertile sites (Clark et al., in press). Like quaking aspen, the abundance of bigtooth aspen increased in many portions of the study region following extensive logging in the 19th century. However, given the comparatively demanding site requirements of this species, the increase has been less extensive. Bigtooth aspen provides food and habitat for many bird species, including the ruffed grouse, as well as moose, deer, and beavers. This species is tolerant of poor soils and can be used to reclaim contaminated soils. The fine textured, soft wood is used primarily for pulp.

Of the 37 million acres of the study area that are occupied by bigtooth aspen, 31 million acres are classified by NCLAS as in exceedance. This accounts for 84% of its extent in the region, highlighting its widespread sensitivity to acid deposition. Across FIA plots, bigtooth aspen growth was significantly negatively correlated with exceedance (Duarte et al., 2013), although few other studies directly link bigtooth aspen to acid deposition.

Temperature and precipitation were the abiotic factor with sub-optimal conditions most frequently adjusting the critical load for bigtooth aspen into the lower end of its reported critical load range (more susceptible to detrimental effects of N deposition). Both factors were above the optimal range in parts of most ecoregions in the study area; the January temperature was above optimal in the majority of the Erie Drift Plain, Northeastern Coastal Zone, and the Southern Michigan/Northern Indiana Drift Plains; annual precipitation was above optimal in the majority of northeastern ecoregions. Projected increases in temperature and annual precipitation in the eastern ecoregions (Horton et al., 2014) would render a greater proportion of bigtooth aspen's current habitat above the optimal range. Modeling areas of suitable habitat also indicate diminishing habitat area for bigtooth aspen across the region (Iverson et al., 2008).

4.6. Red pine

Red pine is used for lumber and pulpwood and has been planted extensively across portions of the upper Lake States and northeastern

United States for wood production (Gilmore and Palik, 2006). Like pitch pine, red pine forests are fire-dependent communities and naturally occur on coarse textured soils or ridgetop communities. Red pine provides nutrition via seeds, bark, and seedlings to both small and large mammals and is the exclusive habitat (in white-jack-red pine stands) for two species of warblers, including the federally endangered Kirtland's warbler (Clark et al., in press).

Red pine occupies a relatively small proportion of the study area (8 million acres). However, over 95% of its extent (7.7 million acres) is classified as in exceedance by NCLAS. Because of its sensitivity, red pine has been suggested as an indicator species for harmful effects of SO_x pollution (Smith, 1990). Acid deposition has also been implicated in tree declines and increased frost risk of red pine in Japan (Shan et al., 2000). While red pine has fewer commonly damaging agents than most associated species when growing under conditions natural to its native range, under sub-optimal conditions it is susceptible to secondary stress agents (Burns and Honkala, 1990).

Elevation falls below the optimal range for most of the area in the coastal ecoregions.

Red pine is native to areas with cool-to-warm summers, cold winters, and low-to-moderate precipitation. Within our study area, at the southern end of the native range, both annual and growing season precipitation were often above the optimal range. January temperature tends to be higher than the optimal range for southern and western ecoregions (Erie Drift Plain, Southern Michigan/Northern Indiana Drift Plains, and Northern Minnesota Wetlands). The only exceptions occurred in the two northernmost ecoregions on the western side of the study region, where annual precipitation fell below the optimal range, and the Northeast Coastal Zone where January temperature was below optimal range. Given the drought tolerance of mature red pines, the projected decreases in growing season precipitation (Horton et al., 2014; Ning et al., 2015) may not increase the area of red pine at risk. However, the projected increases in annual precipitation projected for the eastern part of the region would increase the portion of these ecoregions with precipitation above the optimal range.

4.7. Chestnut oak

Chestnut oak is most commonly found in dry upland sites in the Appalachian region, with the best growth occurring on well-drained soil along streams in mountainous areas (McQuilkin, 1990). Chestnut oaks can become dominant on sites with a disturbance regime, including fire or land clearing. In the absence of disturbance, shade tolerant species such as red maple (*Acer rubrum*) and yellow birch eventually outcompete chestnut oak (Mikan et al., 1994). Acorns from this oak are an important food source for many wildlife species. While most trees are medium sized with low branches, high quality trees are marketed as white oak (McQuilkin, 1990).

Chestnut oak occurs in 5.6 million acres in the study area; the majority of the range for this species extends further south. Five million acres are classified as in exceedance in NCLAS, about 89% of the total area it occupies. Declines in chestnut oak growth have been linked to acid deposition (Puckett, 1982), and growth was significantly negatively correlated with critical loads exceedance across the region (Duarte et al., 2013). Increased nitrogen deposition has also been correlated with increased mortality (Thomas et al., 2010).

As expected for a species near the northern extent of its range, temperatures for chestnut oak were sub-optimal across most of the study area, including portions of the North Central Highlands, the Northern Allegheny Plateau, and the Northern Appalachian and Atlantic Maritime Highlands. Growing season and January temperatures were the primary factors that resulted in an adjusted critical load to the lower end of its reported critical load range (more susceptible to detrimental effects from N deposition). Increasing temperatures as projected by Horton et al. (2014) could result in increased areas with optimal temperature conditions for chestnut oak in the study area,

leading to greater tolerance of N deposition.

4.8. Pitch pine

While occupying the smallest area within the region (5 million acres), pitch pine is classified in exceedance over 100% of this extent. Pitch pine is the dominant conifer species in pine barrens across the northeastern United States, including on extensive outwash and moraine deposits on Cape Cod, MA, Long Island, NY, and southern New Jersey. Historically, this species was used for turpentine and, due to its tolerance of harsh habitats, can be used in site reclamation of degraded areas (Clark et al., *in press*). Given the suitability of areas supporting pitch pine barrens for development, the extent of pitch pine forests has been greatly reduced, with these ecosystems now recognized as globally rare (Jordan et al., 2003).

Pitch pine is in exceedance across the highest percentage of area of any species in this study area. This may be due, in part, to its typical location on acidic, coarse soils where capacity to mitigate acid deposition is limited. Studies have linked soil acidification as a result of acid deposition to reductions in pitch pine growth (Johnson et al., 1981; Rhyu et al., 1994), alterations in seedling growth and nutrient relationships (Schier, 1986) and inhibited root growth (Schier, 1987).

Because of the study area's location at the northern end of its native extent, temperature is often lower than optimal where pitch pine occurs across the study area, while elevation is higher than the optimal range in mountainous regions. A previous study indicated that increases in acid deposition resulted in physiological stress which made climate conditions that were normally tolerated, limiting to tree growth (Puckett, 1982), which presents a quantitative link between suboptimal climate conditions and sensitivity to acid deposition. The two western ecoregions where pitch pine occurs have precipitation lower than the optimal range, while precipitation extends higher than the optimal ranges in the Appalachian Mountains.

5. Conclusions

Our analysis predicts that most forests in the northeastern United States are at risk of detrimental effects from N deposition, although the extent and magnitude of the risk varies considerably. It also highlights the variation in susceptibility to N deposition by species and, thus, the importance of considering individual tree species responses.

N-CLAS provides a major step forward for resource managers and policy makers by providing a simple tool that can be used to assess current and future risk from N deposition and the relative significance of climatic conditions, site and soil characteristics in determining forest susceptibility in different locations (<http://nadp.slh.wisc.edu/committees/clad/links.aspx>). N-CLAS has multiple user and application scenarios built in to facilitate its use. Resource managers can use N-CLAS to determine how many acres are currently in exceedance and which species are most susceptible to N deposition. Policy makers can use N-CLAS to determine the extent of area at risk at given N deposition levels and how exceedance will shift with future deposition scenarios. Scientific modelers can use the synthesis of the influence of abiotic factors on tree growth provided by N-CLAS in the development of dynamic models.

N-CLAS also provides a customizable analysis by allowing the user to select the area of interest, the tree species to include, and the level of protection (e.g., the critical load, which is the most protective, or a less protective target load). Depending on management objectives, a resource manager might produce output tables, figures, and maps to protect: the most sensitive species across the whole area; a key species of management, cultural, or aesthetic significance; or a specific rare species. As an example, for a species of management concern like northern red oak, whose regeneration has posed a challenge over some decades in Vermont, N-CLAS provides information about the spatial distribution of areas where northern red oak is more susceptible (i.e.,

shifted to the lower, more N sensitive end of the critical load range because of site conditions) and also allows interpretation of the spatial patterns in the climatic conditions, site and soil characteristics that drive that sensitivity.

N-CLAS also has a number of uses not directly related to air pollution assessments. N-CLAS provides easy access to high quality, seamless abiotic data layers and histograms describing the distribution of the abiotic factors within a user-selected region. Management uses of the tool beyond CLs include understanding potential sensitivities to various abiotic factors, with the potential to map risk or niche locations.

Ultimately, it would be useful to model competition and to incorporate the differing responses of individual tree species to N deposition dynamically, and to evaluate how that would affect species composition over time and under varying climate scenarios (Van Houtven et al., 2019). In the future, we plan to expand N-CLAS to the national scale by incorporating information from a national-scale analysis for tree growth and survival responses to air pollution (Horn et al., 2018). In the meantime, N-CLAS represents a significant refinement in empirical critical loads with improved spatial resolution and provides an easy-to-use management tool that allows resource managers to benefit from the current state-of-the science understanding of the potential risk to forests in the northeastern United States.

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Appendix A. Supplementary material

Supplementary data to this article can be found online at <https://doi.org/10.1016/j.foreco.2019.117528>.

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