



Applying Mycorrhizal Critical Loads of Nitrogen to US Federal Lands Containing Forested and Mediterranean Shrubland Ecosystems



A mushroom rising from the forest floor at the Potomac Heritage National Scenic Trail in Maryland.
NPS / MONICA LARCOM

Applying mycorrhizal critical loads of nitrogen to US federal lands containing forested and Mediterranean shrubland ecosystems

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Abstract

Mycorrhizal fungi (MF) play a crucial role within ecosystems by forming mutually symbiotic relationships where they share water, carbon, nutrients, and other benefits with plants they have inoculated. Since these plant communities depend on MF for survival, the status of MF communities can be used as a proxy for the health of the plants they support. Anthropogenic nitrogen (N) deposition can disrupt the symbiotic relationship between the plants and MF by causing a shift in mycorrhizal community composition, and in turn a shift in the plant structure within an ecosystem. Lilleskov et al. (2019) summarized recent research on critical loads (CLs) of N for a shift from N-sensitive to N-tolerant mycorrhizal and tree communities, setting CLs to protect conifer-associated MF (5–6 kg-N ha⁻¹ yr⁻¹), and broadleaf-associated MF (10–20 kg-N ha⁻¹ yr⁻¹). Allen et al. (2016) developed CLs of N for shifts in arbuscular MF communities in California coastal sage scrub which contribute to the conversion of native shrubland to exotic annual grassland (10–11 kg-N ha⁻¹ yr⁻¹).

Here we apply the CL-N for forest mycorrhizae to forested areas in the contiguous United States (CONUS), and the CL-N for southern California shrubland mycorrhizae to shrublands and grasslands within the Mediterranean ecoregion of California. The National Atmospheric Deposition Program (NADP) Total Deposition model (TDep) for total N deposition from 2018–2020 (v2018.02) is used to calculate exceedances of the CLs and evaluate potential risk to forest health. The areas of exceedance are calculated for all units within CONUS managed by the Fish and Wildlife Service (FWS), National Park Service (NPS), and Forest Service (USFS).

Within CONUS, 68% of federal land managed by the three agencies is forest: 76% is conifer, 17% is broadleaf, and 7% is a mixture of both tree communities. The USFS manages 93% of this forested land, and 30% of USFS forests are in exceedance of CLs-N for MF. The NPS manages a smaller portion of federal forested land at 6%, with exceedance occurring in 29% of that area. The FWS controls only 1% of forested land but has exceedance of CLs in 43% of that area.

Within Mediterranean California (CA), 29% of federal land managed by the three agencies is shrubland or grassland. Federal shrublands are in exceedance of the CL-N for MF in 25% of the area. The USFS manages 91% of federal shrublands in Mediterranean CA, with 27% of USFS CA shrublands in exceedance of the CL. The NPS manages 8% of federal shrublands in Mediterranean CA, of which only 3% is experiencing exceedance. The FWS is only responsible for 1% federal shrublands in Mediterranean CA, with exceedance occurring in 22% of that area.

This analysis shows the effects that N deposition has on forest and shrubland ecosystems occurring within federal lands across CONUS. Knowing the extent of exceedance observed within federal lands informs natural resource management. On smaller scales, this analysis enables federal land managers to better understand what is happening on their lands, effectively guiding local management decisions. On larger scales, the analysis outlines a portion of the overall effects that N deposition has on ecosystems within CONUS, providing policymakers with the scientific evidence required to support future policy actions aimed at protecting natural resources.

Introduction

A priority of the National Park Service (NPS) is to ensure the continued protection of natural resources found within national parks. Vegetation is a widespread resource throughout parks and plays a crucial role in maintaining ecosystem function. Many plants have mutually symbiotic relationships with mycorrhizal fungi (MF) that attach to their roots and form a mycelial network within the soil, connecting individual plants together and facilitating the uptake and transfer of nutrients. The plants supply the MF with organic material that the fungi use for growth, and in return the MF supply the plants with water, nutrients, and various other benefits (Simard et al., 2012).

Nitrogen (N) is an important nutrient that determines the rate of growth and photosynthesis for many plants. MF enhance plant access to N and other soil nutrients, increase the drought tolerance of plants, and provide physical resistance to soil erosion (George et al., 1995; Cheng et al., 2021; Burri et al., 2013). Human activities have increased N pollution through the burning of fossil fuels and the application of N-rich fertilizers for agriculture. Excess N can disrupt the symbiosis of MF and their associated plant communities. When anthropogenic pollution increases N availability in the soil, MF become less important for the acquisition of N and many plants will cease the exchange of nutrients altogether (Lilleskov et al., 2019). Although the plants obtain their required amounts of N, they lose the other benefits MF normally provide, including enhanced water and micronutrient uptake. The loss of the mycorrhizal symbiosis makes plants more vulnerable to other environmental stressors such as drought. N deposition can thus lead first to a decline in MF and then to changes in plant abundance and composition.

Numerous studies have explored the response of both forest and shrubland ecosystems to levels of N pollution that affect mycorrhizae through the use of critical loads (CL). A CL is “the quantitative exposure to one or more pollutants below which significant harmful effects on sensitive elements of the environment do not occur, according to present knowledge” (Nilsson and Grennfelt, 1988). Land managers utilize CLs to determine what species or communities are likely being impacted within their ecosystems and estimate how much damage is likely occurring. When N deposition occurs at a rate higher than the CL the area is said to be in exceedance of the CL. CLs of N for a shift in mycorrhizal communities have been developed for both forest and southern California shrubland ecosystems.

Tree species across the US have growth and survival rates dependent on relationships with N deposition (Horn et al., 2018). Many conifers associate with MF that are sensitive to N deposition, leading to a loss in diversity in coniferous forests, and a potential shift to broadleaf dominant forest under high N deposition (Lilleskov et al., 2019). Lilleskov et al. (2019) synthesized recent research on the effects of N deposition upon MF and published CLs to prevent declines in N-sensitive ectomycorrhizal fungal species. This synthesis uses multiple lines of evidence from US and European forests to suggest that increasing N deposition or increased time under N deposition could cause a cascade of changes in mycorrhizal and plant communities. Excess N deposition may:

1. trigger declines in N-sensitive ectomycorrhizal fungi that form symbioses with individual conifer species (based on long-term European ICP Forest monitoring), then
2. trigger declines in N-sensitive arbuscular mycorrhizal fungi (AMF; based on eastern US sugar maple forests), then
3. trigger increases in N-tolerant ectomycorrhizal fungi that are generalists and form symbioses with conifer or broad-leaf tree species (empirical CL synthesis for EU forests, European ICP Forest monitoring), and then
4. trigger shifts from conifer- to broadleaf-dominated forests, since broadleaf tree species are more likely to form symbioses with N-tolerant AMF (Lilleskov et al., 2019).

The CLs in the synthesis are meant to prevent the first step in that cascade. A CL of 5–6 kg-N ha⁻¹ yr⁻¹ protects N-sensitive ectomycorrhizal fungi in conifer-dominated forests, and a CL of 10–20 kg-N ha⁻¹ yr⁻¹ protects N-sensitive ectomycorrhizal fungi and N-sensitive arbuscular mycorrhizae in broadleaf forests (Lilleskov et al., 2019).

The Mediterranean California ecoregion is a biodiversity hotspot consisting of numerous ecosystems that support a variety of endemic plants. Allen et al. (2016) synthesized evidence of N deposition effects on plant and fungal communities in California coastal sage scrub from long-term vegetation surveys, deposition gradient studies, N addition field experiments, microcosm studies, and greenhouse studies. California sagebrush (*Artemisia tridentata*) and other native shrub species have died back since 1930 in many areas of Mediterranean California receiving high N deposition (Talluto and Suding, 2008; Cox et al., 2014). In contrast, exotic annual grasses invading these shrublands tend to have neutral or positive responses to increases in N deposition (Rao and Allen, 2010). Mycorrhizal communities shift along with plant communities as N deposition increases; AMF associated with sagebrush decrease in richness, abundance, and in their symbiosis with plant roots, and fine AMF species that benefit invasive grasses become dominant (Allen et al., 2016). An ecosystem-level conversion takes place as native shrubs are replaced by exotic annual grasses (Allen et al., 2016), which in turn provide a constant source of flash fuels and lead to increased fire risk (Cione et al., 2002). Given these measured responses in southern California's coastal sage scrub, Allen et al. (2016) established CLs for a shift in arbuscular mycorrhizal communities and plant richness at 10–11 kg-N ha⁻¹ yr⁻¹.

This report applies CLs of N for forest and shrubland ecosystems to appropriate landcover classes to determine the location and distribution of areas at risk from N deposition. Understanding the spatial relationships between N deposition and exceedance helps federal land managers predict the impact of current N deposition in their local areas of concern, as well as inform future land management strategies.

Methods

Critical Loads

Forests

Critical loads of nitrogen (N) for a shift in mycorrhizal communities and associated forest communities are summarized by Lilleskov et al. (2019). The CLs for conifer-associated MF are 5–6 kg-N ha⁻¹ yr⁻¹ and the CLs for broadleaf-associated MF are 10–11 kg-N ha⁻¹ yr⁻¹. To determine where the CLs are applicable within parks, the CL values were applied to forest land cover (Figure 1) as defined by the 2019 National Land Cover Database (NLCD; Dewitz, 2021). The NLCD defines forest cover as either evergreen, deciduous, or mixed. Since the majority of evergreen trees in the US are conifer, we apply the CL for conifer-associated MF (5–6 kg-N ha⁻¹ yr⁻¹) to evergreen forest cover. Similarly, since most of deciduous trees in the US are broadleaf, we apply the CL for broadleaf-associated MF (10–20 kg-N ha⁻¹ yr⁻¹) to deciduous forest cover. For mixed forests, the lowest minimum (min) and highest maximum (max) from both the CL for conifer-associated (5 kg-N ha⁻¹ yr⁻¹) and broadleaf-associated (20 kg-N ha⁻¹ yr⁻¹) MF were chosen. These CLs ensure that even the most sensitive species are protected at the low end of the range and all species are at risk at the high end of the range. The cell size for forested land cover was aggregated from 30 m × 30 m to 240 m × 240 m to match the cell size of the N deposition surface. A cell was only designated as ‘forested land’ when forest made up 10% or more of the 240 m × 240 m cell’s total area.

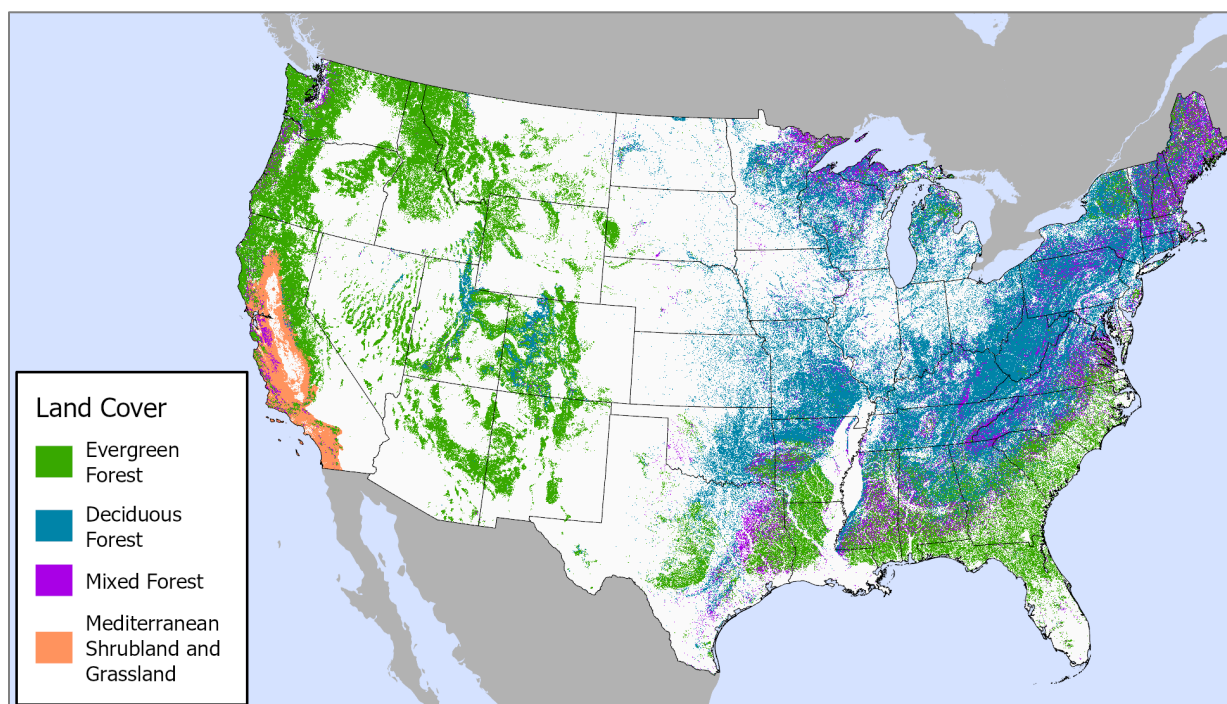


Figure 1. Land cover categories where critical loads of nitrogen for a shift in mycorrhizal community composition are applied. Land cover classes obtained from the National Land Cover Database.

Shrublands

For southern California's coastal sage scrub, Allen et al. (2016) established CLs of N for a shift in arbuscular mycorrhizal communities as 10–11 kg-N ha⁻¹ yr⁻¹. We apply these CLs to the shrublands and grasslands (Figure 1) within the Mediterranean California ecoregion level I as defined by Omernik and Griffith (2014). Areas containing shrublands and grasslands were determined using the NLCD categories for shrub/scrub and grassland/herbaceous. The cell size for land cover was aggregated from 30 m × 30 m to 240 m × 240 m, and cells were only designated 'shrubland' if the 240 m × 240 m cell contained over 10% of shrubland and/or grassland. The min and max CLs for shrubland-associated MF are 10 kg-N ha⁻¹ yr⁻¹ and 11 kg-N ha⁻¹ yr⁻¹, respectively.

Deposition and Exceedance

N deposition values across the contiguous United States are from the National Atmospheric Deposition Program (NADP) Total Deposition model (TDep) mean annual total N deposition from 2018–2020 (v2018.02; NADP, 2020). To estimate total N, the models incorporate measured NH₄⁺ (wet), NO₃⁻ (wet/dry) and HNO₃ (dry) deposition, and model dry deposition of NH₃, PAN, N₂O₅, NO₂, HONO, and organic nitrates (Schwede and Lear, 2014). Levels of N deposition greater than or equal to the CL indicate the community is likely to experience negative effects caused by N deposition. CL exceedance is calculated by subtracting the CL from the level of N deposition being experienced. Exceedance of the min CL indicates the most sensitive mycorrhizal community in an area is likely to experience harm due to N deposition. Exceedance of the max CL indicates that the least sensitive mycorrhizal community in an area is at risk, and therefore all mycorrhizal communities are also at risk.

Min and max CL exceedances were calculated for conifer-, broadleaf-, and mixed-associated MF and applied to their respective land cover categories. Min and max CL exceedances were also calculated across the Mediterranean California ecoregion for a shift in shrubland-associated arbuscular mycorrhizal communities.

CL Exceedances in Federal Lands

To measure the extent of CL exceedances occurring within federal lands, we considered land cover type and deposition within all land units managed by Fish and Wildlife Service (FWS), National Park Service (NPS), and the US Forest Service (USFS; Figure 2). This report only includes units that both contain plant communities with CLs-N for MF (forest within CONUS or shrubland within Mediterranean California) and that have deposition data available. It is important to note that the Wilderness Areas included in this study are all subsets of National Forests that have been given special protections based on their natural resources. For both ecosystem types, these overlaps were taken into consideration when calculating area-based statistics to avoid double-counting land. However, when looking at an individual land unit or unit type, all land within a unit's boundary was considered, regardless of any overlaps with other units.

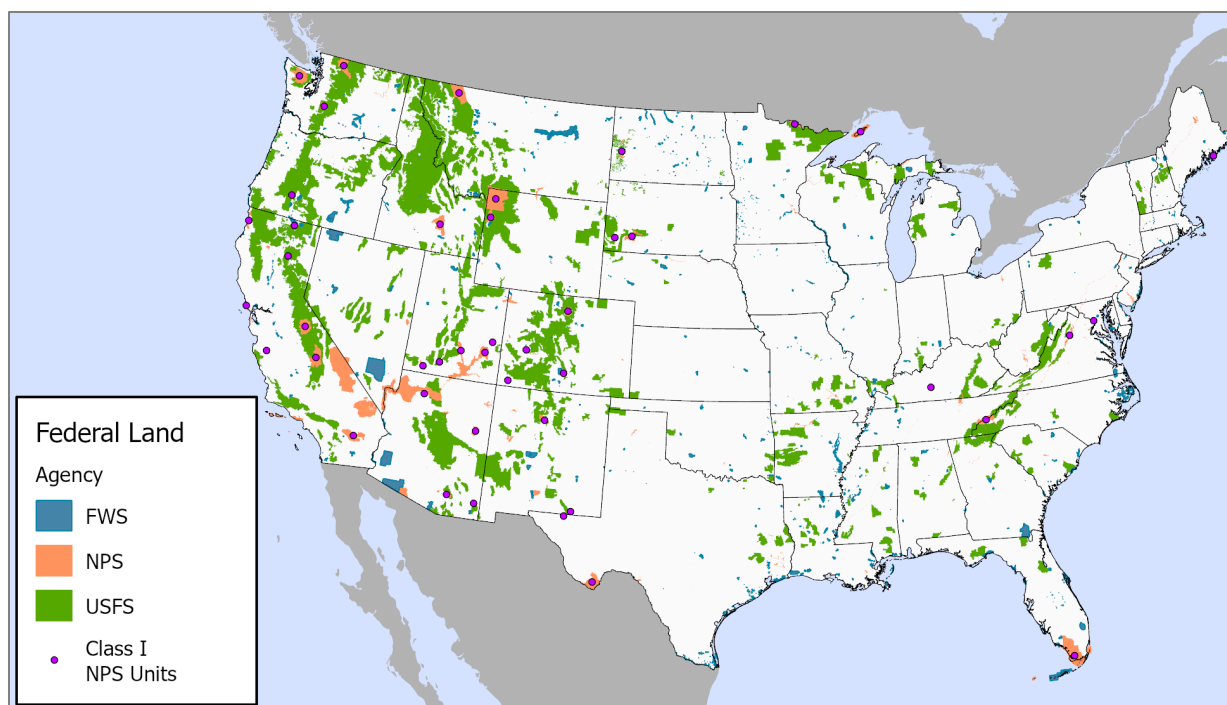


Figure 2. Federal lands of the contiguous US managed by the Fish and Wildlife Service (FWS), National Park Service (NPS), and US Forest Service (USFS). Class I NPS units are also included.

The Clean Air Act 1977 Amendments designated certain federal lands as Class I areas which have stricter air quality standards for protecting visibility and preventing air quality deterioration. Of the 147 Class I units containing forested land, 16 are managed by the FWS, 42 are managed by the NPS, and 89 are managed by the USFS (Figure 2). There are 11 Class I units containing federal shrubland in Mediterranean California, of which 3 are managed by the NPS and 8 are managed by the USFS. The remaining lands are considered Class II areas and are protected by the founding legislation of each agency and the Wilderness Act, but do not have additional Clean Air Act protections. Of the 1,047 Class II units containing forest land, 377 are managed by the FWS, 224 are managed by the NPS, and 446 are managed by the USFS. There are 60 Class II units containing federal shrubland in Mediterranean California, of which 20 are managed by the FWS, 9 are managed by the NPS, and 31 are managed by the USFS. This report refers to the lands managed by these three agencies where the CLs of N for MF are applied as ‘federal forests’ and ‘federal shrublands’ even though the report does not include federal lands managed by other agencies.

Results

Regional Exceedance Patterns

Forests

Forests account for two-thirds of all land area within the contiguous US; 46% is primarily evergreen forest, 41% is deciduous forest, and 13% is mixed evergreen-deciduous forest. The forests in continental zones east of the Rockies are dominated by deciduous species (broadleaf forest, min CL = 10 kg-N ha⁻¹ yr⁻¹). In determining minimum CLs, evergreen forests and mixed evergreen-deciduous forests are grouped together; these are found in the West, the Gulf and Atlantic coastal plains, and boreal forests along the Canadian border in the East and Midwest (conifer forest, min CL = 5 kg-N ha⁻¹ yr⁻¹, Figure 1). In contrast, higher minimum (10 kg-N ha⁻¹ yr⁻¹) and maximum (20 kg-N ha⁻¹ yr⁻¹) critical loads (CLs) define the East (Figures 3 and 4).

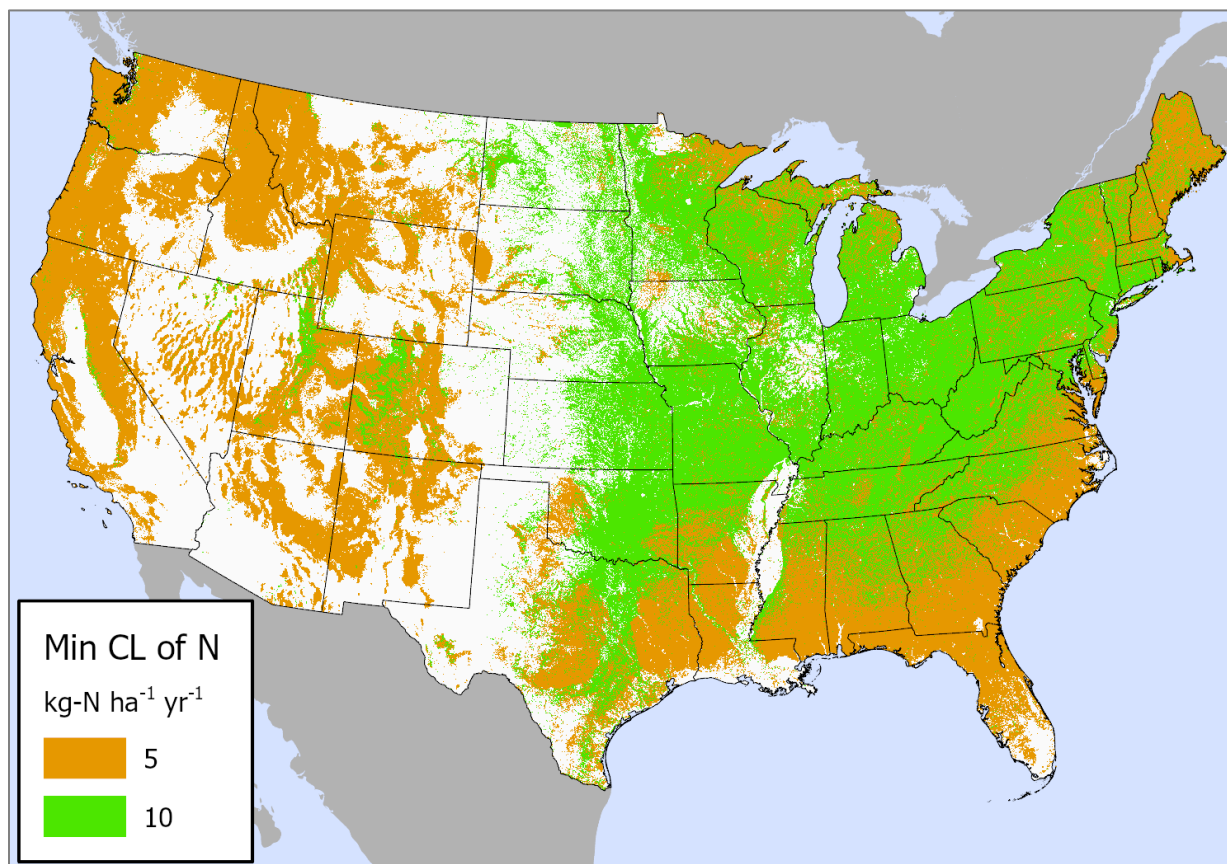


Figure 3. Minimum (min) forest critical loads (CLs) of nitrogen (N) for a shift in mycorrhizal community composition in a given forest type. Conifer and mixed forests are represented by a CL of N value of 5 kg-N ha⁻¹ yr⁻¹ and broadleaf forests are represented by a CL of N value of 10 kg-N ha⁻¹ yr⁻¹.

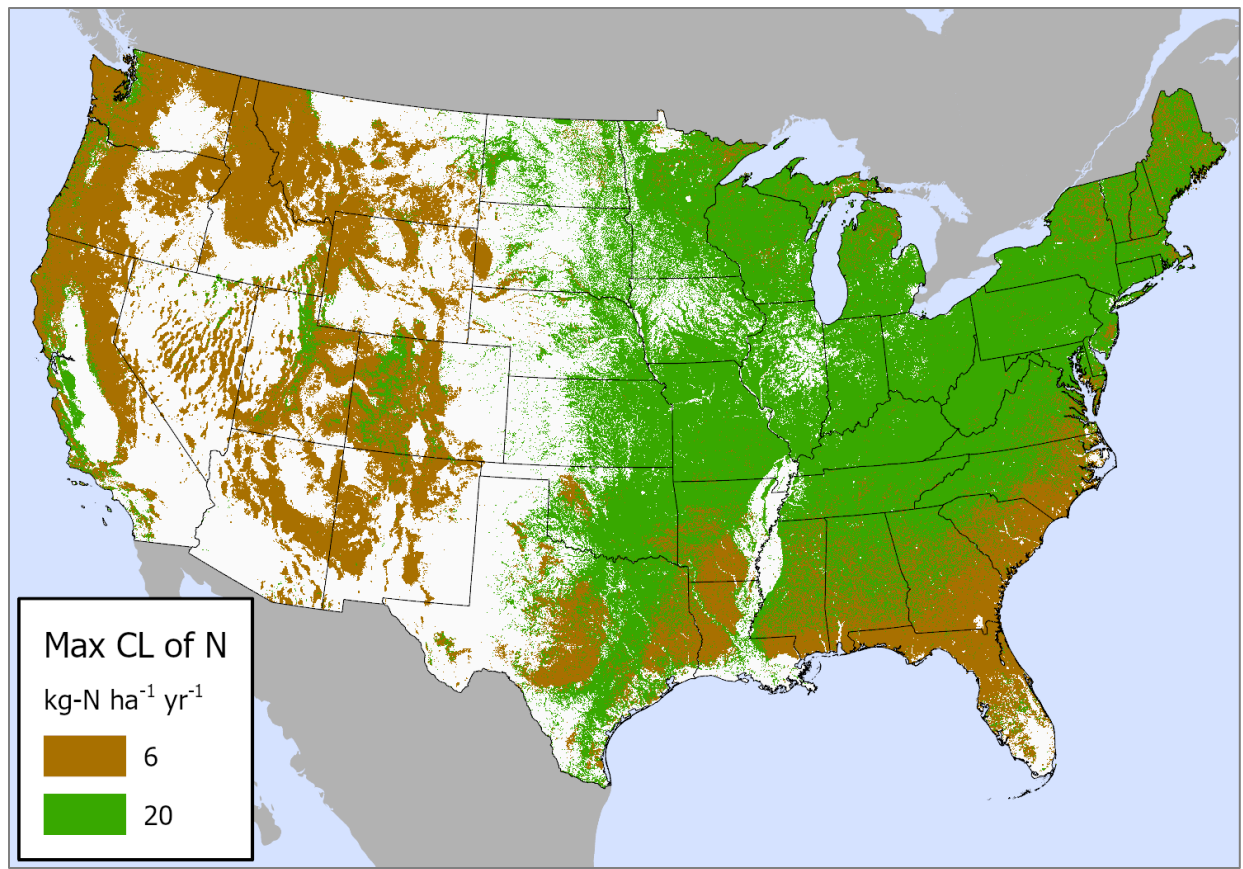


Figure 4. Maximum (max) forest critical loads (CLs) of nitrogen (N) for a shift in mycorrhizal community composition in a given forest type. Conifer forests are represented by a CL of N value of 6 kg-N ha⁻¹ yr⁻¹ and broadleaf and mixed forests are represented by a CL of N value of 20 kg-N ha⁻¹ yr⁻¹.

Exceedances of the min CLs are varied throughout the East, with some areas experiencing high levels of exceedance (e.g., Florida forests) and other areas experiencing no exceedance at all (e.g., Maine forests), regardless of varying forest types and CLs (Figure 5). The West consists mostly of coniferous forest, leading to lower min (5 kg-N ha⁻¹ yr⁻¹) and max (6 kg-N ha⁻¹ yr⁻¹) CLs defining the region (Figures 3 and 4). Although N deposition in the West is generally lower than the East, the increased conifer sensitivity to N still leads to exceedances of the min and max CLs (Figures 5 and 6). These exceedances generally occur in areas of higher elevation due to the increased precipitation and N deposition. Exceedances of CLs range from less than -2 kg-N (i.e., not in exceedance, total N deposition is 2 kg less than CL value) to more than 5 kg-N ha⁻¹ yr⁻¹. This categorization allows for a visual assessment of the level of harm likely to be experienced by the soil community. Our application of max CLs groups together deciduous and mixed forest types (broadleaf forest max CL = 6 kg-N ha⁻¹ yr⁻¹). Geographic patterns of exceedance are clearer, with regions of exceedance along the Sierra Nevada and along the Gulf and Coastal Plains. Much of the southeast is in exceedance of both the min and max CLs.

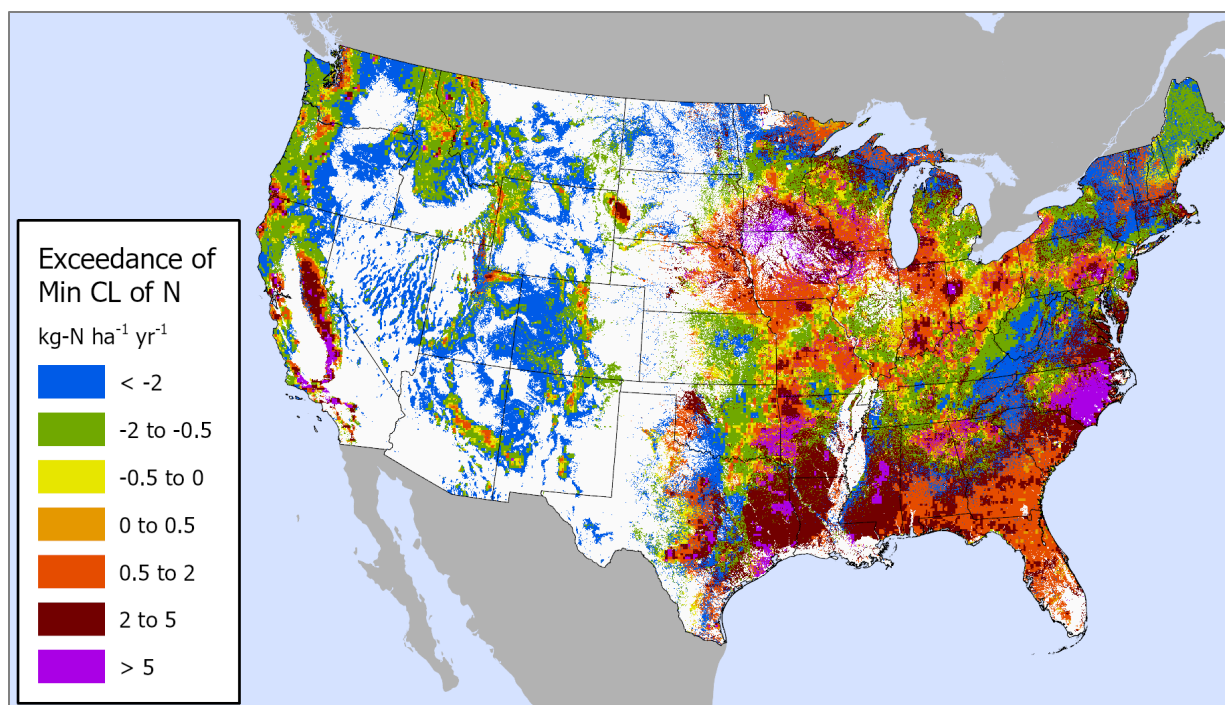


Figure 5. Exceedance of minimum (min) forest critical loads (CLs) of nitrogen (N) for a shift in mycorrhizal community composition. Deposition data used to calculate exceedance sourced from TDep mean annual total N deposition from 2018–2020 (v2018.02).

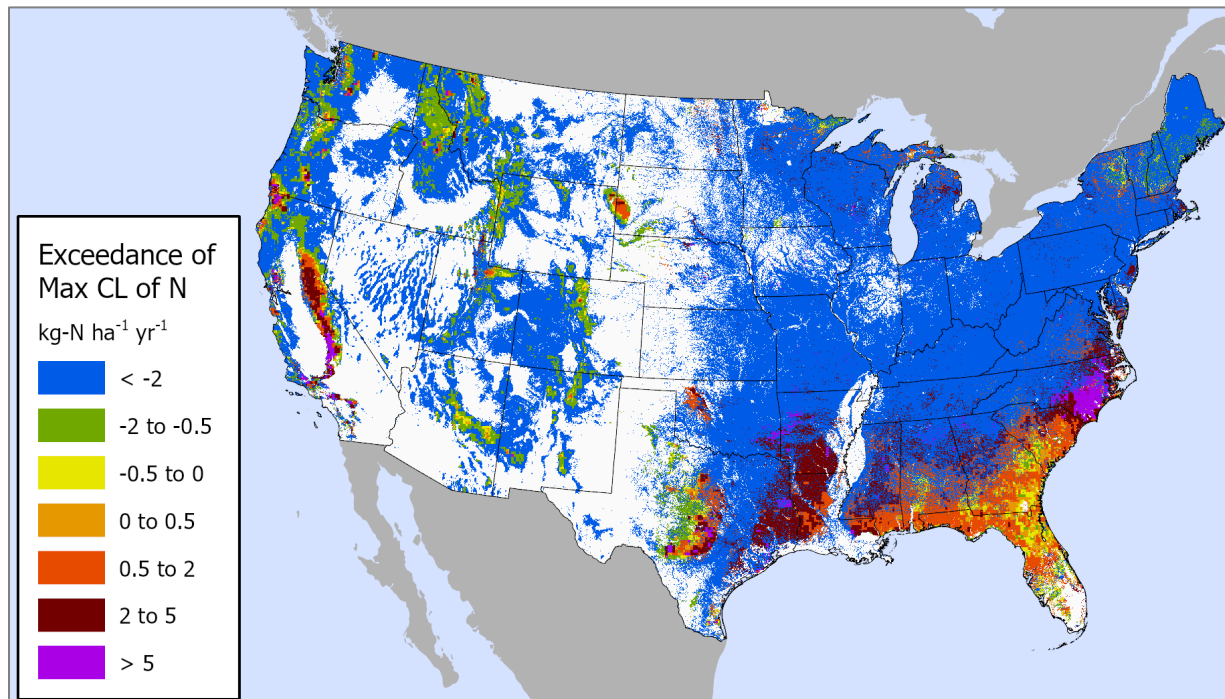


Figure 6. Exceedance of maximum (max) forest critical loads (CLs) of nitrogen (N) for a shift in mycorrhizal community composition. Deposition data used to calculate exceedance sourced from TDep mean annual total N deposition from 2018–2020 (v2018.02).

Shrublands

Eighty-five percent of the shrubland and grassland in Mediterranean California are not experiencing any exceedance of the min ($10 \text{ kg-N ha}^{-1} \text{ yr}^{-1}$) or max ($11 \text{ kg-N ha}^{-1} \text{ yr}^{-1}$) CL for shrubland-associated MF. The main areas in exceedance occur in the southern Sierra Nevada mountains east of the CA central valley, the San Bernardino mountains on the east of Los Angeles Air Basin, and the Santa Monica Mountains north of Los Angeles. Exceedance maps for the min and max CL for shrubland-associated MF are very similar (Figure 7).

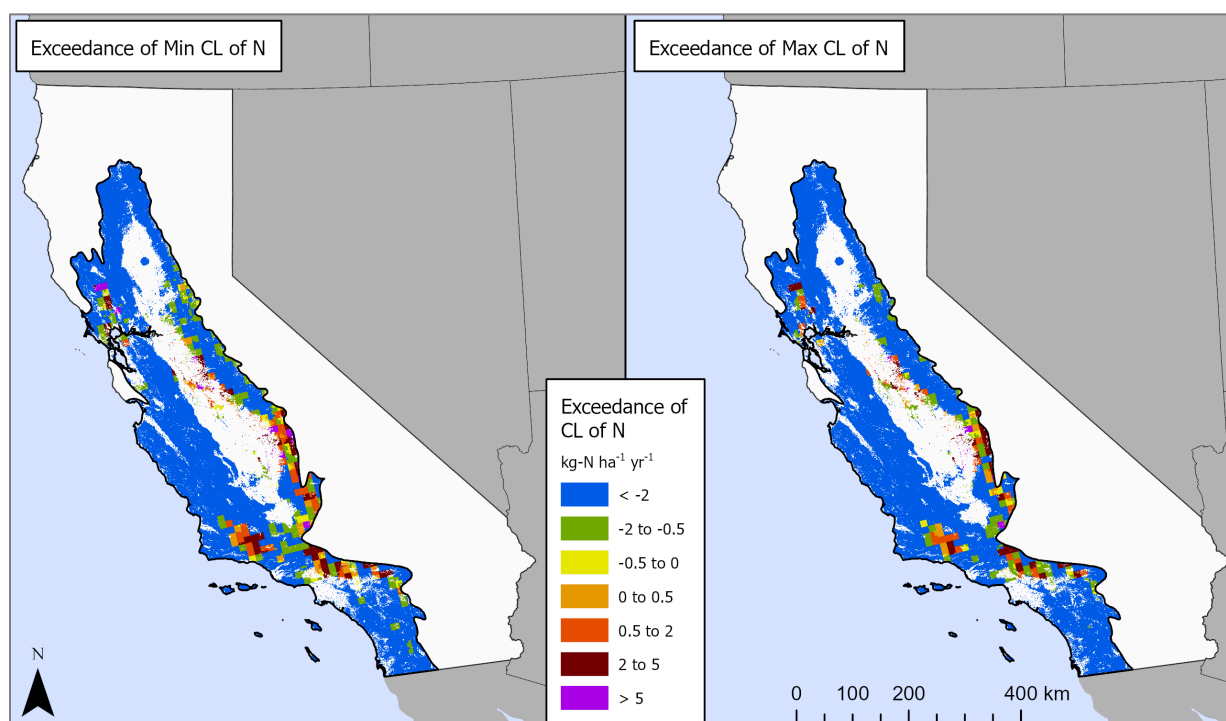


Figure 7. Exceedance of minimum (min; left panel) and maximum (max; right panel) shrubland critical loads (CLs) of nitrogen (N) for a shift in arbuscular mycorrhizal communities and plant richness, where the min CL of N is $10 \text{ kg-N ha}^{-1} \text{ yr}^{-1}$ and the max CL of N is $11 \text{ kg-N ha}^{-1} \text{ yr}^{-1}$. Deposition data used to calculate exceedance sourced from TDep mean annual total N deposition from 2018–2020 (v2018.02).

Federal Units

Forests

There are 768 federal units within the contiguous US managed by FWS, NPS, or USFS (Table 1) that together contain $697,708 \text{ km}^2$ of forested land, which is 68% of their total land area (Table 2). Of these units, 510 (66% of units) have an exceedance of the min CL and 342 (45% of units) have an exceedance of the max CL. Thirty percent of federal forested land area is in exceedance of the min CL and 13% is in exceedance of the max CL. USFS forested lands account for 93% of the total protected forested area managed by the three agencies, followed by the NPS with 6%, and the FWS at 1%. As a proportion of the total land area managed within its boundaries, the USFS also contains the highest percentage of forested land within its boundaries at 76% forested land of total USFS land area, with the NPS at 34% forested land of total NPS land area, and the FWS at 14% forested land of total FWS land area.

Table 1. Federal units containing forested land managed by FWS, NPS, and USFS with exceedances of critical loads (CLs) of nitrogen (N) for forest mycorrhizal fungi (MF). The CLs of N for broadleaf-associated MF are 10–20 kg-N ha⁻¹ yr⁻¹ and the CLs of N for conifer-associated MF 5–6 kg-N ha⁻¹ yr⁻¹.

Group	Subgroup	Total Units	Units with Exceedance of Min CL	Units in Exceedance of Min CL (%)	Units in Exceedance of Max CL	Units in Exceedance of Max CL (%)
All 3 agencies	All	768	510	66%	342	45%
	Class I	147	84	57%	65	44%
	Class II	1047	705	67%	477	46%
FWS	All	393	239	61%	145	37%
	Class I	16	8	50%	6	38%
	Class II	377	231	61%	139	37%
NPS	All	266	170	64%	108	41%
	Class I	42	17	40%	14	33%
	Class II	224	153	68%	94	42%
USFS	All	109	101	93%	89	82%
	Class I	89	59	66%	45	51%
	Class II	446	321	72%	244	55%

Table 2. Area of federal forested land managed by FWS, NPS, and USFS with exceedances of critical loads (CLs) of nitrogen (N) for forest mycorrhizal fungi (MF). The CLs of N for broadleaf-associated MF are 10–20 kg-N ha⁻¹ yr⁻¹ and the CLs of N for conifer-associated MF 5–6 kg-N ha⁻¹ yr⁻¹.

Group	Subgroup	Total Area (km ²)	Forest Area (km ²)	Forest Area (%)	Forest Area in Exceedance of Min CL (%)	Forest Area in Exceedance of Max CL (%)
All 3 agencies	All	1,024,217	697,708	68%	30%	13%
	Class I	134,909	71,109	52%	30%	12%
	Class II	1,014,311	713,334	70%	30%	13%
FWS	All	42,705	5,846	14%	43%	19%
	Class I	8,232	1,433	17%	24%	14%
	Class II	34,473	4,413	13%	49%	21%
NPS	All	120,232	40,508	34%	29%	11%
	Class I	64,243	27,472	43%	29%	13%
	Class II	55,990	13,036	23%	28%	6%
USFS	All	861,280	651,354	76%	30%	13%
	Class I	62,434	42,204	68%	31%	11%
	Class II	923,848	695,884	75%	30%	13%

There are 147 Class I units managed by the three agencies that in total contain 71,109 km² of forested land, where 84 (57% of Class I units) have an exceedance of the min CL and 65 (44% of Class I units) have an exceedance of the max CL. Of the 84 units that have an exceedance of the min CL, 55 are located in the western half of the US and 29 in the eastern half. There are 63 Class I units remaining that experience no exceedance of the forest CLs-N for MF, 60 of which are in the western half of the US leaving the remaining 3 in the eastern half. In terms of forested area, 30% of the total land area designated Class I is in exceedance of the min CL and 13% is in exceedance of the max CL. There are 1,047 Class II units managed by the three agencies containing 713,334 km² of forested area, where 705 (67% of Class II units) have an exceedance of the min CL and 477 (46% of Class II units) have an exceedance of the max CL.

The highest exceedance of the min forest CL-N for MF on FWS managed land was experienced by Balcones Canyonlands National Wildlife Refuge at 35.4 kg-N ha⁻¹ yr⁻¹ over the CL. On NPS managed land, Yosemite National Park had the highest exceedance of the min forest CL-N for MF at 26.8 kg-N ha⁻¹ yr⁻¹ over the CL. The highest exceedance of the min forest CL-N for MF on USFS managed land was in the Siskiyou Wilderness at 27.1 kg-N ha⁻¹ yr⁻¹ over the CL. There are 105 units that have an exceedance of the min CL of less than 1 kg-N ha⁻¹ yr⁻¹, 475 units that have an exceedance of 1–5 kg-N ha⁻¹ yr⁻¹, 183 units that have an exceedance of 5–10 kg-N ha⁻¹ yr⁻¹, and 26 units that have an exceedance of 10 kg-N ha⁻¹ yr⁻¹ or more.

Shrublands

There are 43 federal units among the three agencies (Table 3) that together contain 19,072 km² of shrubland and grassland in the Mediterranean ecoregion of California (Table 4). Federal shrubland accounts for 29% of the total land area managed by the three agencies in the ecoregion. Of these units, 12 (28%) have an exceedance of both their min and max CLs. The USFS manages the most federal shrubland in Mediterranean California, accounting for 91% of the total federal shrubland area, followed by the NPS at 8%, and the FWS at 1%. Although the min and max CL for shrubland-associated MF define a narrow range of deposition, only differing by 1 kg-N ha⁻¹ yr⁻¹, there is a notable difference in the amount of area experiencing exceedance for FWS and USFS units. FWS federal shrubland is in exceedance of the min shrubland CL for 22% of its area, but in exceedance of the max shrubland CL for only 5% of its area. This difference in FWS units occurs entirely within the San Luis National Wildlife Refuge and the Merced National Wildlife Refuge, which both receive N deposition just over 10 kg-N ha⁻¹ yr⁻¹ throughout the majority of their area. Furthermore, the USFS federal shrubland is in exceedance of the min shrubland CL for 27% of its area, but in exceedance of the max shrubland CL for only 18% of its area. Although NPS only manages a small fraction of the federal shrubland, all of the NPS shrubland in exceedance of a CL is in the Class I area within the boundary of Sequoia National Park.

Table 3. Federal units containing shrubland and grassland managed by FWS, NPS, and USFS with exceedances of critical loads (CLs) of nitrogen (N) for shrubland mycorrhizal fungi (MF). The CLs of N for a shift in arbuscular mycorrhizal communities and plant richness are 10–11 kg-N ha⁻¹ yr⁻¹.

Group	Subgroup	Total Units	Units in Exceedance of Min CL	Units in Exceedance of Min CL (%)	Units in Exceedance of Max CL	Units in Exceedance of Max CL (%)
All 3 agencies	All	43	12	28%	12	28%
	Class I	11	5	45%	3	27%
	Class II	60	17	28%	16	27%
FWS	All	20	6	30%	6	30%
	Class I	0	–	–	–	–
	Class II	20	6	30%	6	30%
NPS	All	12	1	8%	1	8%
	Class I	3	1	33%	1	33%
	Class II	9	0	0%	0	0%
USFS	All	11	5	45%	5	45%
	Class I	8	4	50%	2	25%
	Class II	31	11	35%	10	32%

Table 4. Area of federal shrubland and grassland managed by FWS, NPS, and USFS with exceedances of critical loads (CLs) of nitrogen (N) for shrubland mycorrhizal fungi (MF). The CLs of N for a shift in arbuscular mycorrhizal communities and plant richness are 10–11 kg-N ha⁻¹ yr⁻¹.

Group	Subgroup	Total Area (km ²)	Shrubland Area (km ²)	Shrubland Area (%)	Shrubland Area in Exceedance of Min CL (%)	Shrubland Area in Exceedance of Max CL (%)
All 3 agencies	All	65,055	19,072	29%	25%	17%
	Class I	6,472	2,209	34%	36%	28%
	Class II	64,187	21,193	33%	25%	17%
FWS	All	673	227	34%	22%	5%
	Class I	0	–	–	–	–
	Class II	673	227	34%	22%	5%
NPS	All	6,015	1,551	26%	3%	3%
	Class I	3,890	305	8%	17%	17%
	Class II	2,125	1,246	59%	0%	0%
USFS	All	58,367	17,295	30%	27%	18%
	Class I	2,582	1,904	74%	39%	30%
	Class II	61,389	19,721	32%	27%	18%

Discussion

This study applied critical loads of nitrogen (N) for a shift in mycorrhizal fungal communities to forests in the contiguous US and shrubland and grassland communities in the Mediterranean ecoregion of California. CL exceedances were then determined by comparing the CLs to TDep modeled total N deposition from 2018–2020. Areas in exceedance were evaluated within federal lands managed by FWS, NPS, and USFS to explore variation in risk of mycorrhizal community shifts. In terms of administrative boundaries, FWS has the highest number of units in which the MF CLs are applied for both land management units which contain forested land and land management units which contain federal shrubland. However, USFS manages the highest number of Class I areas in which the CLs-N for MF are applied for both forested land and federal shrubland. In terms of land area, the USFS manages the greatest area to which the CLs-N for MF are applied, over 90% of both federal forests and federal shrublands.

Overall, we found that 30% of federal forests are in exceedance of a forest CL-N for MF. Units managed by USFS contain 93% forests, and 30% of USFS forested land is in exceedance of a forest CL-N for MF and at risk of a mycorrhizal community shift. Of the 6% of federal forests managed by the NPS, 29% are in exceedance of a forest CL-N for MF. The remaining 1% of the total federal forest land is managed by the FWS with 43% of the land in exceedance of a forest CL-N for MF.

In addition, we found that 25% of federal shrublands in Mediterranean California are experiencing an exceedance of a shrubland CL-N for MF. The USFS manages 91% of total federal shrublands, with 27% undergoing some level of exceedance of a shrubland CL-N for MF. The NPS manages 8% of federal shrubland in Mediterranean California, with only 3% undergoing exceedance of a shrubland CL-N for MF. The FWS manages 1% of federal shrubland in the US, with 22% in exceedance of a shrubland CL-N for MF. Although N deposition may have profound effects within specific units managed by the NPS or FWS, these agencies control less than 2% of federal shrublands in Mediterranean California that are experiencing exceedance.

Critical Loads and Exceedance

The availability of CL data is vital for determining the impact that atmospheric deposition has on ecological communities and processes. When CL data are available, we can determine where and to what extent certain communities are likely to experience harm, which ultimately provides further insight on their chance of persistence into the future. While these data generalize responses across conifer and broadleaf communities, they allow us to identify areas where forest health is most likely to be in decline and help prioritize future research and analyses. Having site specific data would be ideal but is unrealistic due to the time and money constraints.

When minimum (min) and maximum (max) CLs are close together, as is seen in conifer-associated MF, it suggests that there is little variation in species-level responses and any exceedance of the min CL will likely have impacts on the most resilient species. In contrast, when min and max CLs are further apart, as is seen in broadleaf-associated MF, it suggests that species-level responses are highly variable, and an exceedance of the lower CL will only impact the sensitive species while

leaving other more resilient species unaffected. A larger amount of mycorrhizal community shift is expected with increasing levels of deposition over the CL. Furthermore, assuming a reduction of deposition did occur, more time is expected for areas previously experiencing high levels of exceedance to return to a baseline state (Stevens, 2016).

The median of the highest exceedance of the max CL for all forested federal lands experiencing some level of exceedance is $2.1 \text{ kg-N ha}^{-1} \text{ yr}^{-1}$. In 23 units, the exceedance of the max CL was greater than $10 \text{ kg-N ha}^{-1} \text{ yr}^{-1}$, with the highest exceedance of $34.4 \text{ kg-N ha}^{-1} \text{ yr}^{-1}$ occurring at Balcones Canyonlands National Wildlife Refuge. Looking closer at the deposition model in areas with exceedances over $20 \text{ kg-N ha}^{-1} \text{ yr}^{-1}$, it appears the deposition model is likely overpredicting high levels of dry deposition of NH_3 in a few cells relative to surrounding areas. This provides a good example of additional uses of these analyses to check the consistency of the modeled deposition data across space and time. These results were reported to the developers of the TDep model and modifications were made to constrain deposition values to more appropriate values (TDep v2023.01). Using the updated data, the areas in exceedance remain the same, but the intensity of the exceedance is lower.

Responses Relative to Dominant Forest Type

Given there are 1194 federal units included in this analysis, grouping them by dominant forest type allows for a more general analysis that can be applied to any federal unit containing forest cover. A selection for each dominant forest type was chosen (Table 5) to highlight what conclusions can be drawn once N deposition data are also considered. Detailed data for all federal units analyzed in this report are available online on IRMA in association with this study (Clemens et al., 2024).

Table 5. Forested area by type in Mammoth Cave National Park, Crater Lake National Park, and Voyageurs National Park.

Federal Unit	Total Park Area (km²)	Forest Area (km²)	Conifer Component of Forest Area (%)	Broadleaf Component of Forest Area (%)	Mixed Forest Component of Forest Area (%)
Mammoth Cave National Park	209.2	208.5	9%	84%	7%
Crater Lake National Park	740.7	590.5	100%	0%	0%
Voyageurs National Park	826.9	544.7	14%	12%	74%

Broadleaf Dominant Units

Federal land units that consist of mainly broadleaf forest cover have higher max CLs that help protect them from moderately high levels of N deposition. They also tend to occur in the central- and northeastern-half of the US where deposition occurs at higher levels than in the west. Mammoth Cave National Park forested land is 84% broadleaf, 9% conifer, and 7% mixed (Table 5). Seventy-five percent of Mammoth Cave National Park receives between $10\text{--}20 \text{ kg-N ha}^{-1} \text{ yr}^{-1}$, which guarantees the min CL will be in exceedance in these areas (Figure 8). Since the majority of forest cover is broadleaf, it also means that the max CL is rarely in exceedance. N deposition in the east

peaked around 1990 and these historically elevated levels combined with other stressors, may have caused shifts in mycorrhizal communities that shifted community structure and are still slowly recovering.

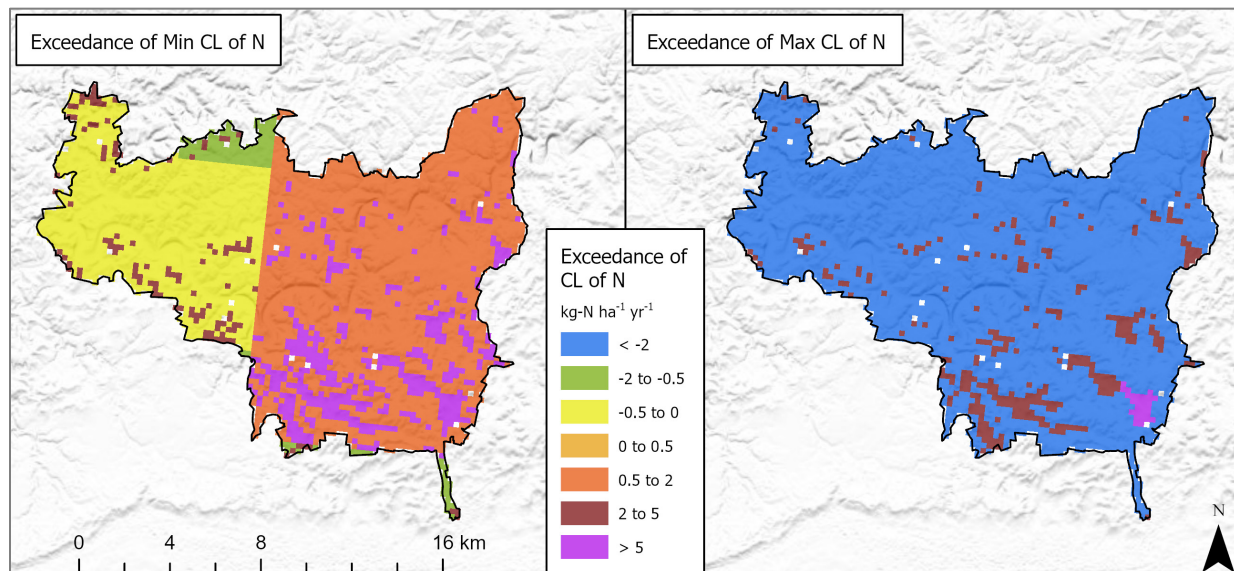


Figure 8. Exceedance of minimum (min; left panel) and maximum (max; right panel) forest critical loads (CLs) of nitrogen (N) for a shift in mycorrhizal community composition at Mammoth Cave National Park. Deposition data used to calculate exceedance sourced from TDep mean annual total N deposition from 2018–2020 (v2018.02).

Conifer Dominant Units

Although units consisting of predominantly coniferous forest cover have low min and max CLs, they tend to occur in the western US where N deposition is lower than in the east. Crater Lake National Park consists entirely of coniferous forest cover (Table 5). Exceedance is lowest in the northeastern portion of the park, where N deposition is consistently less than 5 kg-N ha⁻¹ yr⁻¹ (Figure 9). The southern portion of the park has slightly higher levels of deposition from 5–6 kg-N ha⁻¹ yr⁻¹, and the western portion experiences much higher levels ranging from 6–20 kg-N ha⁻¹ yr⁻¹. The wide variety of deposition experienced within the park makes it an ideal place for future experimentation comparing mycorrhizal communities exposed to various levels of deposition. Tree communities can also be studied to see how tree species responses compare to the responses of their associated MF.

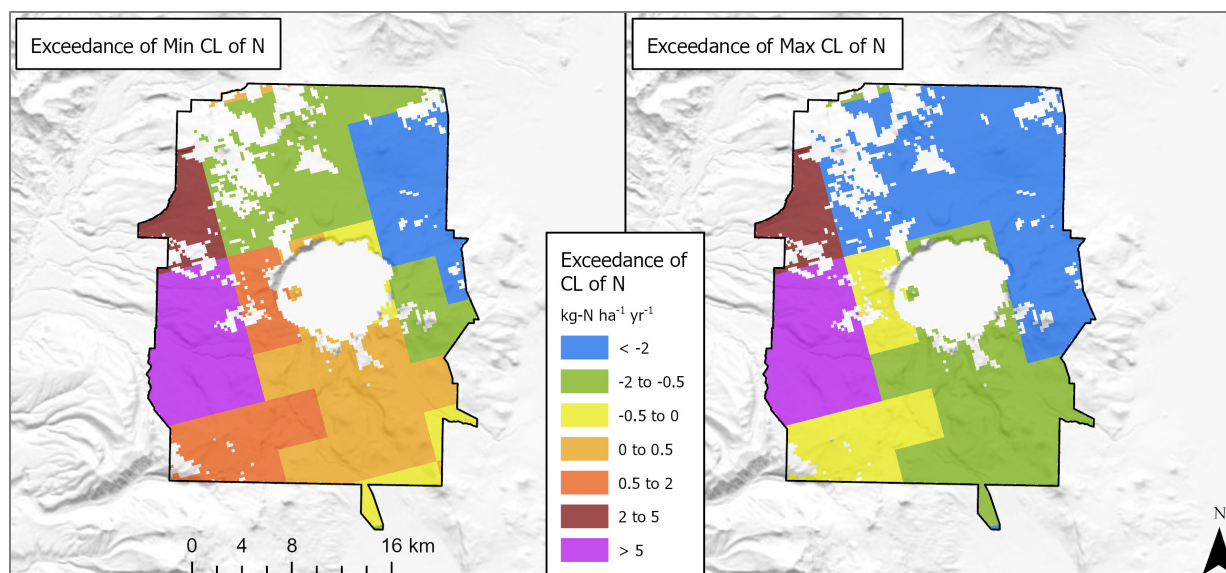


Figure 9. Exceedance of minimum (min; left panel) and maximum (max; right panel) forest critical loads (CLs) of nitrogen (N) for a shift in mycorrhizal community composition at Crater Lake National Park. Deposition data used to calculate exceedance sourced from TDep mean annual total N deposition from 2018–2020 (v2018.02).

This report uses NLCD evergreen forest to assign CLs protective of conifer forest mycorrhizae. There are evergreen forests, particularly in central Texas and along the southeast coastal plain, where oak species, *Quercus virginiana* and *Quercus fusiformis*, retain their leaves year-round. However, until research confirms the sensitivity of the mycorrhizae associated with evergreen oak species, we believe that it is appropriate to apply the conifer CL to forested areas that include both live oaks and junipers or pines.

Mixed Forest Dominant Units

Determining the appropriate CLs for the protection of mixed forest cover requires additional research. Here we use 5 kg-N ha⁻¹ yr⁻¹ for the min CL of the range to protect all coniferous- and broadleaf-associated mycorrhizal species, and 20 kg-N ha⁻¹ yr⁻¹ for the max CL of the range to indicate the level above which all coniferous- and broadleaf-associated species are likely to experience harm. Since conifer-associated MF will be impacted due to their relatively lower CLs, this could lead to vegetation community shifts from mixed to broadleaf dominated forests. In addition, broadleaf tree species with ectomycorrhizal associations tend to be more sensitive to N deposition than those with arbuscular mycorrhizal associations (Horn et al., 2018), causing a shift in broadleaf community structure. When lowering the max mixed forest CL from 20 to 6 kg-N ha⁻¹ yr⁻¹, the number of federal units experiencing exceedance rises from 342 to 461. Of these additional 119 units, 117 of them are located east of the Rocky Mountains where N deposition tends to be higher and broadleaf and mixed forests are more prevalent.

Units with high amounts of mixed forest cover that also experience N deposition at moderate (5–10 kg-N ha⁻¹ yr⁻¹) levels are at risk for their coniferous trees being converted to broadleaf. At these levels deposition is higher than the CL for conifer-associated MF but still lower than the CL for

broadleaf-associated MF, so conifers are the only community experiencing harm. This gives the broadleaf tree communities an opportunity to outcompete the conifers, potentially leading to the conversion of forests from mixed to broadleaf. Voyageurs National Park embodies this scenario since the forests are 74% mixed, 12% broadleaf, and 14% conifer (Table 5), and all N deposition within the park is $6 \text{ kg-N ha}^{-1} \text{ yr}^{-1}$ or less (Figure 10). Over 80% of this N deposition is in the $5\text{--}6 \text{ kg-N ha}^{-1} \text{ yr}^{-1}$ range, which is harmful to only conifer-associated MF.

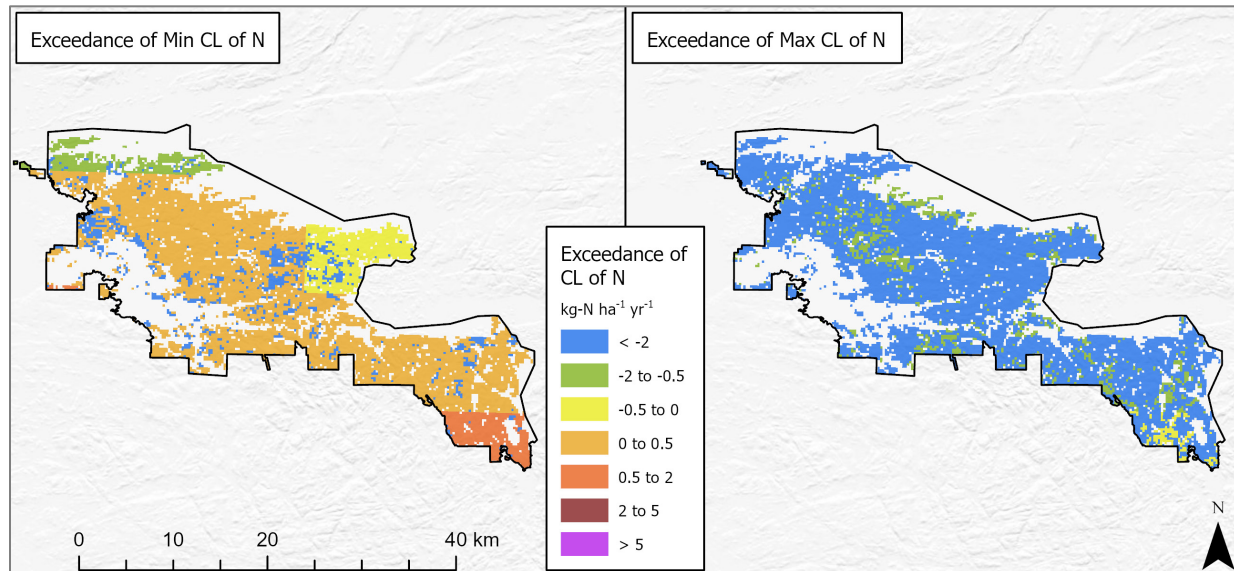


Figure 10. Exceedance of minimum (min; left panel) and maximum (max; right panel) forest critical loads (CLs) of nitrogen (N) for a shift in mycorrhizal community composition at Voyageurs National Park. Deposition data used to calculate exceedance sourced from TDep mean annual total N deposition from 2018–2020 (v2018.02).

Shrubland Units

Although the min and max CL exceedance map for shrublands and grasslands throughout the Mediterranean California ecoregion was difficult to distinguish because the CLs differ by only $1 \text{ kg-N ha}^{-1} \text{ yr}^{-1}$, some exceedance maps (Figure 11) for specific units may still show noticeable differences. When factoring in both the uncertainty in N deposition models and the uncertainty in CL values, $1 \text{ kg-N ha}^{-1} \text{ yr}^{-1}$ is likely too precise a difference to accurately differentiate between the min and max CLs. The value of comparing the differences between the min and max values is to identify the areas that may be on the edge of exceedance and where management action could have the largest impact.

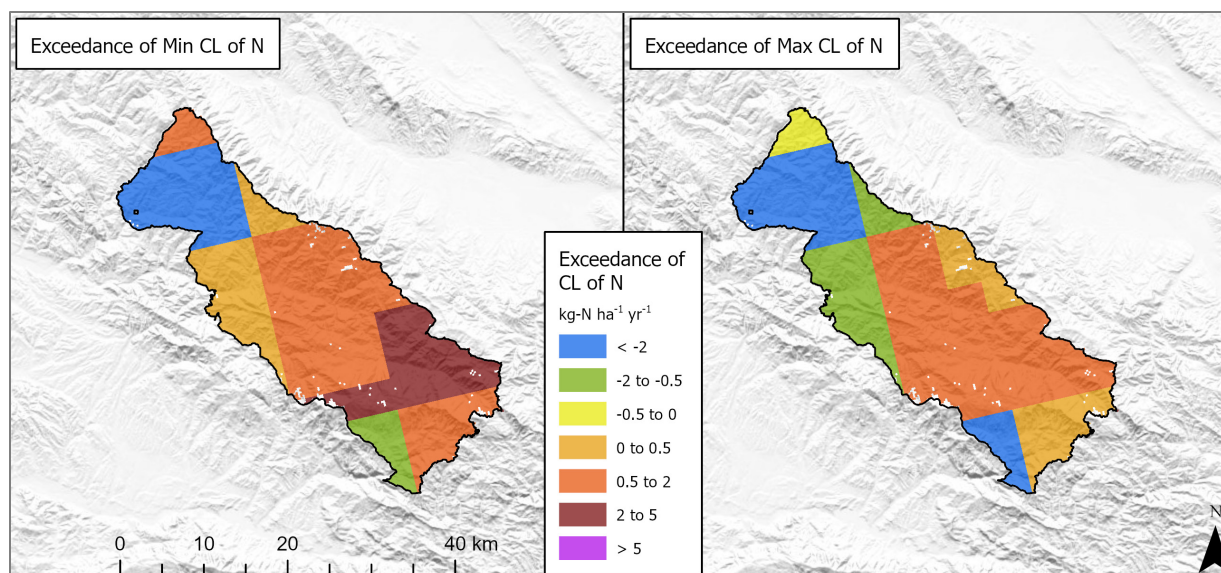


Figure 11. Exceedance of minimum (min; left panel) and maximum (max; right panel) shrubland critical loads (CLs) of nitrogen (N) for a shift in mycorrhizal community composition at San Rafael Wilderness. Deposition data used to calculate exceedance sourced from TDep mean annual total N deposition from 2018–2020 (v2018.02).

Future Research

Further research is needed that compares the continuity of response of western- vs eastern-coniferous forests to N deposition. The majority of current data is based on studies conducted within the eastern US that is then extrapolated for use in west. Western coniferous forests are subject to different growing conditions than those in the east with varying temperature, precipitation, and soil conditions. All of these factors may influence how N deposition interacts with coniferous species, and ultimately lead to changes in the CL. Even small changes in the CL could lead to differing results from those outlined in this report. Response curves for specific species should be created across deposition gradients to determine how much harm can be expected at a given deposition and inform at what level recovery can begin to occur.

In addition, tree community diversity can influence an area's ability to recover from loss of species due to acid deposition. Conifer dominant NPS units host less acid-sensitive species than either broadleaf or mixed dominant units (NPSpecies, 2023) and may therefore have less species to replace the ones being removed by N deposition. The extent of exceedance occurring within MF communities can inform individual tree responses to N deposition (Jo et al., 2019). Areas experiencing acidification for an extended period may have already experienced tree community shifts resulting from the loss of acid-sensitive species.

For shrublands, there are strong relationships between N deposition, precipitation, and species recovery from disturbance (Valliere et al., 2017). Developing better understanding of the variability of mycorrhizal community response across different Mediterranean shrubland and grassland communities can help guide restoration and mitigation actions as the climate continues to change and urbanization increases the rate of disturbances outside NPS lands.

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