

ARTICLE

Developing spatially explicit critical loads for herbaceous species across the United States using convex hulls

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Abstract

Atmospheric deposition of nitrogen and sulfur, after land use change, is one of the most impactful stressors to terrestrial biodiversity. Deposition effects on ecosystems are pervasive, impacting species distributions and disrupting natural communities and associated ecosystem services. Decision makers in particular areas have in the past been limited to using critical loads from faraway research sites or from networks of plots that may or may not overlap with or represent their particular management area. That potential mismatch between the management area and available data presents scientific and possibly legal challenges. Here, we develop spatially explicit critical loads using convex hulls to fill this key knowledge gap in the translation of science to decision making. Specifically, we used convex hulls to understand how representative critical loads are to the broader landscape by comparing the environmental conditions from a set of roughly 15,000 sampled locations with critical loads to a broader landscape for which there is no direct sampling. We performed separate analyses for critical loads of forest and grassland biodiversity and of individual herbaceous species. We found that the sampled plots, though unevenly distributed across the landscape, represented forest and grassland canopy communities very well across the contiguous United States aside from areas in the Southeast and the coastal Pacific Northwest. For the 198 species assessed, 161 species (81%) had 50% or more of their historical range inside the convex hull, and 197 species (99%) had 50% or more of their historical range within 1 SD of the convex hull. These results indicate that most critical loads may be used with confidence across species' ranges to support decision making. These results also can guide future sampling efforts in strategic areas. Further, the use of convex hulls as a general tool for other efforts may greatly increase the utility of various existing datasets to support land managers and decision makers charged with protecting ecosystems.

KEYWORDS

biodiversity, convex hulls, critical loads, herbaceous species, NAAQS, nitrogen deposition

INTRODUCTION

Atmospheric deposition of nitrogen (N) and sulfur (S) is a longstanding stressor to terrestrial ecosystems in the United States and other developed countries (Bobbink et al., 2010; Clark et al., 2018; Pardo, Fenn, et al., 2011). Both can have many effects, including soil acidification, which can lead to cation imbalances in growing plants, mobilization of and damage from aluminum in the soil, decreased cold tolerance, and leaching of nutrients and cations from the watershed (Burns et al., 2011; Cronan et al., 1989; EPA, 2020; Schaberg et al., 2002). For N deposition, there are additional effects from nutrient enrichment, which can lead to increases in growth for some often-weedy species, decreases in light availability, and competitive exclusion of many species in the community (Clark et al., 2019; Hautier et al., 2009; Simkin et al., 2016; Suding et al., 2005). Over evolutionary time, N availability was usually low, and most terrestrial ecosystems were N limited or co-limited, with few species able to capitalize on high rates of N (Aerts & Chapin, 2000; Elser et al., 2007). Thus, evolutionarily, N deposition favors a small number of species, and often leads to significant shifts in the plant community. Ultimately, these effects can reduce the biodiversity of the plant community and the ecosystem services that the plant community provides (Bell et al., 2017; Clark et al., 2017).

Over the past several decades, researchers have developed “critical loads” or “CLs” to help identify important thresholds of deposition below which specified harmful ecological effects do not occur (Porter et al., 2005). CLs are formally defined as “A quantitative estimate of exposure to one or more pollutants below which significant harmful effects on specified sensitive elements of the environment do not occur according to present knowledge” (Nilsson, 1988). In the United States, CLs have been quantified for many different ecological end points of concern (Lynch et al., 2013; Pardo, Fenn, et al., 2011), including for N and S effects on aquatic acidification (Lawrence et al., 2015; McDonnell et al., 2014), forest soil acidification (McNulty et al., 2007; Simkin et al., 2016), tree species growth and survival (Horn et al., 2018; Pavlovic et al., 2023), herbaceous communities (Clark et al., 2019; McDonnell et al., 2020; Simkin et al., 2016; Wilkins et al., 2022), lichen species (Geiser et al., 2019, 2021), and other end points (Pardo, Robin-Abbott, et al., 2011). More recently, researchers have demonstrated that CLs are not fixed for a particular species and may vary across its range; and, that even different species within the same genera or functional group may have different CLs based on ecological context (Clark et al., 2019; Coughlin et al., 2024; Dalton et al., 2024; Horn et al., 2018). In the United States, CLs are compiled into the National Critical Loads Database (Lynch et al., 2022),

which is accessed by decision makers and the public. CLs have been used to support policymaking in Europe for years (UBA, 2004) and are beginning to be utilized by policymakers in the United States in the EPA (EPA, 2017), the Forest Service (Porter et al., 2005), and the National Park Service (USFS, 2011).

One of the core limitations in using CLs for the United States is uncertainty about where they are applicable across the landscape. For example, there are dozens of CLs from detailed field studies conducted historically (Pardo, Fenn, et al., 2011), but it is unclear whether those are applicable to other areas. Local and regional decision makers are uncertain whether the CLs developed in one ecosystem or region are applicable to another. This is not an issue for many of the CLs that are based on the USFS Forest Inventory and Analysis (FIA) database (e.g., trees and lichen; Geiser et al., 2021; Horn et al., 2018; Pavlovic et al., 2023) because the FIA was designed to be a fully randomized sample across the contiguous United States (CONUS), and thus, the samples are statistically representative of the broader landscape by design. On the other hand, the herbaceous community and species CLs (Clark et al., 2019; Simkin et al., 2016) are derived from a set of 22 individual datasets that were combined from the literature and available at the time. These are not a randomized plot design for the CONUS, and no such dataset yet exists for the United States (Appendix S1: Figure S1). There are clear gaps in the dataset in the southwest, California, southeast, and other areas, and hotspots with greater sampling in Minnesota, Virginia, and western Montana (Appendix S1: Figure S1). Thus, it is unclear to what degree these herbaceous CLs are applicable to other areas in the country.

Here, we attempt to fill this knowledge gap by utilizing the convex hull statistical approach (Baillio & Chacón, 2021). Put simply, the convex hull defines the multidimensional cloud of environmental conditions sampled by a dataset (e.g., temperature, precipitation; Figure 1). We then compare these environmental conditions with a broader geographic region to see how similar or different the dataset is from the broader conditions where no observations exist. The central thesis of this approach is that the geographic location of a plot is not important (e.g., lat/lon)—rather, what is important are the ecological conditions at that geographic location (e.g., temperature, precipitation, soil pH). If those ecological conditions in sampled areas are similar to conditions in unsampled areas, we hypothesize that the response to N or S deposition may be similar as well in these unsampled areas. In essence, this helps to quantify explicitly the domain of inference for these CLs—where they are applicable. By assessing the multidimensional range of conditions spanned by the underlying dataset, we then compare that with the CONUS to determine

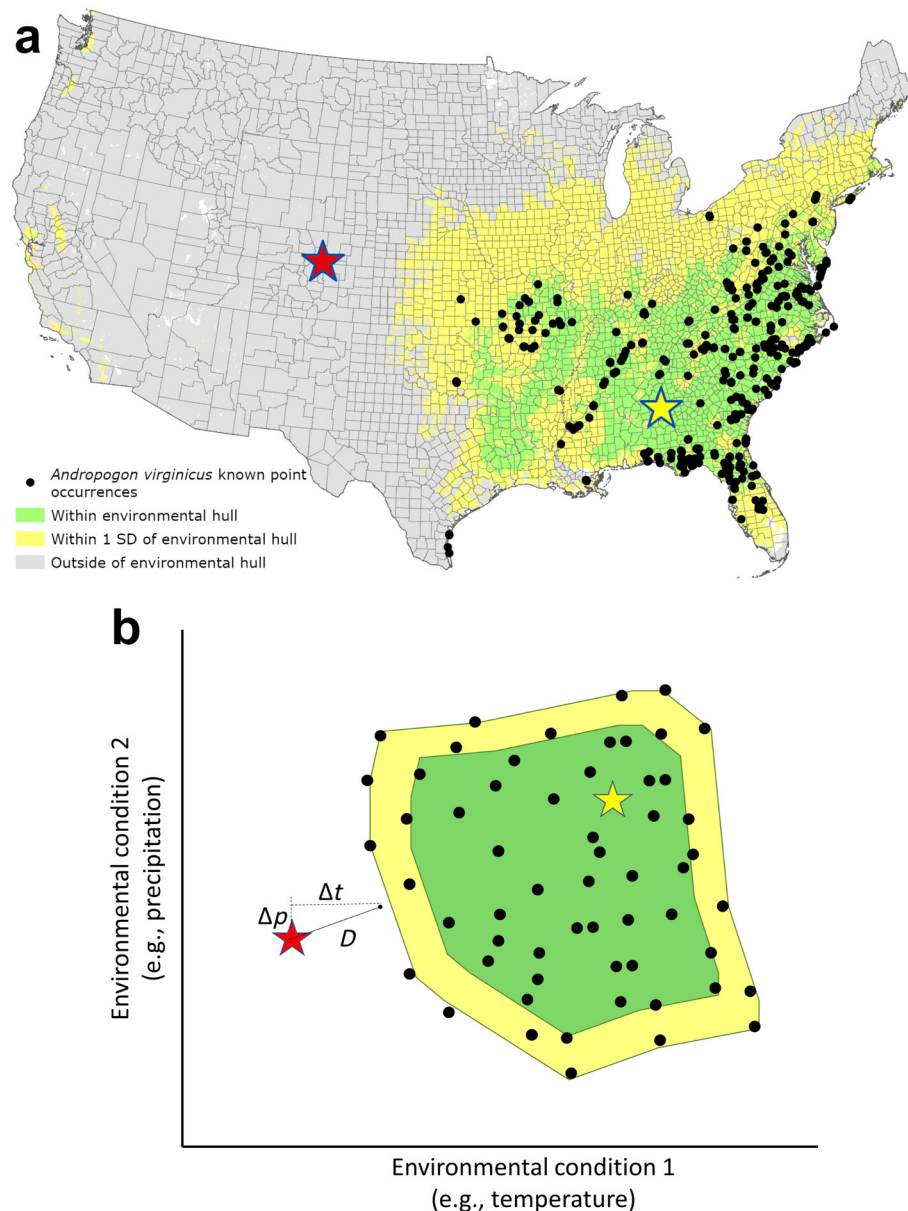


FIGURE 1 Conceptual diagram of the approach for one species (*Andropogon virginicus*). The environmental conditions for the plot samples (a, dots) are used to estimate the convex hull which defines the volume of environmental space sampled (b, example for two dimensions, green polygon). Then, we may compare other areas (continental United States [CONUS], and red and yellow stars as example) that were not sampled with the convex hull. For some areas, the conditions will be similar (yellow star is inside the convex hull but not a sampled location, Mahalanobis distance $D < 0$), and for others, they may be quite different (red star is outside the convex hull, $D > 0$). We decided to allow for some extrapolation that is outside the convex hull by a small amount ($0 < D < 1$, yellow band). For areas outside the convex hull, we may decompose the minimum distance to the hull surface to determine which variable(s) are responsible for $D > 0$ (for the red star, temperature).

whether the set of points in the underlying dataset are representative of other areas. For areas that are similar, we recommend using the CL with confidence. For areas that are not similar, we recommend either not using the CLs or using them with caution.

Conceptually, our use of convex hulls is similar to various applications of “climate envelopes” (Elith et al., 2006; Guisan & Thuiller, 2005; Hijmans &

Graham, 2006). Climate envelopes, generally speaking, examine the current or past distribution of a species based on various climatic (or other) conditions that define the potential or realized habitat for the species (Leibold, 1995). Researchers then compare those climate envelopes with conditions in other locations or with conditions projected in the future to answer specific questions. Climate envelopes have been used to address

questions related to invasiveness (Bradley et al., 2010), bioenergy (Barney & DiTomaso, 2010), climate change (Pearson et al., 2002; Pearson & Dawson, 2003), and a host of other questions. The key difference between our work and this body of literature is on the application—we are interested in where the estimates of vulnerability to atmospheric deposition are applicable, rather than where a species may or may not be able to disperse or migrate to in the future. Mathematically and statistically, though, the analytical approach applied to answer these questions are similar.

Our approach is more generally similar to the use of convex hulls or other statistical approaches to define outliers from a multidimensional cloud of data (Pierna et al., 2002). Here, again, the application differs—we are interested in finding areas that are similar to our dataset (and thus, the CLs are likely applicable), to separate those from areas that are different (and thus, the CLs are likely not applicable). Regardless, the use of convex hulls to define areas where CL estimates may be applied is novel to our knowledge.

METHODS

We used two datasets that estimated CLs: for herbaceous species richness (Simkin et al., 2016) and for the occurrence probability of individual herbaceous species (Clark et al., 2019). We used a four-step process in our approach: Step 1 used the CL equations from Simkin et al. (2016) (richness) oClark et al. (2019) (species occurrence) to develop spatially explicit estimates of CLs across the CONUS; step 2 derived the convex hull for the set of geographic points that represent the sampled conditions; step 3 assessed conditions across the CONUS to determine areas inside (i.e., similar to) and outside (i.e., different from) the convex hull, and step 4 for regions inside or “near” the hull, we used the interpolated (inside the hull) or extrapolated (outside the hull) CLs from step 1. These concepts are summarized in Figure 1 and are described in more detail below.

Convex hulls—Species richness CLs

Simkin et al. (2016) estimated CLs for species richness for two herbaceous community types: open canopy (representing grasslands, shrublands, and woodlands) and closed canopy (representing deciduous, evergreen, and mixed forests) communities based on the 2016 National Land Cover Dataset (NLCD) (Homer et al., 2020). There were 3317 open canopy plots and 11,819 closed canopy plots for a total of 15,136 plots

(Appendix S1: Figure S1). Simkin et al. (2016) extracted four environmental predictors at each of these plot locations: (1) N deposition (from a combination of modeled [Community Multiscale Air Quality, CMAQ] and observed [National Atmospheric Deposition Program, NADP] data), (2) soil pH (from a combination of US Department of Agriculture [USDA] [Soil Survey Geographic Database, SSURGO]) and local field measurements, (3) temperature (from Parameter-elevation Regressions on Independent Slopes Model, or PRISM), and (4) precipitation (from PRISM). Additional information on the data sources is found in Simkin et al. (2016).

Simkin et al. (2016) then regressed the response of species richness against N deposition (N), temperature (T), precipitation (P), soil pH (pH), and select interactions of ecological interest (Equation 1). The CL for each community type was based on the partial derivative with respect to nitrogen of Equation (1). After terms with a nonsignificant coefficient were dropped, the CL for open canopy sites depended on soil pH, temperature, and precipitation (Equation 2), while the CL for closed canopy sites only depended on soil pH (Equation 3). Thus, Equations (2 and 3) were applied to spatially continuous data across the CONUS to generate a continuous estimate of CLs for open and closed canopy sites.

$$\begin{aligned} \text{CL} = \partial/\partial N [\beta_0 + \beta_1 N + \beta_2 \text{pH} + \beta_3 T + \beta_4 P \\ + \beta_5 N^2 + \beta_6 N \text{pH} + \beta_7 NP + \beta_8 NT]. \end{aligned} \quad (1)$$

$$\text{CL}(\text{open canopy}) = 4.75 + 0.48 \text{pH} + 0.0018P - 0.074T. \quad (2)$$

$$\text{CL}(\text{closed canopy}) = 1.80 + 2.17 \text{pH}. \quad (3)$$

To apply Equations (2 and 3) to the CONUS for this study (step 1), we first identified areas that were open or closed canopy as in Simkin et al. (2016). We used the 2016 NLCD to identify grid cells that were open canopy (i.e., NLCD class 71, 72, 52) or closed canopy (i.e., NLCD 41, 42, 43) ecosystems. Next, we assembled spatial data layers for the environmental variables in Equations (2 and 3): nitrogen deposition, temperature, precipitation, and soil pH. Three of the four original data sources were continuous across the CONUS (i.e., temperature, precipitation, N deposition). Thus, we used the CONUS-wide original data for the conditions across the CONUS for temperature and precipitation to derive spatially continuous CLs based on Equations (2 and 3). At the time of analysis for Simkin et al. (2016), only the 4-km PRISM grids were available. Since then, 800-m climate grids have become available for the same climate normal (1981–2010). The 4-km and 800-m climate normals were highly

correlated for the 15,136 plot locations in Simkin et al. (2016), allowing us to upgrade to the 800-m climate normals for this study (Appendix S1: Figure S2). We resampled all input rasters to 1600 m for faster computation and easier storage of the species-level output rasters. As noted above, for soil pH, there was a mixture of point-location data and spatial data from the USDA SSURGO used in the original analysis. The SSURGO data layer was the only CONUS-wide data layer available at the time of the analysis in Simkin et al. (2016). We evaluated whether we could switch to a newly available gNATSGO soil pH data product from the USDA (2020). gNATSGO is also based partly on SSURGO and other datasets, and estimates soil pH at smaller scales (30 m resolution) and at multiple depths. The soil pH from Simkin et al. (2016) and gNATSGO were highly correlated ($R^2 = 0.7442$ – 0.7825 ; Appendix S1: Figure S3); thus, we upgraded to use soil pH from gNATSGO in this study. CLs between Simkin et al. (2016) and the continuous version here, resampled at the point locations, were very similar, with 95% of the open canopy CLs within -0.6 and $+0.57$ kg N ha $^{-1}$ year $^{-1}$ and 80% of the closed canopy CLs within -2 and $+1$ kg N ha $^{-1}$ year $^{-1}$. We used the 0- to 20-cm depth from gNATSGO to best represent the soil depth that is most relevant to herbaceous species roots. With these spatial data sources, we were able to generate continuous estimates of CLs for open (Equation 2) and closed canopy (Equation 3) sites across the CONUS.

Next (step 2), we generated convex hulls from the gridded values at the plot locations of the 3317 open and 11,819 closed canopy plots sampled in Simkin et al. (2016). Because the CL is based on the partial derivative of the full statistical model (i.e., Equation 1), the hull was derived based on all four of the original environmental variables, not just the subset upon which the CLs were based. For example, if the original plots only sampled a small range of temperature, which then yielded no temperature effect on the CL, that would be important to capture in the hull analysis. For each of the two community types, we derived the convex hull for the observed plot locations using the `convhulln()` function in the R geometry package (version 0.4.6). The two convex hulls (open and closed communities) thus defined the four-dimensional (4-D) environmental space sampled by the open and closed canopy plots in the dataset. We used the 95th percentile for the convex hull to exclude outlier plots from the estimate of the convex hull. With the convex hull for the two community types, we then compared the conditions sampled by the 95th convex hulls (hereafter simplified to be termed “convex hull”) with the conditions across the CONUS (step 3). Each grid cell had information on the four environmental variables, which defined a location in 4-D space. For all grid cells, we

estimated the shortest distance to the convex hull using the Mahalanobis multivariate distance (D) in R (from the `disthulln()` function in the R geometry package version 0.4.6). Mahalanobis distance is in the units of SDs. If the conditions of that grid cell were inside the convex hull ($D < 0$), we assumed the equations (e.g., Equation 2 or 3) to be robust for that location. If the conditions of that grid cell were outside the convex hull ($D > 0$), the equations may or may not be robust depending on how far outside the convex hull the plot location was and the uncertainty the user is willing to accept. That distance was then decomposed into the four axes to determine which variables were responsible for being outside the hull.

For step 4, we used the notion that the further outside the hull, the less confident we were in the application of the CL equations. Grid cells very close to the convex hull are similar in confidence to grid cells inside the convex hull. As noted above, we assumed that any grid cell inside the hull was well represented by the 15,136 sampled plots, and thus, Equations (2 and 3) could be applied. We assumed that any grid cell that had environmental conditions within 1 SD of the hull ($D < 1$) was useful but had a lower confidence than grid locations inside the hull ($D < 0$). Grid conditions more than 1 SD outside of the hull ($D > 1$) were considered very low confidence. There is no “bright line” for how far outside the convex hull is too far, but we feel that within 1 SD is lower confidence than inside the convex hull but acceptable for most uses.

Convex hulls—Species occurrence CLs

For the species-level CLs from Clark et al. (2019), the same general four-step process was applied with some minor modifications noted here. First, the CLs from Clark et al. (2019) are species-level, not community-level. Thus, the NLCD is not relevant because some species are not in all closed canopy areas (or open canopy) and some species are found in both open and closed canopy sites. We focused on the 198 out of 348 species that were determined to have a robust relationship in Clark et al. (2019). Each of the 198 species had a different set of plots that were used in the derivation of the hull based on where that species had been observed. Second, rather than relying on the NLCD to identify broad community types (i.e., open vs. closed canopy), we used the USDA PLANTS database to identify the historical range of each species where the CL equations were most applicable historically. The USDA PLANTS database provides standardized information about the vascular plants, mosses, liverworts, hornworts, and lichens of the United States.

Among the information are range maps at the county level of where the species has been observed historically from herbarium and other collections. Third, in addition to the four environmental variables above, the Clark et al. (2019) study included S deposition. Thus, there were five environmental variables used for the derivation of the species-level hulls (i.e., temperature, precipitation, soil pH, N deposition, S deposition). Sulfur deposition in Clark et al. (2019) was estimated using the same approach as N deposition. Other than the above three differences, the species-level analysis was the same four-step process described above with (step 1) estimation of species-level CONUS-wide CLs using the CL equations in Clark et al. (2019), (step 2) estimation of the 5-D convex hull for each species based on the subset of plots where they were observed, (step 3) comparison of the convex hulls with conditions across the CONUS, and (step 4) subsetting the species-level CONUS-wide CLs based on the historical ranges of the PLANTS USDA database and the areas inside and within 1 SD of the convex hulls using a basic GIS spatial analysis. We recognize that most

herbaceous species are not found throughout the CONUS, but with climate change, historical ranges may be a poor predictor of future observations (Parmesan, 2006); thus, we wanted to be expansive in our assessment of the convex hulls.

RESULTS

Species richness: Continuous CLs and hulls

We found that closed canopy CLs varied widely across the country ($6.1\text{--}23.7\text{ kg N ha}^{-1}\text{ year}^{-1}$) and were generally lower in the eastern United States ($10\text{--}14\text{ kg N ha}^{-1}\text{ year}^{-1}$) and higher in the western United States ($>14\text{ kg N ha}^{-1}\text{ year}^{-1}$; Figure 2a). This was primarily a pH effect, as that was the only factor affecting the closed canopy CLs (Equation 3), with higher CLs in the more alkaline soils of the west. In the more acidic soils of the east, the Pacific Northwest, and the upper Midwest, the CLs were lower. The convex hulls indicated

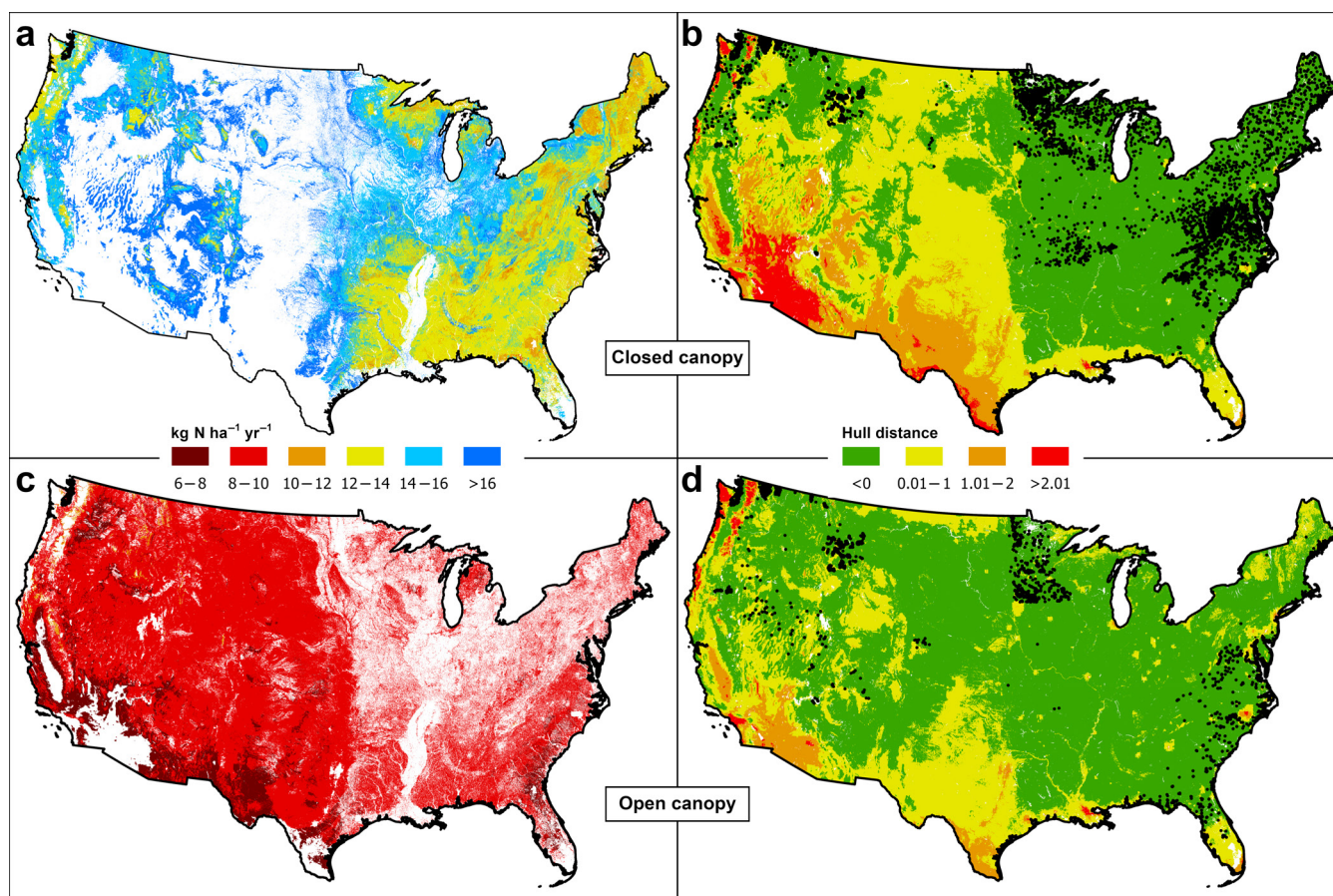


FIGURE 2 Species richness critical loads for (a) closed and (c) open canopy communities, as well as the Mahalanobis distance (D) to the convex hull for (b) closed and (d) open canopy communities. Key in panel (c) is the same as in panel (a). Areas without an open or closed canopy critical load (CL), white in panel (a) or (c) are any areas that are assigned a land cover of something other than grasslands, shrublands, woodlands, or forests in the National Critical Loads Database (NCLD) (e.g., urban, agricultural).

good (inside the hull, $D < 0$) or acceptable (within 1 SD, $0 < D < 1$) representation of the four environmental variables for most of the forested areas of the CONUS (Figure 2b). It was interesting to note that even though the bulk of the western plots were in the Northern Rockies of Idaho and Montana, and the Northern Cascade Range of Washington, large areas to the south in connected mountain ranges had good ($D < 0$) representation (e.g., central and southern Rockies of Colorado, Sierras of California). Portions of the Pacific Northwest and much of the Southwest were not well represented ($D > 1$) (Figure 2b). The primary variable responsible for $D > 1$ varied by region. In the Southwest, it was temperature (Figure 3a), while in the Pacific Northwest, it was precipitation (Figure 3c). Soil pH and N dep were well represented for closed canopy sites (Figure 3e,g).

Open canopy CLs were much lower (6–10 kg N ha⁻¹ year⁻¹) and less variable across the country (Figure 2c). The lower variability was interesting given that the open canopy CLs were influenced by more factors (i.e., pH, temp, and precip; Equation 2), but it appeared that these effects counteracted one another to result in a relatively consistent CL. The convex hulls indicated good ($D < 0$) or acceptable ($0 < D < 1$) representation of the four environmental variables for most of the relevant areas of the CONUS (Figure 2d). It was interesting to note that—similar to the closed canopy CLs—even though the bulk of the plots were in Minnesota, Montana, and the southeastern United States, much of the rest of the CONUS had good or acceptable representation. Similar areas were poorly represented, again primarily the Southwest (from temperature; Figure 3b) and the Pacific Northwest (from precipitation; Figure 3d). There were also a few areas where N deposition pushed conditions outside the convex hull, particularly around emission sources in Louisiana, North Carolina, and southern California (Figure 3h).

Individual species: Continuous CLs and hulls

We found that of the 198 species assessed, 161 species (81%) had 50% or more of their historical range inside the convex hull, while 25 species (13%) had 90% or more of their historical range inside the convex hull (Figure 4). We found even better representation for $D < 1$. We found that 197 species had 50% or more of their historical range with $D < 1$ and 185 had 90% or more of their historical range with $D < 1$. Species with poor representation included *Liatris pycnostachya* (10% with $D < 0$ and 38% with $D < 1$), *Oligoneuron riddellii* (5% with $D < 0$ and 81% with $D < 1$), and *Helianthus grosseserratus* (9% with

$D < 0$ and 80% with $D < 1$), among others. Violations generally were idiosyncratic, with different factors affecting different species in terms of conditions relative to their convex hull (Appendix S1). When summed across species and isolated to $D < 1$, we found that there were 10 or more species in our dataset experiencing an N or S exceedance across much of the CONUS (Figure 5).

Individual species CLs and associated convex hulls for all 198 species are displayed in Appendix S1, and associated data are in Figshare (<https://doi.org/10.6084/m9.figshare.27242094>). Here, we present two example species to convey the richness of information and patterns that emerged: *Actaea rubra* (red baneberry) and *Eryngium yuccifolium* (rattlesnake master).

A. rubra (red baneberry) is a common perennial herb that grows throughout much of the western and northern United States. The plot data for *A. rubra* were relatively well distributed across the northern United States, even though there was a higher concentration of plots in Minnesota (Figure 6a). Most of the northern half of the United States was either inside the hull or within 1 SD (Figure 6b), although there were pockets in the northern Ohio River Valley, the Snake River (ID and OR/WA), and various urban areas with $D > 1$. Thus, the CLs were only reported in these areas inside or near the surface of the hull ($D < 1$; Figure 6c,d). The N CLs for *A. rubra* are lower (<4 kg N ha⁻¹ year⁻¹) in the eastern United States and Northeast, and higher (>10 kg N ha⁻¹ year⁻¹) in the western United States (Figure 6a). Clark et al. (2019) demonstrated that the N CL for this species was lower under more acidic soil conditions and under higher S deposition, both of which are generally more prevalent in the east (Appendix S1: Figure S4). Montane areas in the west also had lower CLs, but these pockets are not visible at the scales displayed in Figure 6 (see Appendix S1 for high-resolution downloadable figures). Note that the N CLs were lower in eastern states where the species was listed as having some form of conservation status (Figure 6a; IL, IN, OH, PA). The S CL for *A. rubra* was very low in the eastern United States and high elsewhere (Figure 6d). This was due to the N × S interaction in Clark et al. (2019), whereby if N deposition was high enough (>6 kg N ha⁻¹ year⁻¹), any amount of S led to a decrease in the probability of occurrence; but if N deposition was below this threshold, the species was relatively unresponsive to S deposition. These areas where the species was not predicted to respond were areas in the west where both N and S deposition were lower, and the soils outside of montane areas are more buffered. The reasons conditions were outside the convex hull ($D > 1$) for *A. rubra* varied by region and were mostly driven by temperature in the southern United States (Figure 7a), S deposition in the Ohio River Valley and other urban

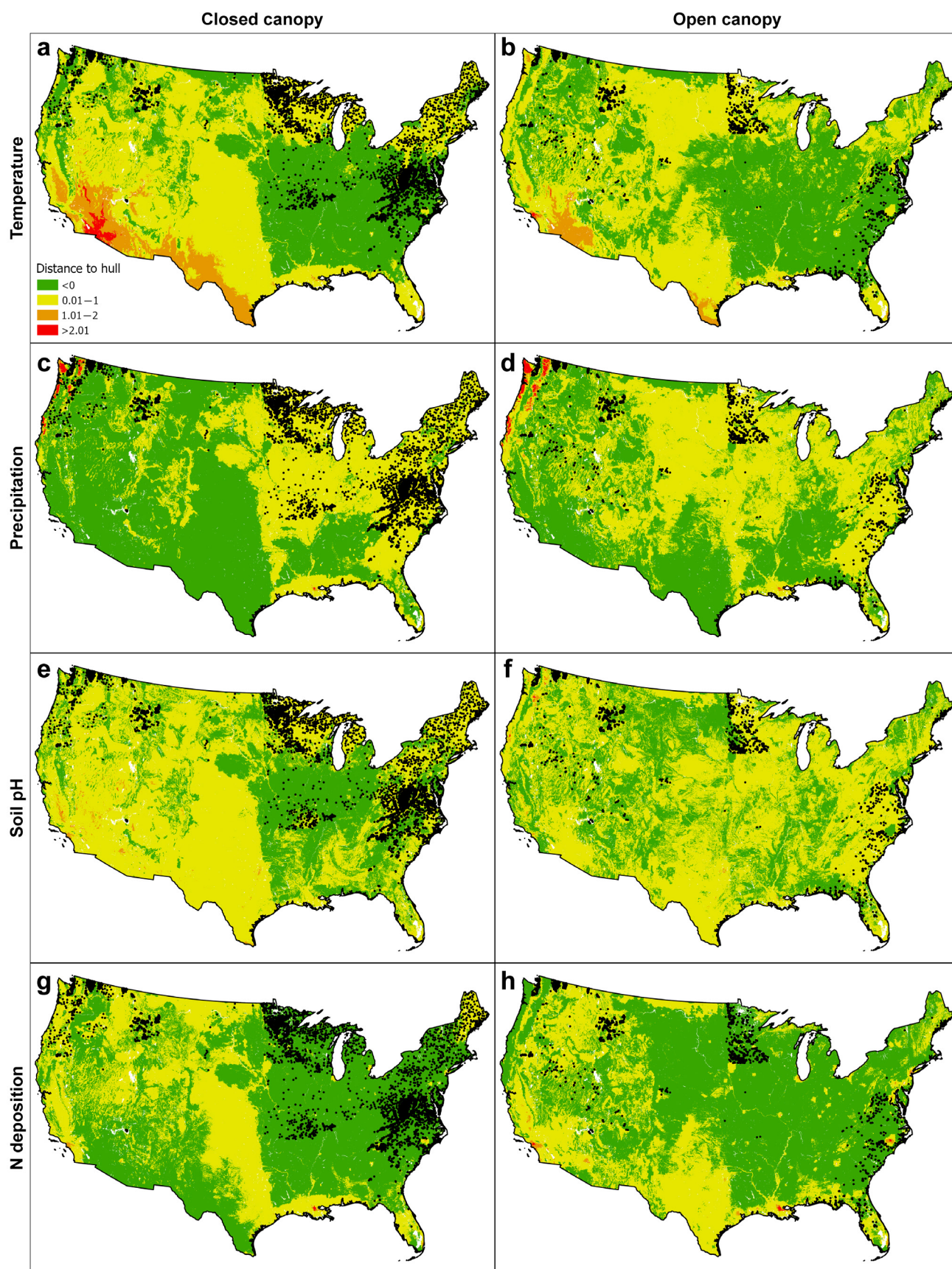


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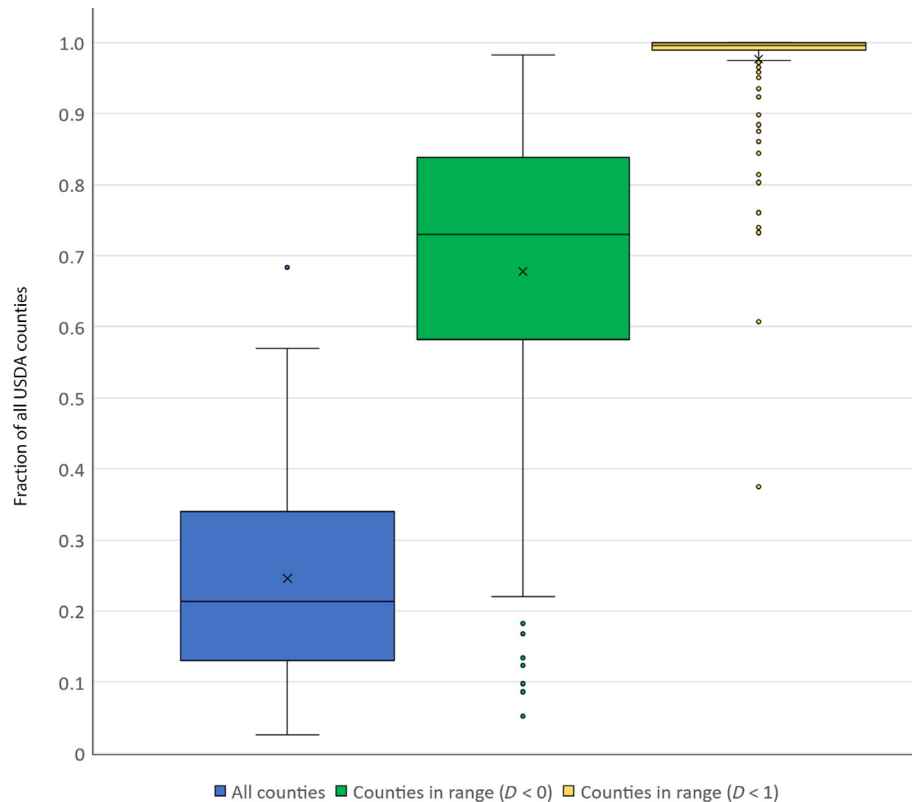


FIGURE 4 Histograms of the fraction of all US Department of Agriculture (USDA) counties in which the 198 species were observed (left), the fraction of all USDA counties that were inside the historical range and in which at least some of the county was inside the convex hull ($D < 0$, middle), and the fraction of all USDA counties that were inside the historical range and in which at least some of the county was inside ($D < 0$) or near the convex hull ($0 < D < 1$, right). Data for all species are available in Figshare (<https://doi.org/10.6084/m9.figshare.27242094>).

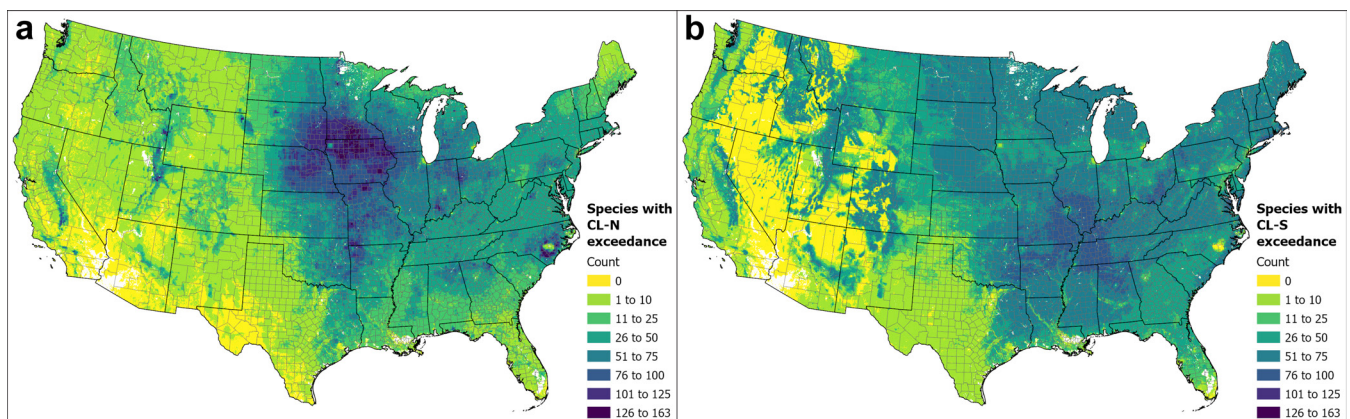


FIGURE 5 Total number of species included in the study in exceedance for (a) N deposition and (b) S deposition. Here, an exceedance was included if the area was inside the convex hull for that species and deposition was above the critical load. Exceedances are summed within a grid cell among the 198 species.

FIGURE 3 Mahalanobis distance (D) to the hull for open and closed canopy communities across the continental United States (CONUS) for each environmental variable and the plot locations for closed and open canopy. In (a)–(b) are the overall Mahalanobis distances across all axes (dimensions) for open and closed canopy communities, respectively; and (c)–(h) are the individual distances for the different environmental axes. All distances are as in the key of panel (a).

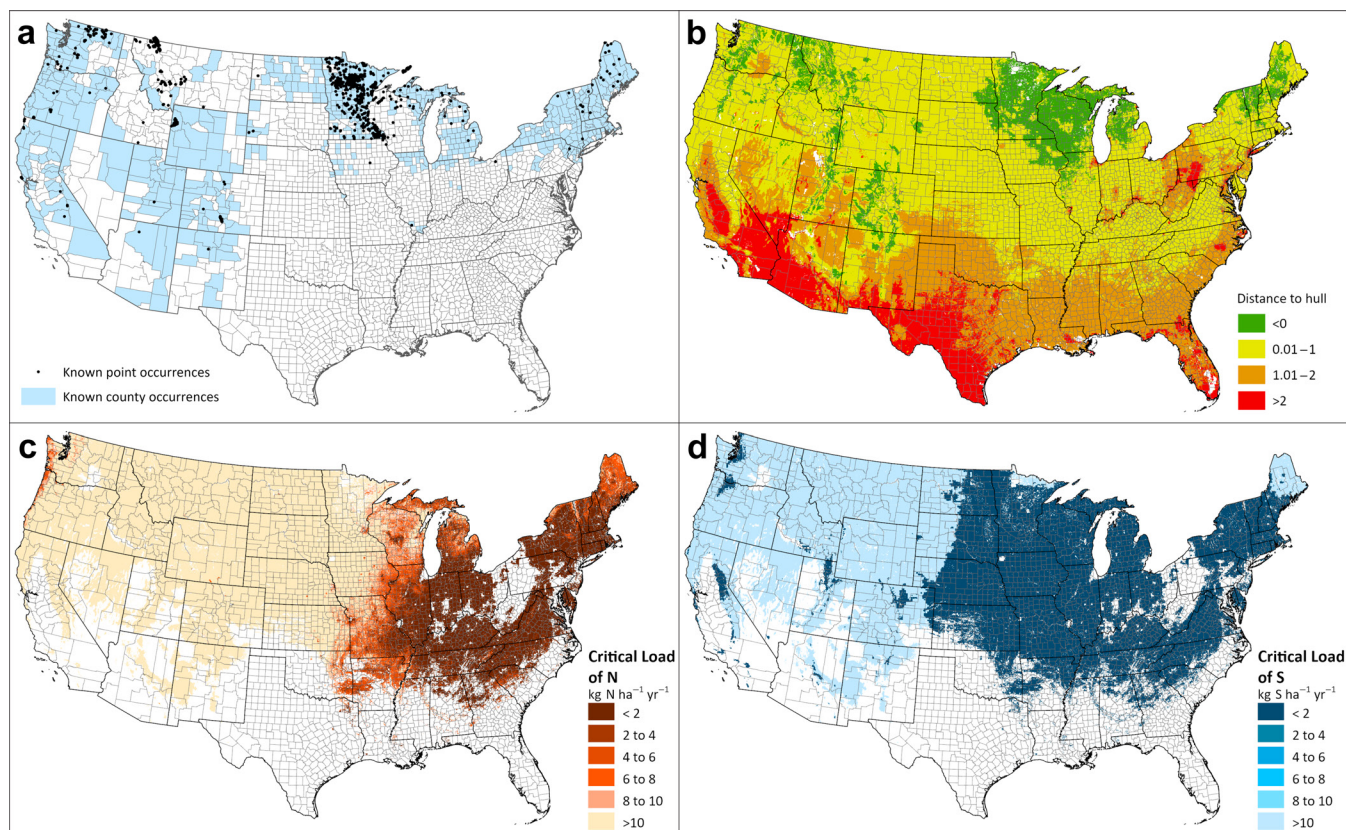


FIGURE 6 Distribution, hull results, and estimated critical loads for *Actaea rubra*. (a) The distribution of *A. rubra*, including counties in which it was reported in the US Department of Agriculture (USDA) PLANTS database (blue), and plots (points) in which it was observed in Clark et al. (2019). (b) The Mahalanobis distance (D) to the hull shows locations inside the hull (green), within 1 SD of the hull (yellow), and further outside (orange and red). (c, d) The estimate of the N and S critical load (CL), respectively, for *A. rubra* for areas inside or within 1 SD of the hull.

pockets (Figure 7b), N deposition in urban pockets in southern California and the eastern United States (Figure 7c), and soil pH in the southwest (Figure 7d). Precipitation was generally not responsible for pushing conditions outside the convex hull ($D > 1$) (Figure 7e).

E. yuccifolium (rattlesnake master) is a perennial native forb normally found in wet or dry prairies and open woods in the Southeast United States, north to Virginia, and throughout the Midwest to Minnesota, Kansas, and Texas (Figure 8a). The plot data available for *E. yuccifolium* was not evenly distributed, with reported occurrences in the warmer areas of the southern and southeastern United States and in cooler areas of southern Minnesota (Figure 8a). With this range of conditions captured, most of the southern United States and eastern portions of the Midwest were either inside or within 1 SD of the hull (Figure 8b); however, the conditions of the western United States were outside 1 SD of the hull. The N CLs were low throughout much of its range ($4\text{--}6\text{ kg N ha}^{-1}\text{ year}^{-1}$) as were the S CLs ($2.2\text{ kg S ha}^{-1}\text{ year}^{-1}$) (Figure 7c,d). The reasons conditions were outside the convex hull ($D > 1$) varied by

region and were due to temperature (Figure 9a) in the southwest, S deposition in the Ohio River Valley (Figure 9b), N deposition in emissions hot spots in southern California and various eastern areas (Figure 9c), soil pH in much of the west and southwest (Figure 9d), and precipitation in the Pacific Northwest (Figure 9e). This species is not historically found in the western United States, so these violations may not be important.

DISCUSSION

This work extends the point-based estimates of ecosystem vulnerability of herbaceous species to atmospheric deposition of N and S to continuous estimates across the CONUS. We find that for species richness, the original set of plots represents environmental conditions over much of the CONUS very well ($D < 0$) or is acceptable ($D < 1$). There is no bright line for where the conditions are sufficiently different that the estimates should not be used. Statistical efforts on outlier detection note that points outside the convex hull may be interpreted as an

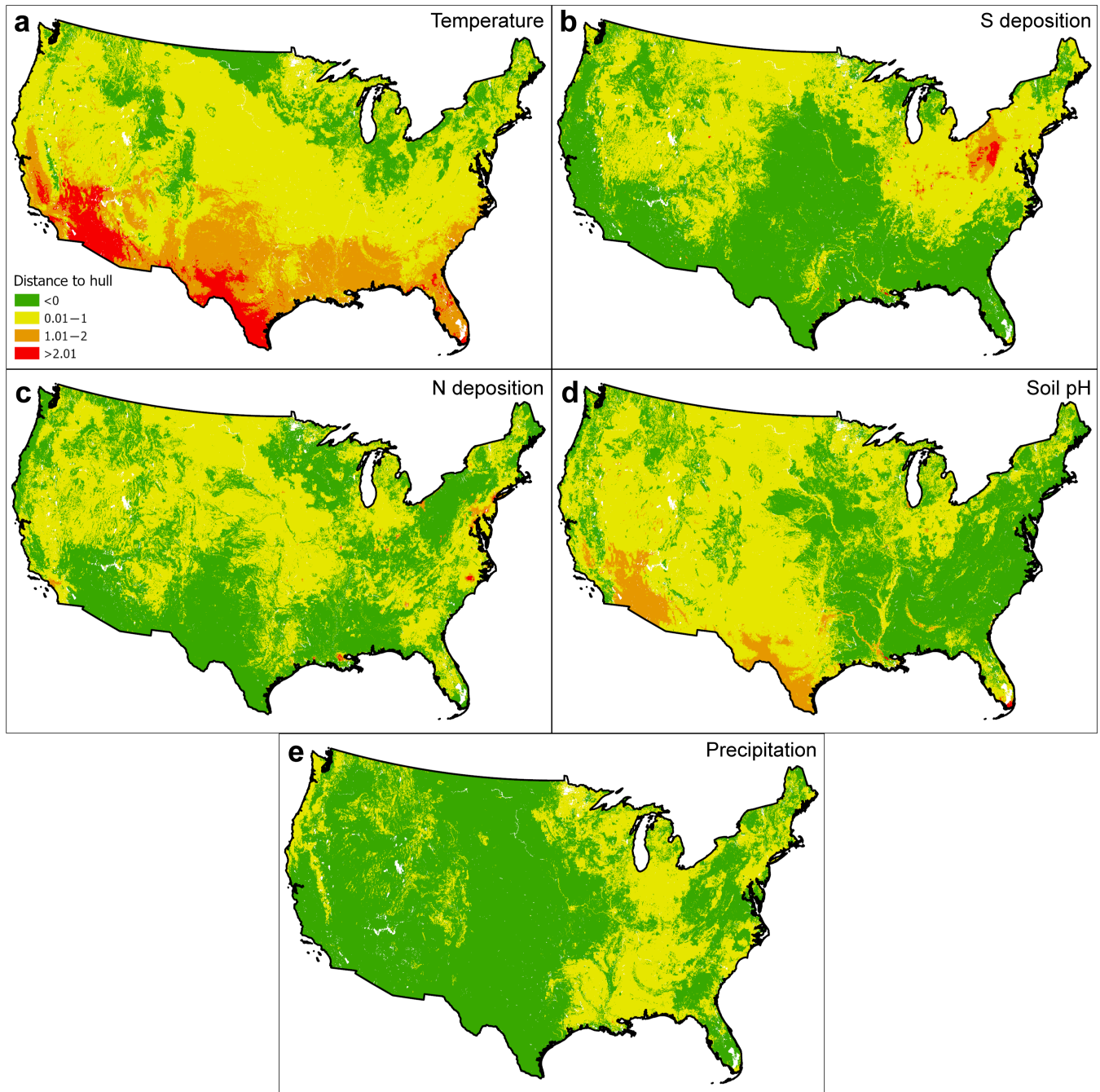


FIGURE 7 Distances to convex hull for *Actaea rubra*. Shown are the distances to the convex hull for (a) temperature, (b) S deposition, (c) N deposition, (d) soil pH, and (e) precipitation. All distances are as in the key of panel (a).

outlier, but also that researchers may want to extend the convex hull to allow for some managed extrapolation (Pierna et al., 2002). We feel that decision makers should be confident when using these estimates from areas that are inside the convex hull ($D < 0$). For areas far outside the convex hull ($D > 1$), we recommend additional lines of evidence prior to using these estimates to support land management decision making. For areas in between ($0 < D < 1$), we recommend using the estimates but recognizing the additional uncertainty.

It is important to remember to focus on not only the overall Mahalanobis distance to the hull (D) but also the variables contributing to that distance. For the example of *E. yuccifolium*, much of the west was well outside the convex hull ($D > 1$; Figure 8b). However, *E. yuccifolium* is not historically found in the west, so the lack of representation of that region is neither surprising nor concerning if one is interested in current or historical risk. On the other hand, with climate change, we may expect species ranges to shift substantially

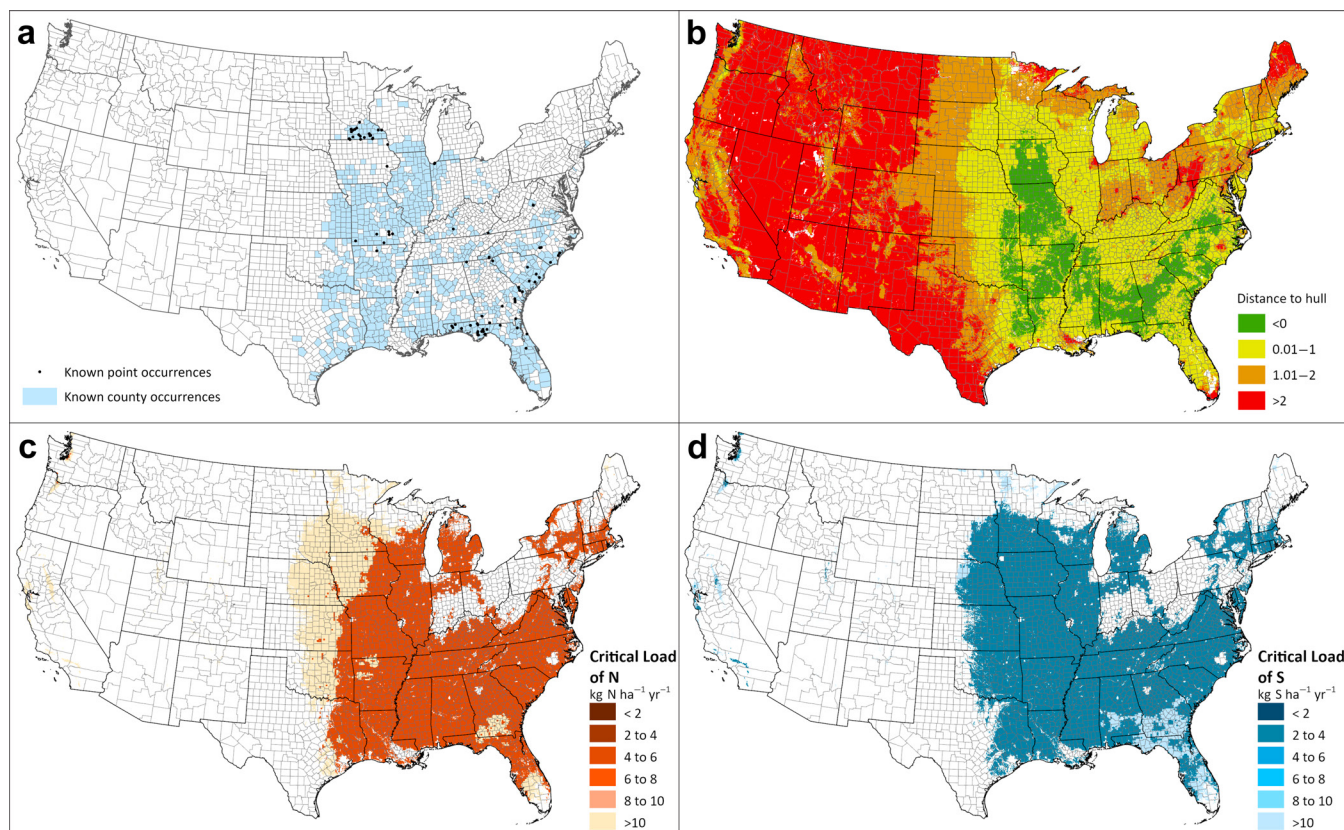


FIGURE 8 Distribution, hull results, and estimated critical loads for *Eryngium yuccifolium*. (a) The distribution of *E. yuccifolium*, including counties in which it was reported in the US Department of Agriculture (USDA) PLANTS database (blue), and plots (points) in which it was observed in Clark et al. (2019). (b) The distance to the hull showing locations inside the hull (green), within 1 SD of the hull (yellow), and further outside (orange and red). (c, d) The estimate of the N and S critical load (CL), respectively, for *E. yuccifolium* for areas inside or within 1 SD of the hull.

(Parmesan, 2006), so having an understanding of how well we might be able to predict responses outside of a species' historical range may be very useful for some purposes. Furthermore, it is important to assess not just which variable is contributing to the violation, but whether that variable matters for the species and particular use case. For example, if a particular location is inside the convex hull for temperature but outside for N deposition, it may be appropriate to use these responses for applications related to climate change but not for N deposition. In addition, if temperature is contributing to the violation in a particular area but does not interact with nitrogen, then the estimate of the nitrogen CL is considered to be unaffected by this violation. Careful consideration of the variables that contribute to D—in the context of the goals of the application—is a good rule of thumb.

Finally, this approach offers a quantitative way to address a common question faced by decision makers: “how applicable is this study to my area?” Researchers and decision makers commonly take results from one study and apply them to their particular case. Underpinning that choice is the assumption, whether stated or

unstated, that the results from one study are applicable to the other areas. The approach here quantifies that assumption, taking the guesswork out of interpolation and extrapolation. This could be used in any number of applications, such as climate change analyses to understand whether there is field data (experimental or observed) that mimics the environmental space sampled in IPCC global change models or socioeconomic analyses to understand whether one study is applicable to an unsampled population (Bastin et al., 2019; Early & Sax, 2014). Convex hulls may be a promising tool to help quantify the broader areas of inference for many studies in the peer-reviewed literature.

As noted in the introduction, this use of convex hulls is similar conceptually to the assessment of “climate envelopes” to assess future species ranges (Pearson & Dawson, 2003). However, there are important differences as well. We are not projecting any future environmental conditions, nor are we assuming that species will be free to move to any new areas or that biotic interactions will be similar or different from the current habitat. We are assessing whether the dataset upon which the CLs were

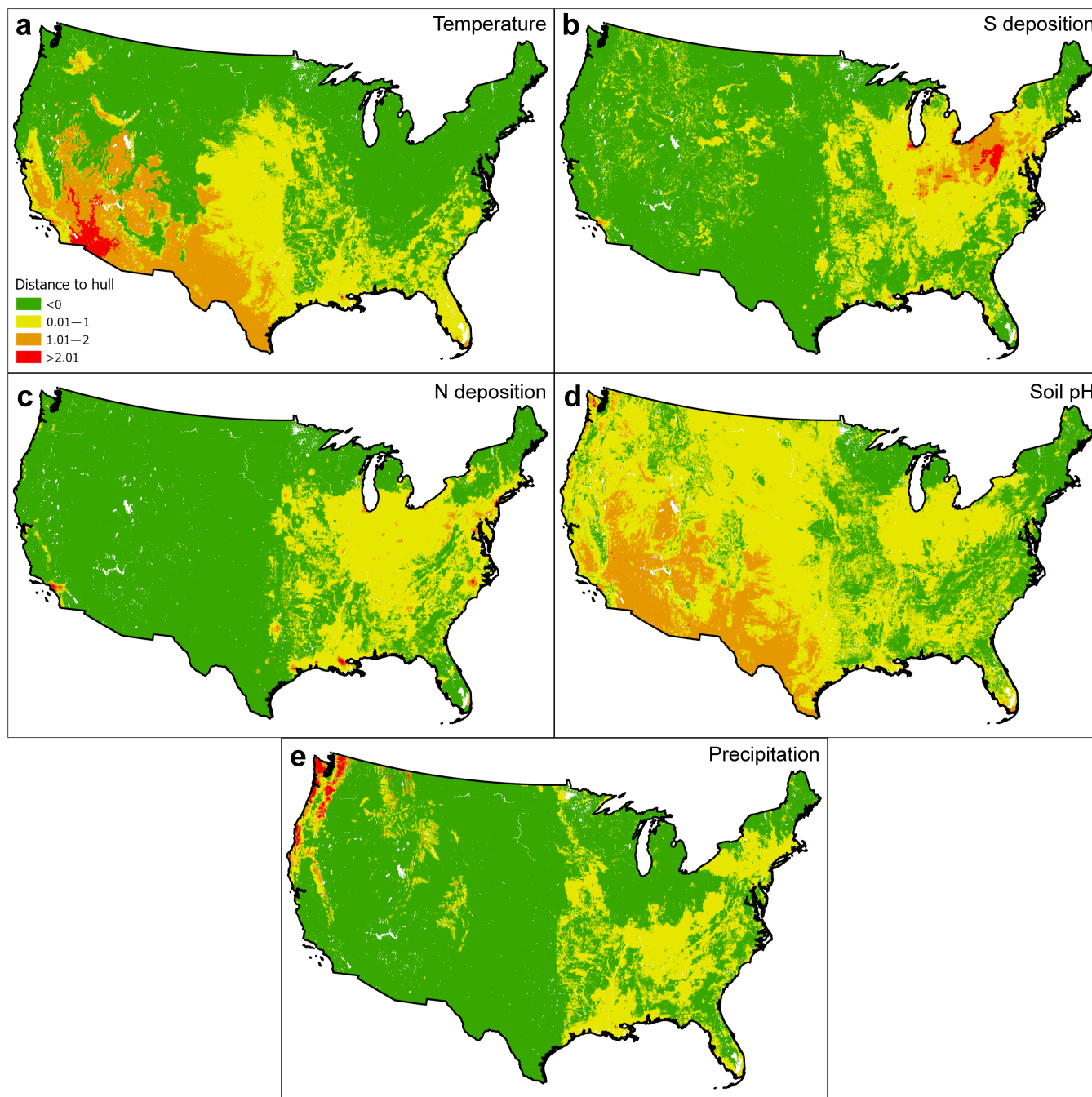


FIGURE 9 Distances to convex hull for *Eryngium yuccifolium*. Shown are the distances to the convex hull for (a) temperature, (b) S deposition, (c) N deposition, (d) soil pH, and (e) precipitation. All distances are as in the key of panel (a).

derived is representative of some larger geographic area, and estimating where in the CONUS that area is using the convex hull. In this way, our approach is less like climate envelope studies and actually more like outlier detection in statistics (Pierna et al., 2002), but with a spatial and ecological goal in mind. More generally, our approach is like a multivariate cluster analysis, in which the question of interest is whether one cluster (areas with CLs) is similar to another cluster (areas without CLs). But in our case, we are less interested in the difference

between two populations and more interested in whether specific areas (i.e., areas with no CL) are similar to some source population (i.e., areas with CLs).

We feel the approach is generalizable and has broad potential applications. It rests on the foundational assumption that the variables for which we have data are relevant to the end point of interest. For our application, we feel confident that vulnerability to N and S deposition is related to the environmental variables examined here (temperature, precipitation, N and S deposition, and soil

pH). However, an unspoken assumption is also the converse, that the end point of interest is not related to excluded variables. We know this is not accurate, as dozens of variables likely affect species vulnerability to N and S deposition, including height in the canopy (Horn et al., 2018), the presence of pests (Bobbink et al., 1998), and soil factors (McNulty et al., 2007). That said, we cannot quantify that which we do not have data for, and so we assume that the omission of these variables merely contributes to the estimates of error in the coefficients (e.g., Equations 1–3), rather than undermining the associations with variables for which we have data.

Using convex hulls allowed us to greatly exceed the areas that we may confidently assess impacts to herbaceous diversity and to assess confidence in these areas. For example, of the 151 Class I areas in the CONUS, only 19 and 8 areas had point estimates of CLs from Simkin for closed and open canopy communities, respectively. However, for closed canopy communities, 124 areas were inside the convex hull ($D < 0$) and 146 areas were inside or near the convex hull ($D < 1$). Thus, the plots sampled in the dataset were likely representative of other sites, and thus, the CLs were applicable. Similar results were found for open canopy sites, where, even though only eight Class I areas had point estimates, 135 areas were inside and all 151 areas were inside or near the convex hull.

CONCLUSIONS

We used convex hulls to greatly increase the applicability of point-based CLs to the CONUS. We found that most of the CONUS was well ($D < 0$) or adequately ($D < 1$) represented by the roughly 15,000 open and closed canopy plots used to derive the CLs for reductions in herbaceous species' biodiversity. We found that of the 198 species assessed, 161 species (81%) had 50% or more of their historical range inside the convex hull ($D < 0$) and 197 species had 50% or more of their historical range inside or near the convex hull ($D < 1$). There is no bright line for where the conditions are sufficiently different that the CL estimates should not be used. However, we feel that decision makers should be confident when using these estimates from areas that are inside ($D < 0$) or even near ($0 < D < 1$) the convex hull. Use of this approach may have widespread application to other uses, ultimately enabling decision makers to better understand community vulnerability to atmospheric deposition today and in the future with potential shifts in species ranges from climate change.

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CONFLICT OF INTEREST STATEMENT

The authors declare no conflicts of interest.

DATA AVAILABILITY STATEMENT

Data (Clark, 2024) are available on Figshare: <https://doi.org/10.6084/m9.figshare.27242094.v2>.

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SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

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