

Declines in native forb richness of an imperiled plant community across an anthropogenic nitrogen deposition gradient

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Abstract. Anthropogenic nitrogen (N) deposition is known to reduce plant diversity in ecosystems worldwide; however, effects on the diversity of Mediterranean-type ecosystems—global hotspots of biodiversity—are relatively unexplored. In California, elevated N deposition due to air pollution has a multitude of ecological effects including the facilitation of nonnative plant invasion and altered ecosystem functioning, but impacts on plant richness have been inadequately quantified. We addressed this research gap by evaluating patterns of plant richness in coastal sage scrub (CSS), a severely threatened, highly diverse Mediterranean-type shrubland, across the Santa Monica Mountains National Recreation Area. This is the largest urban national park in the United States and experiences a strong gradient of N deposition due to its proximity to urban Los Angeles. We measured soil N, plant cover, and richness at 30 CSS sites across this gradient and used regression analyses to explore relationships between richness, N deposition, and other environmental variables. We observed significant declines in plant richness across a steep gradient of soil N availability that paralleled patterns of N deposition, primarily due to decreases in native forb species. Our analyses identified soil N as the best predictor of patterns of native forb richness, but other factors, including nonnative plant cover and aridity, may also drive reduced richness. In addition to the marked decline in the number of native forb species, increasing N deposition was also associated with lower native shrub richness per area and increased cover of nonnatives. These results highlight the threat posed by N deposition to the conservation of this already imperiled ecosystem under continued environmental change.

Key words: atmospheric pollution; coastal sage scrub; Mediterranean-type ecosystems; nitrogen deposition; plant richness; shrublands.

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INTRODUCTION

Increasing atmospheric nitrogen (N) deposition resulting from human activities is a major driver of global environmental change and a growing threat to ecosystems worldwide

(Vitousek et al. 1997, Galloway et al. 2008, Ackerman et al. 2019). While N addition may have complex and variable ecological impacts, reductions in vascular and nonvascular plant richness due to N addition have been widely reported in a number of ecosystems (Stevens et al. 2006,

Bobbink et al. 2010, Maskell et al. 2010, Simkin et al. 2016). However, the impacts of N deposition on the plant diversity of many ecosystems, such as Mediterranean-type ecosystems, and the underlying mechanisms remain unknown (Bobbink et al. 2010, Ochoa-Hueso et al. 2011).

The world's Mediterranean ecoregions—which represent global hotspots of biodiversity—are expected to be particularly vulnerable to environmental change, including increases in N deposition (Phoenix et al. 2006, Ochoa-Hueso et al. 2011). Much of what we know about the response of these ecosystems to N enrichment is from extensive research in California's coastal sage scrub (CSS). This semi-arid plant community consists of a variety of drought-deciduous and evergreen shrubs and a diverse array of perennial and annual forbs, including a number of rare and threatened species (O'Leary 1990). Heavily impacted by grazing, development, and nonnative plant invasion, CSS now occupies as little as ten percent of its historic distribution (Westman 1981).

Much of the remaining CSS in southern California is subject to high levels of N deposition, which may have profound ecological impacts at multiple scales (Fenn et al. 2003, Allen et al. 2016). For example, N deposition is a major contributor to the conversion of CSS to nonnative annual grasslands (Talluto and Suding 2008, Cox et al. 2014). Excess soil N favors nonnative annuals over native species, and the resulting fuel loads lead to larger and more frequent wildfires, facilitating vegetation-type conversion (Fenn et al. 2003). Effects of elevated N deposition may also be exacerbated by drought; together, these stressors can slow post-fire succession, increase shrub mortality, and drive the invasion of nonnatives (Kimball et al. 2014, Valliere et al. 2017, Vourlitis 2017). Altered plant–water relations under high soil N may play a role in shaping community responses to N deposition (Wood et al. 2006, Valliere et al. 2017). Finally, soil N enrichment can induce shifts in soil microbial communities, such as reductions in mycorrhizal diversity, which could promote the growth of invasives over CSS natives (Allen et al. 2016, Valliere and Allen 2016).

Despite a rich body of research exploring the effects of N deposition on CSS, examinations of plant diversity across landscape-level N

deposition gradients are lacking for this and other Mediterranean-type ecosystems (Ochoa-Hueso et al. 2011). The only previous attempt to understand the consequences of anthropogenic N deposition on plant richness of CSS by Allen et al. (2016) was conducted at a very limited number of sites ($n = 7$) in more arid CSS, though a steep drop in forb richness was found at sites receiving high levels of exogenous N. To our knowledge, this is the only study to explore the impact of atmospheric N deposition on plant diversity of any of the world's Mediterranean ecosystems. Several multi-year fertilization experiments have been useful in elucidating impacts of N enrichment in CSS, but these studies found no effect of N addition on native plant richness (Vourlitis and Pasquini 2009, Valliere et al. 2017). Outside of California, the impacts of N deposition on plant diversity of Mediterranean-type ecosystems are virtually unexplored.

To address this research gap, we evaluated potential impacts of elevated N deposition on vascular plant richness of CSS across the Santa Monica Mountains National Recreation Area (NRA) of southern California, United States. We focused our analyses on measures of native forb richness because several previous studies in other systems have reported significant declines in numbers of forb species with increasing N deposition (Stevens et al. 2006, Maskell et al. 2010, Simkin et al. 2016), but we also evaluated impacts on native shrub species and nonnative species. We hypothesized that soil N availability would exhibit a steep east-to-west gradient that parallels patterns of N deposition, with areas closest to urban Los Angeles—the source of much of the region's atmospheric pollutants—being the most N-enriched. We predicted that increased N deposition would be associated with reduced plant richness, especially native forb species. Finally, we predicted that the cover of nonnative species would be positively correlated with N deposition and negatively correlated with native richness. While the primary focus of this study was on atmospheric N deposition, we also considered other environmental variables that could also potentially influence plant community diversity and composition in a landscape-level study such as this (e.g., fire history, soil texture and chemistry, and climate variables).

METHODS

The Santa Monica Mountains NRA (34.103889, –118.6025) is located in the greater Los Angeles area and is the largest urban national park in the United States, representing a high conservation priority. Total land area within the park boundaries is over 62,000 ha, including a mix of privately owned land and parkland managed by the National Park Service, the California State Park system, and Los Angeles County or municipal parks. The park consists of a mosaic of oak woodlands, chaparral, grasslands, and CSS, the ecosystem of interest for this study. The region experiences a hot, dry summer and a cool winter growing season characteristic of a Mediterranean-type climate. In this semi-arid ecosystem, soil water availability is contingent upon precipitation. Most rainfall occurs during the winter growing season (November–March), with high intra- and interannual rainfall variability. Mean annual precipitation ranges from about 300–440 mm in the foothills to 500–625 mm in the mountains (Harrison et al. 1971). The geology of the mountain range is complex, and a variety of parent materials and soil types are present (USDA NRCS 2006).

We utilized data from the Community Multiscale Air Quality (CMAQ) model developed by the U.S. Environmental Protection Agency to estimate rates of N deposition across the study area, ranging $\sim 2\text{--}20 \text{ kg N}\cdot\text{ha}^{-1}\cdot\text{yr}^{-1}$ across the park (Tonnesen et al. 2007, Fenn et al. 2010). We used deposition values from the model for 2002, which is available on a spatial scale of 4-km^2 grid cells. A more recent iteration of the CMAQ model exists for 2012, but on a much coarser spatial scale of 12 km^2 . Prior to conducting our analyses, we compared the 12-km^2 grid values from 2002 and 2012 for our study area. Differences in deposition rates were minimal and suggested a slightly steeper gradient of N deposition across the park (Appendix S1: Fig. S1). Given the relatively small changes over time and the fact that the 4-km^2 grid provides much finer spatial resolution for our analyses, we opted to use the 2002 data from Fenn et al. (2010).

Using aerial imagery and vegetation maps, we identified 30 sites (Fig. 1a) of mature CSS that spanned the N deposition gradient. We selected sites that had previously burned ≥ 10 yr ago and

had at minimum $\sim 50\%$ native CSS shrub cover to ensure our sampling was limited to mature, intact CSS. We sampled vegetation in 2015 during the peak of the spring growing season (April–May). At each site, over an area of approximately one hectare, we randomly placed ten 5-m^2 vegetation sampling plots. To limit effects of aspect, plots were located on south-facing slopes. For each plot, we recorded all species present and estimated percent cover using meter tapes spread along the plot perimeter as a guide. From these data, we calculated total plant richness per site, mean plot richness, and mean percent cover for different plant functional groups, including all natives, native shrubs, native forbs, and nonnatives (Vorobik 2012).

We collected soil samples for analysis in September 2015, when soil N concentrations in this system are typically at their highest (Padgett et al. 1999). We collected ten samples per site, each consisting of two composited 10-cm cores, one from underneath the shrub canopy and one from the adjacent shrub interspace. We analyzed total KCl-extractable soil N from air-dried, 2 mm sieved soil at the University of California, Riverside, using an AQ2 Discrete Autoanalyzer (Seal Analytical, Mequon, Wisconsin, USA). Soils from each site were also analyzed for particle size (i.e., texture), Olsen extractable P, soil C and N by combustion, and exchangeable cation concentrations (K, Ca, Na, and Mg) at the University of California, Davis Analytical Laboratory.

We retrieved climate data from the PRISM Climate Group Web site, Oregon State University (<http://prism.oregonstate.edu>), including mean annual precipitation, mean maximum and minimum temperature, and mean maximum and minimum vapor-pressure deficit (VPD) based on 30-yr normals. Elevation of the study sites was determined using the U.S. Geological Survey's Digital Elevation Models (DEMs). Information on fire history, including time since last fire and fire frequency (since 1925 when historical records began), was determined using maps supplied by the Santa Monica Mountains NRA.

We completed statistical analyses in R (v. 3.5.2). We first used linear regression to explore relationships between N deposition with soil N availability and plant richness and cover across sites ($n = 30$). This included separate analyses of different plant functional groups based on life-

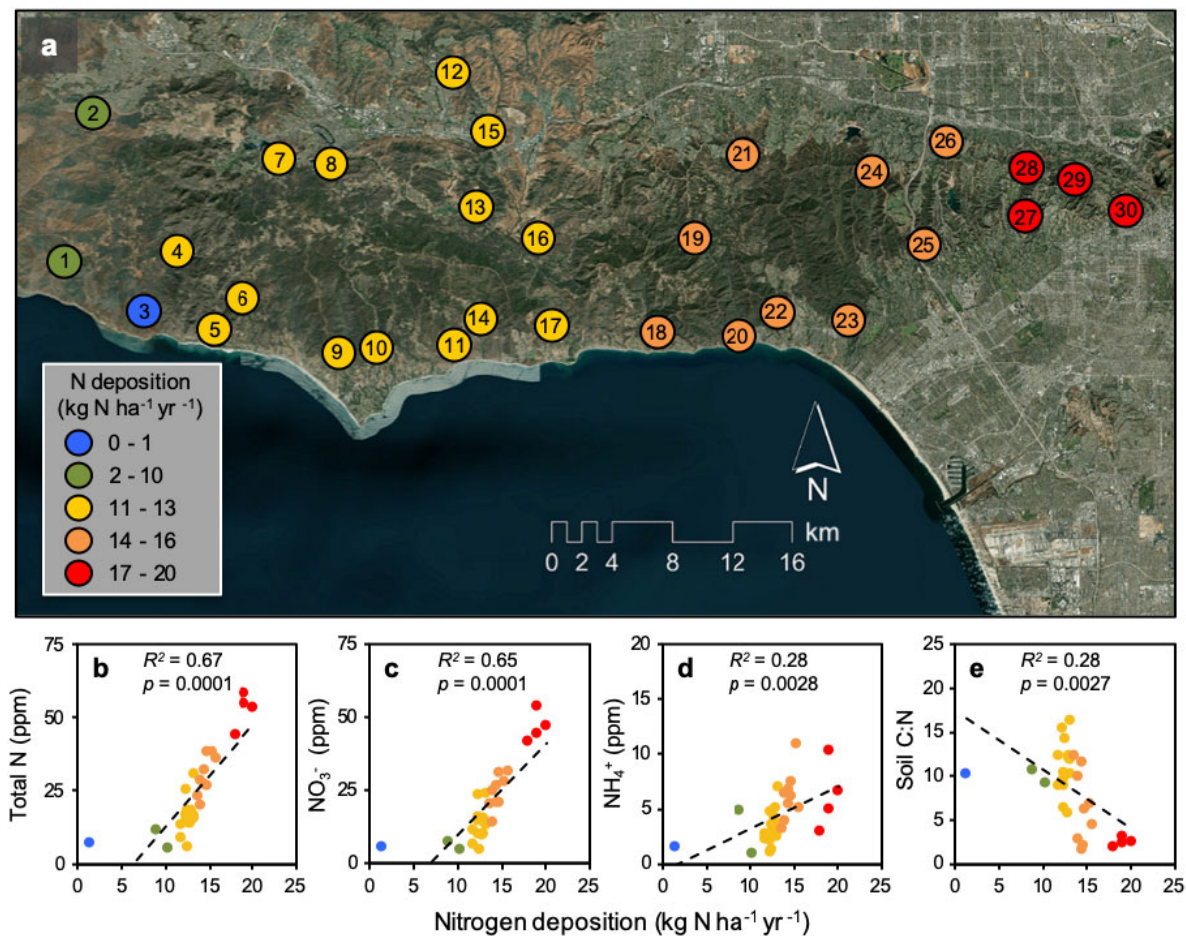


Fig. 1. Location of vegetation sampling sites ($n = 30$) across the Santa Monica Mountains and rates of atmospheric N deposition (a) and correlations between N deposition and (b) total extractable soil N, (c) soil nitrate, (d) soil ammonium, and (e) soil C:N ratios.

form and origin (either native or nonnative), including all natives, native shrubs, native forbs, and nonnative species (which were largely nonnative annuals). We then used Pearson correlation with the `rcorr` function within the `Hmisc` package to produce a correlation matrix to evaluate relationships among all vegetation and environmental variables. Prior to analysis, we tested each variable for normality using the Shapiro-Wilk test, using log and square-root transformations as needed. We then constructed a correlogram using the `corrplot` function.

Finding a significant decline in native forb richness across the N deposition gradient, we then sought to identify environmental variables that best explained this pattern. We completed

independent analyses of total and mean native forb richness using two types of classification and regression tree models. For each analysis, we included predictors based on site-specific values of N deposition, soil N, soil pH, elevation, mean annual precipitation, mean maximum and minimum annual temperatures, mean maximum and minimum VPD, time since last fire, fire frequency, soil nutrient availability (Ca, K, Mg, and P), soil texture (percent sand, silt, and clay), and percent cover of native shrubs, native forbs, and nonnatives. The first models implemented tree regression (TREE v. 1.0-39) and regressed total or mean native forb richness on our set of predictors. Tree regression uses a binary recursive partitioning method to build a classification tree that

hierarchically ranks variables according to how well and at what level they explain variance in response variables (De'ath and Fabricius 2000). We then constructed models that applied tree regressions using the randomForest (v. 4.6-14) framework (Liaw and Wiener 2002). This algorithm iteratively and randomly removes a subset of variables to determine the rank relationships between predictors and response variables based on changes to model error. We chose this approach because randomForest is a non-parametric procedure with no underlying assumptions about data distribution compared to more traditional linear regression. Furthermore, these models have been shown to outperform traditional regression tests, handle complex interactions between variables, and, relevant to our study, assess the role of continuous variables across a landscape (Prasad et al. 2006, Cutler et al. 2007). To assess model robustness, we computed *P*-values ($\alpha = 0.05$) for each predictor by producing a null distribution of 1,000 permutations of each randomForest model with rfPermute (v. 2.1.6).

RESULTS

Total extractable soil N was positively correlated with N deposition across sites (Fig. 1b). This was driven largely by increases in soil nitrate (NO_3^-) but also soil ammonium (NH_4^+) at high deposition sites (Fig. 1c–d). Rates of N deposition were negatively correlated with soil CN ratios (Fig. 1e). We detected no effect of N deposition on soil pH across study sites ($R^2 = 0.01$, $P = 0.7582$). Total native richness (Fig. 2a) and total native forb richness (Fig. 2b) were negatively correlated with N deposition, while total numbers of native shrub species (Fig. 2c) and nonnative species (Fig. 2d) showed no relationship. The mean number of native species per plot was also negatively correlated with N deposition (Fig. 2e), including both native forbs (Fig. 2f) and, to a lesser extent, native shrubs (Fig. 2g). Mean nonnative richness was unrelated to N deposition (Fig. 2h). Total native plant cover decreased with N deposition (Fig. 2i), but not the cover of native forbs (Fig. 2j) and shrubs (Fig. 2k) individually. Total nonnative cover showed a positive relationship with N deposition (Fig. 2l). Correlogram analysis (Fig. 3)

further illustrated negative relationships between measures of native forb richness and N deposition, as well as with soil N, nonnative cover, and climate variables such as higher mean annual temperatures and maximum VPD.

Given the number of correlated environmental variables in a landscape-level study such as this, tree regression and random forest analyses aided in the identification of those with the greatest explanatory power. Tree regression showed that soil N was the most important predictor for both total and mean native forb richness (Fig. 4a, b), as indicated by the length of the first node branch. Other variables, such as soil pH and elevation for total native forb richness and percent sand and forb cover for mean forb richness, explained relatively minor amounts of variance. Random forest models and permutation tests further identified soil N as the most important and statistically significant predictor of total and mean native forb richness patterns (Fig. 4c, d). In addition to soil N, total native forb richness was best explained by maximum temperature, N deposition, nonnative cover, native forb cover, and maximum VPD. Mean native forb richness was best explained by the same factors, with the addition of soil texture (i.e., percent sand).

DISCUSSION

Our results add to a growing body of evidence showing that N addition exerts a strong influence on plant community diversity (Bobbink et al. 2010, Maskell et al. 2010, Simkin et al. 2016) and highlight the vulnerability of native CSS forb species to anthropogenic N deposition. We explored patterns of richness at two scales, including the total number of plant species per site and the mean number of species per plot (5 m²). Forb richness showed similar steep declines in both of these metrics with increasing N deposition, indicating that greater N availability reduces the overall species pool of native forbs at CSS sites and leads to a more simplified native forb community with fewer species per area. We also found that N deposition appears to concomitantly favor nonnative species, consistent with ecological theory (Davis et al. 2000) and previous observational (Talluto and Suding 2008, Cox et al. 2014) and experimental studies in CSS (Kimball et al. 2014, Valliere et al. 2017). Native

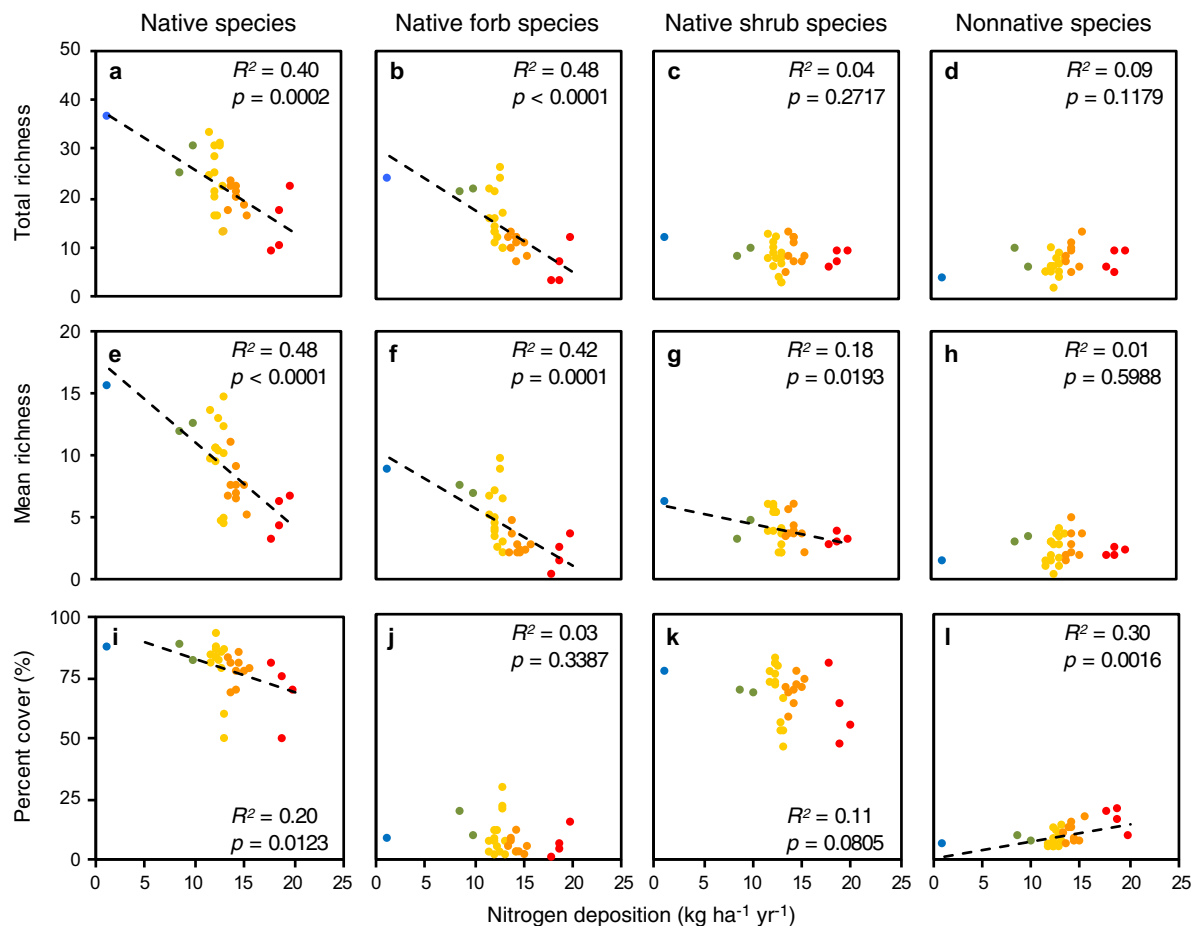


Fig. 2. Correlations between atmospheric N deposition and (a–d) total richness, (e–h) mean richness per plot, and (i–l) percent cover across study sites ($n = 30$) by plant functional group, including all native species, native forb species, native shrub species, and nonnative species. Point colors represent rates of N deposition (see Fig. 1).

forb richness was negatively correlated with nonnative cover, which strongly suggests that the influence of N deposition on CSS diversity is at least partly mediated by nonnative species. In light of predicted increases in global rates of N deposition, these findings have particular relevance to the conservation of biodiversity in Mediterranean-type ecosystems (Phoenix et al. 2006).

Importantly, our analyses revealed that soil N is the best predictor of native forb richness in CSS. As expected, we found a positive correlation between N deposition and soil N availability, largely in the form of soil nitrate. This is similar to other described gradients of atmospheric N pollution and terrestrial N accumulation in the region (Padgett et al. 1999). Given the

uncertainty associated with modeling N deposition (Fenn et al. 2010), it is perhaps unsurprising that soil N was more tightly correlated with plant richness than N deposition. Direct N eutrophication resulting from N deposition may be the primary driver of enhanced soil N availability, but N deposition may also increase rates of decomposition and N mineralization (Sirulnik et al. 2007, Vourlitis et al. 2007). Higher nonnative cover at sites subject to high levels of N deposition could also increase rates of nitrification, contributing to soil N availability (Ehrenfeld 2003, Hawkes et al. 2005).

Reductions in native forb richness with elevated N deposition could be driven by a number of mechanisms. Such species may be easily out-competed by other fast-growing species, for

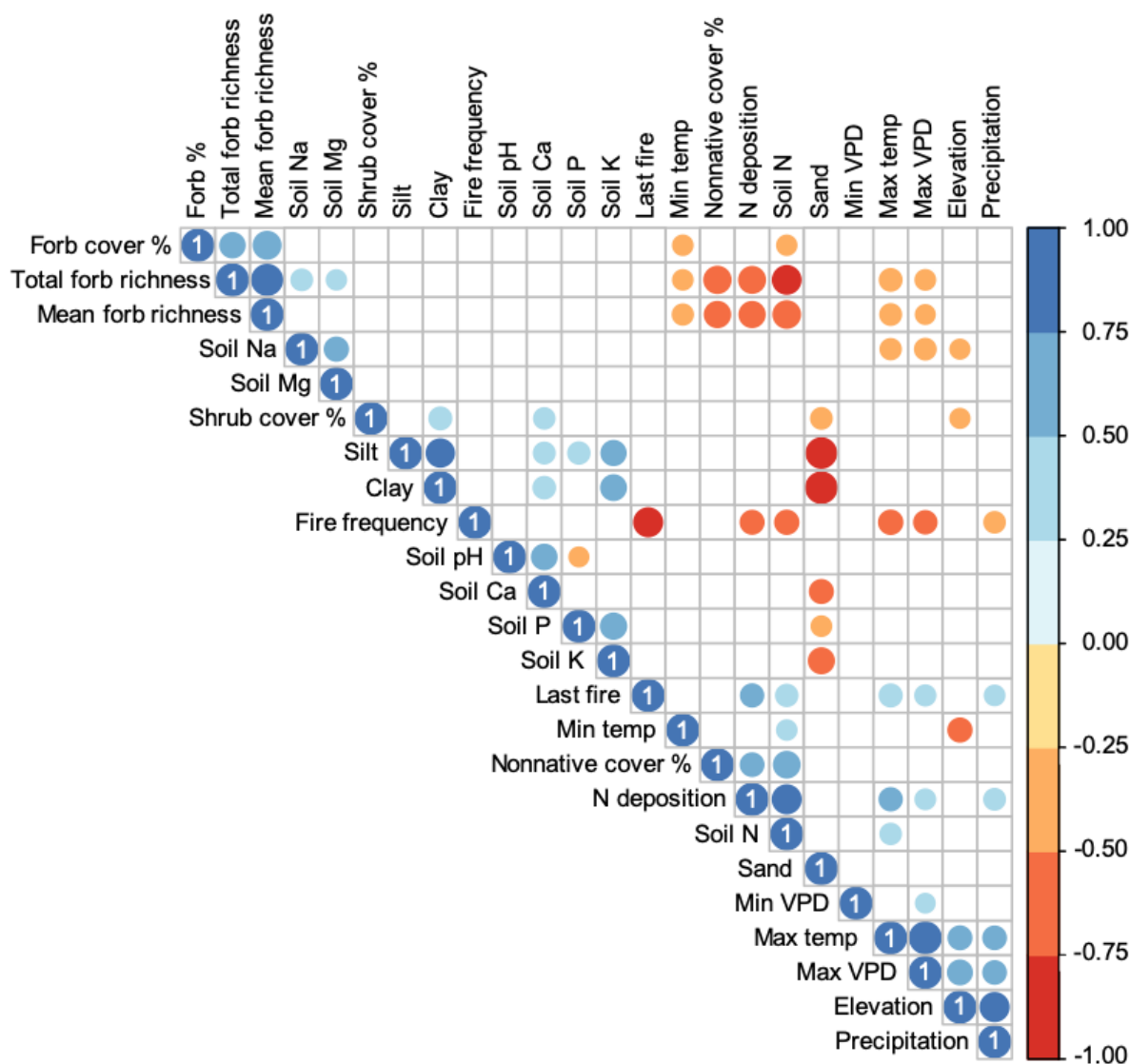


Fig. 3. Correlogram of vegetation and environmental variables across study sites ($n = 30$), including total and mean forb richness, plant cover (native shrubs, native forbs, and nonnatives), N deposition, soil pH, soil nutrients (Ca, K, Mg, N, and P), soil texture (percent clay, sand, and silt), climate variables (elevation and mean annual precipitation, mean annual maximum and minimum temperature, and mean annual maximum and minimum VPD), fire frequency, and time since last fire. Circle size is proportional to the correlation coefficient. Blue indicates a positive correlation, while red indicates a negative correlation. Blank squares indicate the correlation was not significant ($\alpha = 0.05$).

example, nonnative annuals, under high productivity and low-light conditions (Suding et al. 2005). The observed success of nonnative annuals under high N conditions is likely a function of a number of advantageous functional traits: earlier phenology, high germination rates, superior

competitive abilities, and rapid growth rates (Suding et al. 2005, Wainwright and Cleland 2013, Valliere 2019). Increased N may also increase the susceptibility of native plants to secondary stressors or alter interactions with other organisms, both antagonistic and beneficial

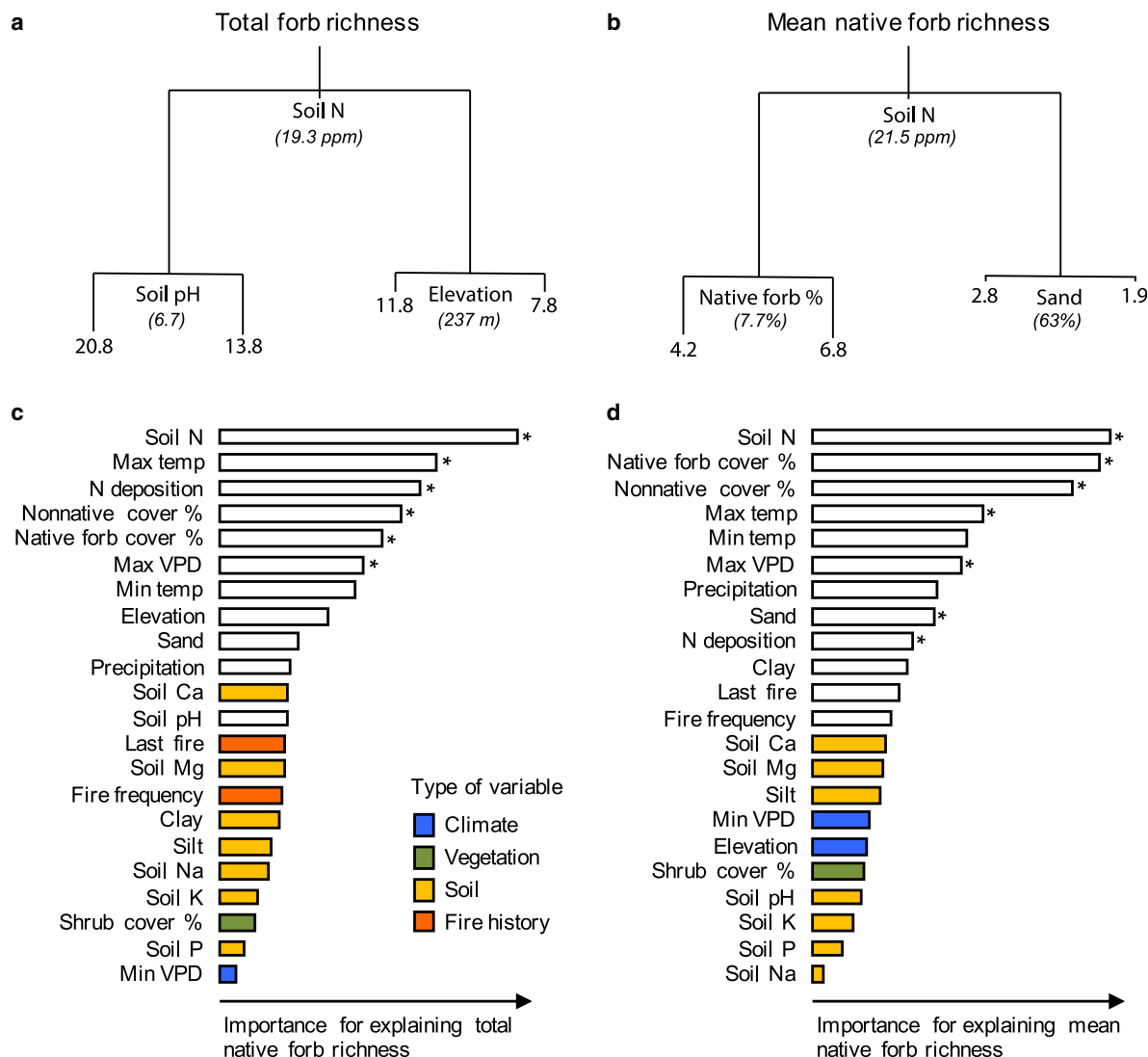


Fig. 4. Tree regression results for (a) total and (b) mean native forb richness illustrating that patterns of richness across the Santa Monica Mountains are best explained by soil N availability. Additional nodes show the next best predictors of richness based on a bifurcated data set split by values that do or do not exceed the first node value (i.e., soil N greater than or less than 19.3 ppm for total native forb richness or 21.5 ppm for mean native forb richness). Random forest models and permutation test results for (c) total and (d) mean native forb richness showed similar results, with soil N identified as the most important predictor of richness along with forb cover, nonnative cover, maximum temperature, maximum VPD, and N deposition ($\alpha = 0.05$).

(Bobbink et al. 2010). For example, elevated N deposition can result in intensified herbivory (Throop and Lerdau 2004), reduced drought tolerance (Valliere et al. 2017), or altered mycorrhizal functioning (Allen et al. 2016). Abundance-based mechanisms may also be at play, with less common species more likely to disappear from the community (Suding et al.

2005). In other ecosystems such as European grasslands and heathlands, soil acidification is the primary driver of forb loss under N deposition (Maskell et al. 2010, Stevens et al. 2010), but we observed no effect of N deposition on soil pH. Regardless of the underlying mechanisms, if native forb species continue to be excluded from the community, they may undergo local, or even

regional, extinction under chronic N deposition (Suding et al. 2005, McClean et al. 2011).

We also identified other environmental variables as important factors influencing forb richness in addition to N deposition, soil N availability, and nonnative cover, such as mean annual maximums in temperature and VPD. These climate variables were negatively correlated with forb richness, suggesting drier and hotter CSS sites are less species-rich. A similar result was found by Westman (1981), where more arid inland CSS sites had lower forb diversity than coastal areas. It is important to note that herbaceous vegetation in this system exhibits high interannual variability depending on precipitation, and our study took place during a multi-year drought. However, our other work in the Santa Monica Mountains during this time found that herbaceous cover and biomass during the drought was relatively high in 2015 (the year we sampled) compared to previous years, despite below-average rainfall (Valliere et al. 2017).

Wildfire is an important ecological process in CSS, but human activities have led to more frequent fires than in the past (Keeley and Fotheringham 2001). Previous work has established a link between elevated N deposition and fire frequency in CSS due to the increased fire risk associated with nonnative annual grasses (Fenn et al. 2003, Talluto and Suding 2008, Cox et al. 2014). While we observed greater nonnative cover with increasing N deposition, fire history parameters were unrelated to forb diversity. This is likely because we restricted vegetation sampling to mature, intact CSS. Furthermore, several high N deposition sites had low fire frequencies, possibly because of fire suppression in areas in close proximity to human property. It is conceivable that low fire return intervals could negatively impact plant richness along with N deposition. For example, fire-following forbs are a key component of plant diversity in CSS (O'Leary 1988). However, these species would not have been an important part of (aboveground) diversity at our sites, which last burned at minimum ten years ago. Understanding the impact of N deposition on the soil seedbanks of such species is an important avenue for future research.

We observed fewer native shrub species per plot with increasing N deposition. Overall,

native shrub cover was similar across sites, showing this is likely due to a simplification of the shrub community and not merely shrub loss. While some CSS shrub species may be negatively impacted by N deposition, others might actually benefit from added N, thereby shifting community composition (Vourlitis and Pasquini 2009). Interactions between seedling recruitment, non-native species, and N deposition probably play an important role in shaping these patterns. For example, Valliere (2019) found that seedlings of native CSS perennials respond positively to soil N in the absence of nonnative annuals, but their growth is severely reduced in invaded communities, especially under high N availability. It is interesting that overall native shrub richness did not show the same negative relationship with N deposition as plot-level shrub richness. Because these plants are longer-lived perennials, it is possible that the negative impacts of N deposition on their diversity are slower to manifest. Our results show that greater N availability can negatively impact shrub richness at smaller spatial scales, and it is possible that over time this will lead to lower overall shrub richness at high deposition sites.

Identifying critical loads, or thresholds, of N deposition for changes in ecosystem properties is useful for developing air quality legislation and land management strategies (Fenn et al. 2010). Previous work suggested a critical load of $\sim 10 \text{ kg N} \cdot \text{ha}^{-1} \cdot \text{yr}^{-1}$ for declines in CSS richness, but this was based on measurements at only seven sites (Allen et al. 2016). The negative relationships we observed between forb richness and N deposition appeared linear, suggesting that any amount of exogenous N could reduce plant diversity in this system. This underscores the significant threat that N deposition poses to the biodiversity of CSS, including a number of rare, threatened, and endangered plant and animal inhabitants (O'Leary 1990, Rubinoff 2001).

A key question that arises from this work is if similar plant richness declines due to N deposition will be observed in the other Mediterranean-type ecoregions of the world. These ecosystems represent global biodiversity hotspots that are predicted to be especially vulnerable to increasing anthropogenic N deposition (Phoenix et al. 2006). Despite this risk, little information exists in the literature regarding how the plant

diversity of such ecosystems will respond (Ochoa-Hueso et al. 2011). Recent reviews by Bobbink et al. (2010) and Ochoa-Hueso et al. (2011) identified only a single study investigating N-induced diversity declines outside of California: an N fertilization experiment in a semi-natural grassland in Italy (Bonanomi et al. 2006). However, some evidence suggests that faster-growing species in these ecosystems will disproportionately benefit from N addition, which could potentially lead to competitive exclusion and reductions in plant richness. For example, N addition has been found to promote the growth of ephemeral plant species in the fynbos of South Africa (Witkowski 1988), nonnative European herbs in the Chilean matorral (Holmgren et al. 2000), and nonnative annual grasses in Western Australia (Hobbs and Atkins 1988). It should not be assumed, however, that all Mediterranean-type ecosystems will respond in the same way. For example, the lower phosphorous availability of the more ancient soils of South Africa and Australia could limit the impacts of N deposition on vegetation in these regions (Ochoa-Hueso et al. 2011). Future studies that explore diversity patterns across gradients of N deposition and in controlled N fertilization experiments will be useful in further evaluating these impacts, particularly in the Southern Hemisphere.

Our results have important implications for the long-term conservation and sustainability of this already imperiled ecosystem and other Mediterranean ecosystems worldwide. While protected areas such as the Santa Monica Mountains NRA are critical for the conservation of biodiversity, park boundaries cannot shield landscapes from atmospheric pollution and the resulting deposition of reactive N. Ultimately, the only way to truly protect ecosystems from the impacts of N deposition is to reduce atmospheric N emissions, but management strategies aimed at controlling nonnative plant species, reducing the amount of N in the system (e.g., through biomass removal), and restoring at-risk natives could help mitigate the negative impacts on plant diversity (Fenn et al. 2010).

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