

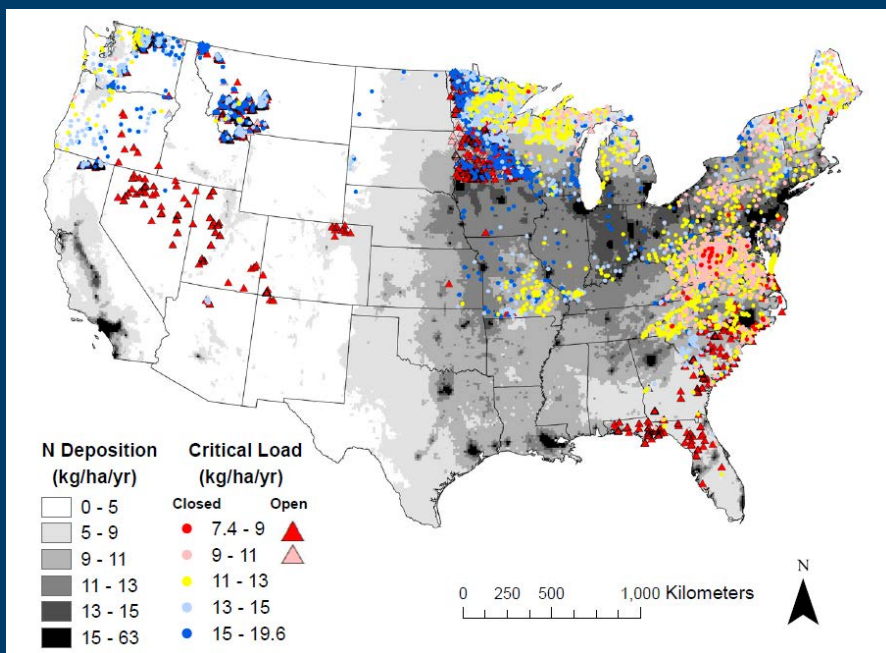
Differential vulnerability of 348 herbaceous species to atmospheric deposition of nitrogen and sulfur across the contiguous U.S.

Christopher M. Clark, Samuel M. Simkin, Edith B. Allen, William D. Bowman, Jayne Belnap, Matthew L. Brooks, Scott L. Collins, Linda H. Geiser, Frank S. Gilliam, Sarah E. Jovan, Linda H. Pardo, Bethany K. Schulz, Carly J. Stevens, Katharine N. Suding, Heather L. Throop, and Donald M. Waller



*The findings and conclusions in this report (presentation) have not been formally disseminated by the U.S. EPA and should not be construed to represent any agency determination or policy..

- Recent study on the sensitivity of herbaceous total richness in grasslands and forests to N deposition from ~15,000 plots nationwide.
- Which species are increasing and which are decreasing?



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Conditional vulnerability of plant diversity to atmospheric nitrogen deposition across the United States

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Atmospheric nitrogen (N) deposition has been shown to decrease plant species richness along regional deposition gradients in Europe and in experimental manipulations. However, the general response of species richness to N deposition across different vegetation types, soil conditions, and climates remains largely unknown even though responses may be contingent on these environmental factors. We assessed the effect of N deposition on herbaceous richness for 15,136 forest, woodland, shrubland, and grassland sites across the continental United States, to address how edaphic and climatic conditions altered vulnerability to this stressor. In our dataset, with N deposition ranging from 1 to 19 kg N ha⁻¹ yr⁻¹, we found a unimodal relationship; richness increased at low deposition levels and decreased above 8.7 and 13.4 kg N ha⁻¹ yr⁻¹ in open and closed-canopy vegetation, respectively. N deposition exceeded critical loads for loss of plant species richness in 24% of 15,136 sites examined nationwide. There were negative relationships between species richness and N deposition in 36% of 44 community gradients. Vulnerability to N deposition was consistently higher in more acidic soils whereas the moderating roles of temperature and precipitation varied across scales. We demonstrate here that negative relationships between N deposition and species richness are common, albeit not universal, and that fine-scale processes can moderate vegetation responses to N deposition. Our results highlight the importance of contingent factors when estimating ecosystem vulnerability to N deposition and suggest that N deposition is affecting species richness in forested and nonforested systems across much of the continental United States.

nitrogen deposition | plant species richness | diversity | soil pH | climate

Global emissions of reactive nitrogen (N) to the atmosphere and subsequent deposition into terrestrial ecosystems have tripled in the last century (1). This N deposition has been identified as a threat to plant diversity (2–4), and plant diversity is linked to ecosystem stability (5), productivity (6), and other ecosystem services (7). Elevated nitrogen inputs have been shown to cause decreases in species richness over time in small plot experiments (8–10) and in regional gradient studies in Europe (11, 12). Although these studies and others have led to some generalizations about the impacts of N deposition on plant diversity, most of these studies have focused on grassland ecosystems and/or, in the United States, have been fine-scale field experiments where N is added experimentally as fertilizer. Thus, translation of these findings to nongrassland systems or to large regions of

the United States may not be appropriate. Unlike grasslands, where elevated N has often led to light limitations and subsequent competitive exclusion (13), plant growth in the herbaceous layers of forest understories is typically primarily light-limited (14) regardless of the extent of N inputs. Moreover, soil chemistry can be heterogeneous, influencing the potential of soil acidification by nitrogen deposition (15). In most arid ecosystems, moisture may be more important than nutrients in controlling plant growth during the growing season (16, 17). Finally, the level of N input at which diversity is first impacted (18) is often unknown for many regions because most studies use a fairly coarse experimental approach to estimate thresholds of response or have been conducted where there have already been high inputs of N for decades (e.g., Northern Europe). To address these critical gaps in our knowledge of continental-scale relationships between N deposition and plant diversity, we used data from herbaceous ground-layer communities within 15,136 forest, woodland, shrubland, and grassland sites spanning N deposition gradients across the continental

Significance

Human activities have elevated nitrogen (N) deposition and there is evidence that deposition impacts species diversity, but spatially extensive and context-specific estimates of N loads at which species losses begin remain elusive. Across a wide range of climates, soil conditions, and vegetation types in the United States, we found that 24% of >15,000 sites were susceptible to N deposition-induced species loss. Grasslands, shrublands, and woodlands were susceptible to species losses at lower loads of N deposition than forests, and susceptibility to species losses increased in acidic soils. These findings are pertinent to the protection of biodiversity and human welfare and should be considered when establishing air quality standards.

Author contributions: S.M.S., E.B.A., W.D.B., C.M.C., J.B., and M.L.B. designed research; S.M.S., E.B.A., W.D.B., C.M.C., J.B., M.L.B., B.S.C., S.L.C., L.H.G., F.S.G., S.E.J., L.H.P., B.K.S., C.J.S., K.N.S., H.-T., and D.M.W. wrote the paper.

The authors declare no conflict of interest.

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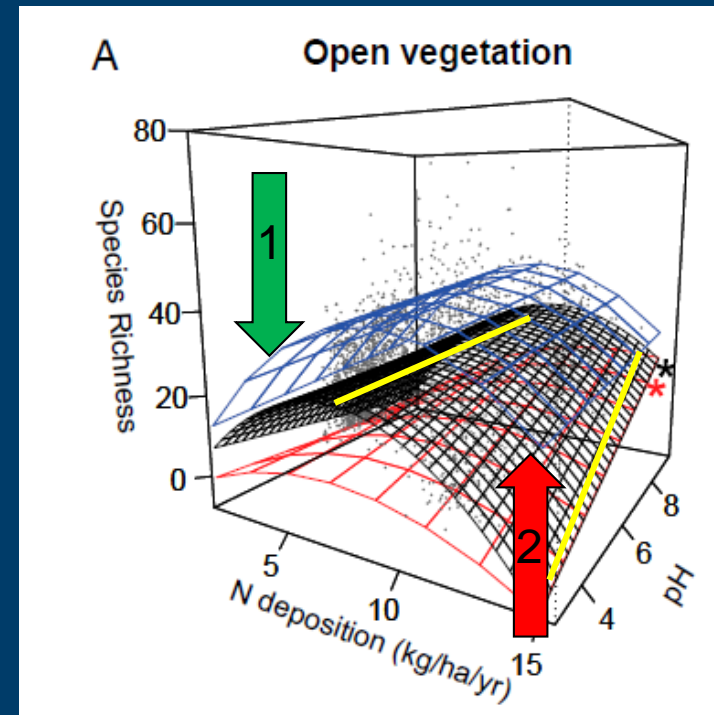
Data deposition: The data reported in this article have been deposited in the Dryad Digital Repository, [doi:10.1038/549241113](https://doi.org/10.1038/549241113).

To whom correspondence should be addressed: samuel.simkin@ucr.edu. This article contains supporting information online at www.pnas.org/lookup/suppl/doi/10.1073/pnas.1515241113/-DC1.

Example from Simkin et al. (2016)

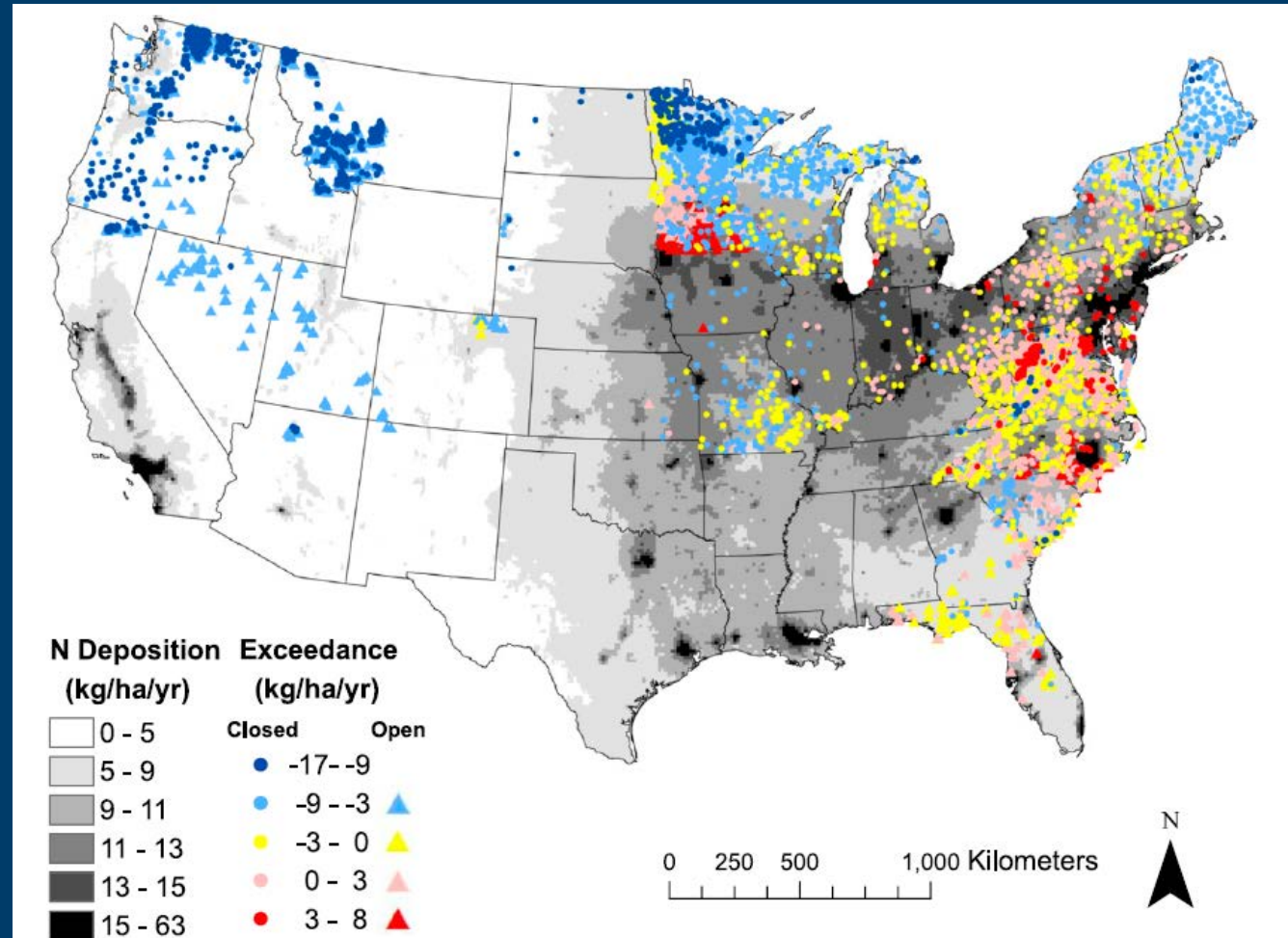
Patterns in total richness suggest:

1. At low N dep there are more species are increasing than decreasing.
2. At high N dep, more species are decreasing than increasing.
3. That relationship is pH-dependant, with stronger decreases at lower pH.



Geographic patterns

- High dep areas, may lose many species, but not always.
- Low dep areas, may lose a few species, or none at all.
- There may be losses of some species even in areas with no net loss
- **Therefore, composition matters!**

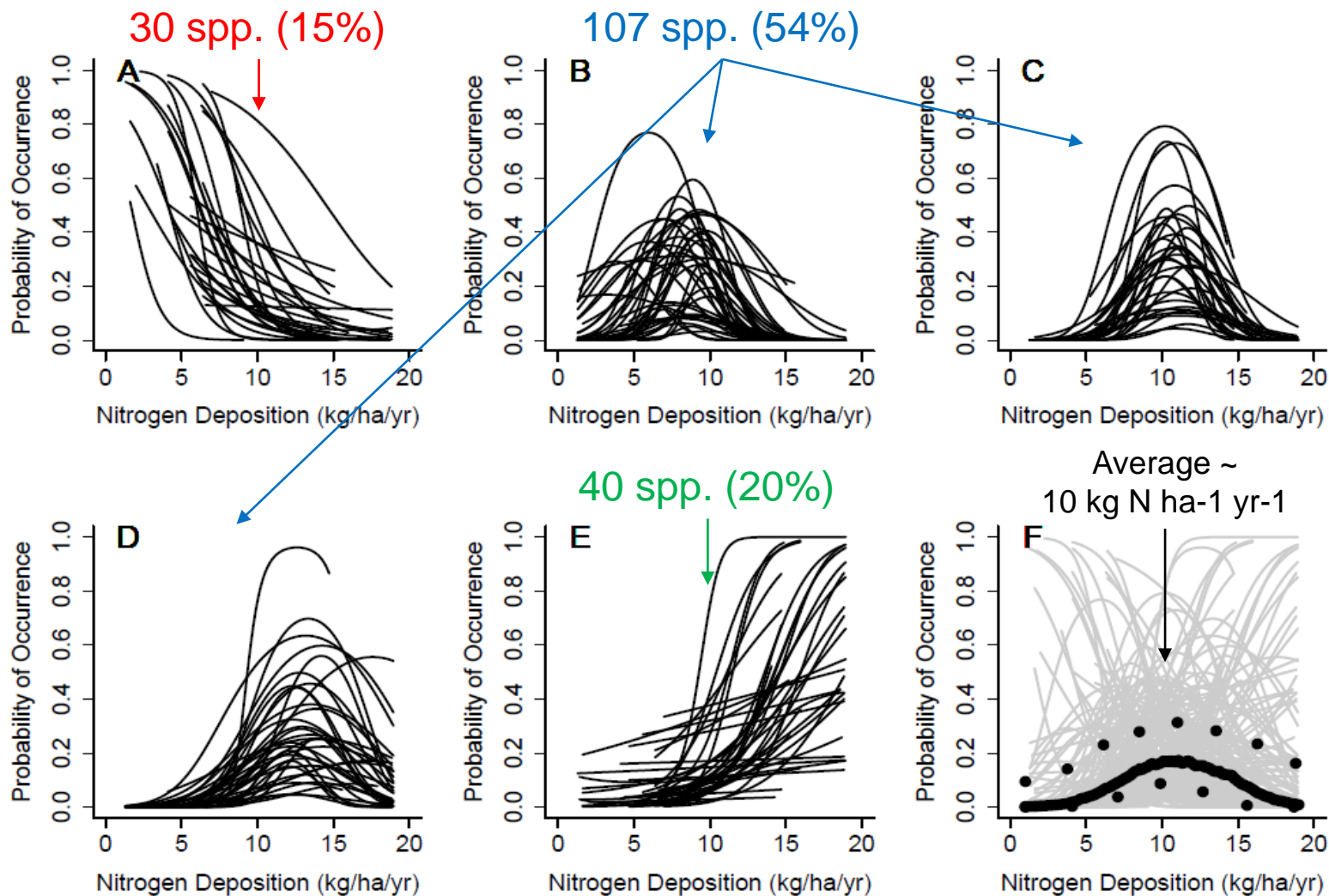


Unpacking the total richness results: Statistical analysis

- Assess separately for ~4000 species the sensitivity to N and S.
- Species screening:
 - most species were too rare to assess (<50 occurrences),
 - Or only appeared locally (thus no deposition gradient).
 - 348 species have enough data and a gradient to asses.
- Statistical analysis:
 - Response: probability of occurrence
 - Run all possible models with up to 12 predictors
 - Compare all models with AICc and AUC.
 - Select the best model that optimizes AICc and AUC
 - Calculate critical loads and assess vulnerability.
 - Focus on those with “robust results” (R2 > 0.1 and AUC >0.7, 243 spp.)

$$Pr = \beta_0 + \beta_0N + \beta_0S + \beta_0T + \beta_0P + \beta_0pH + \beta_0N^2 + \beta_0T^2 + \beta_0P^2 + \beta_0pH^2 + \beta_0NpH + \beta_0NS + \beta_0SpH$$

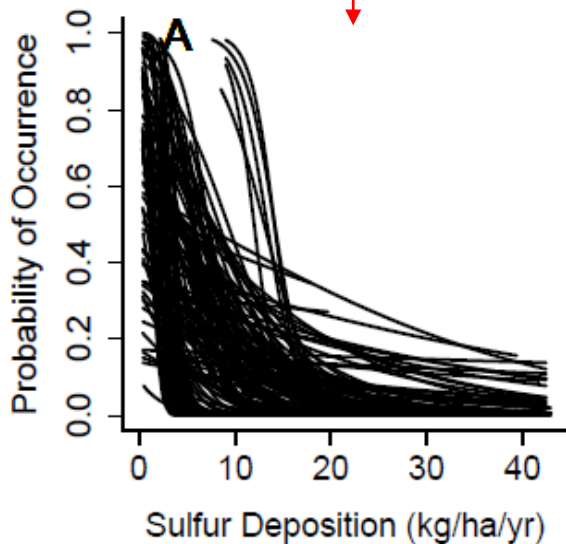
The spaghetti diagrams: N



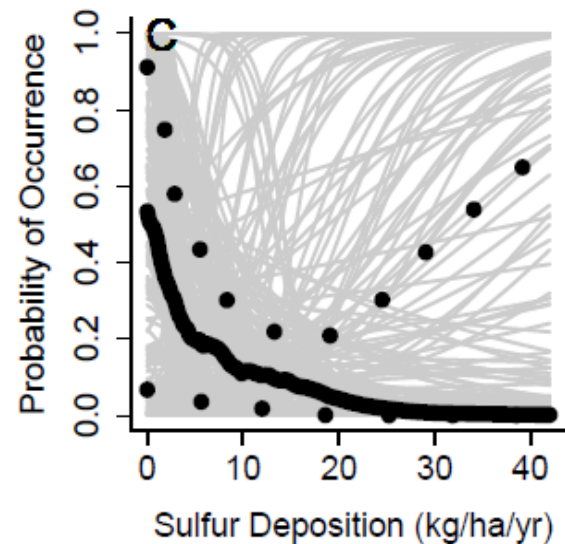
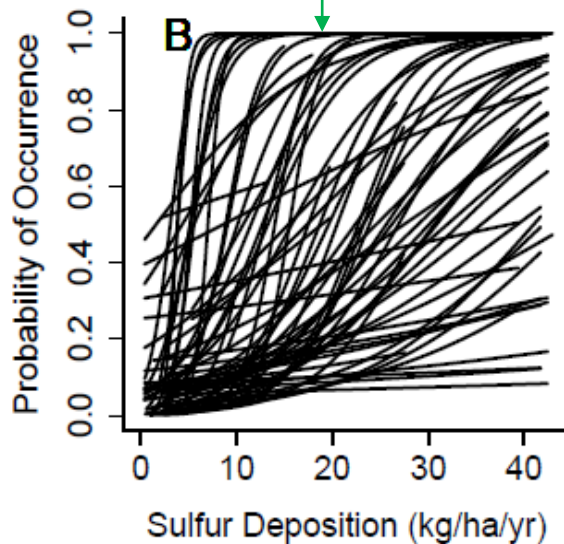
21 spp. (11%) had no relationship and 45 (19%) had nonsensical (i.e. U", not shown).

The spaghetti diagrams: S

137 spp. (57%)



40 spp. (20%)



37 spp. (15%) had no relationship

So...

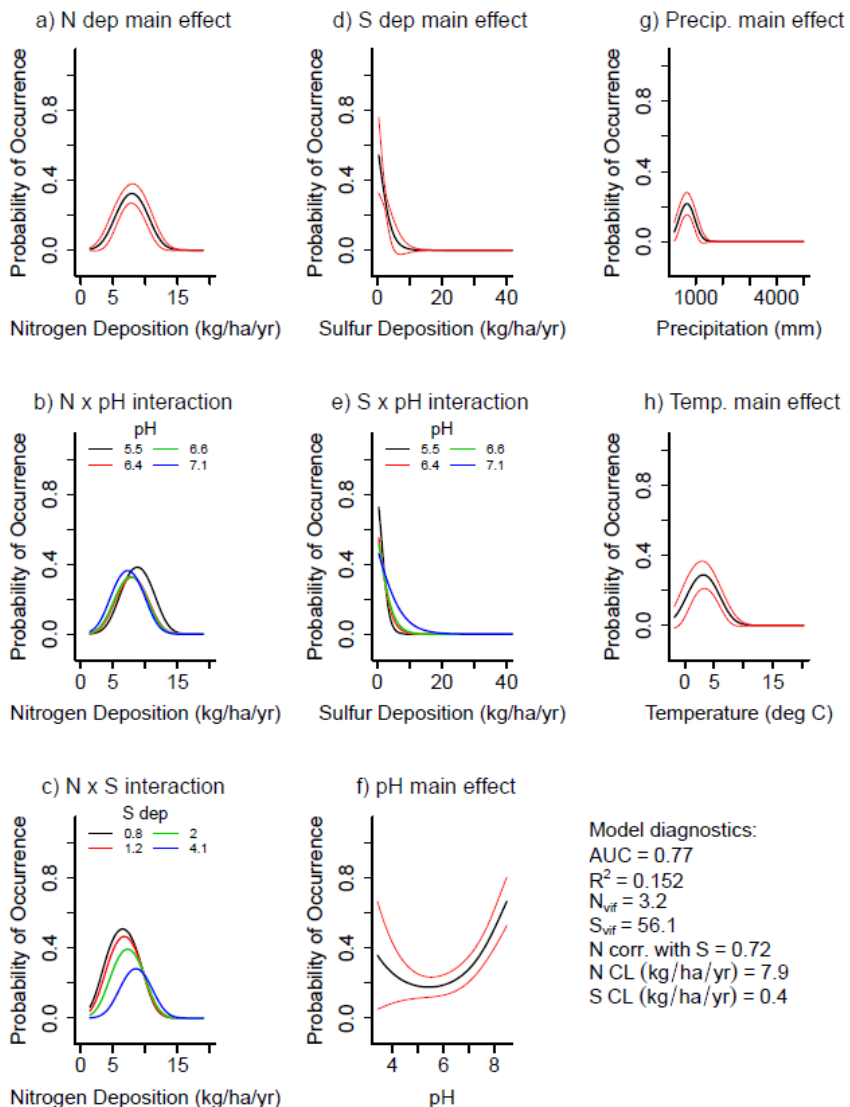
- Lots of variation among species.
- Total richness CLs describe when there are more “losers” than “winners,” but there could be many changes to composition at all deposition levels.

Example species: *Campanula rotundifolia* (harebell, bluebell flower)

- Common native wildflower that does well with drier, colder, conditions on more basic soils.
- Unimodal with N, decreases with S.
- Weak interactions, but sensitivity to N slightly increases if S is higher.
- Better models, N(VIF) good, S(VIF) bad.



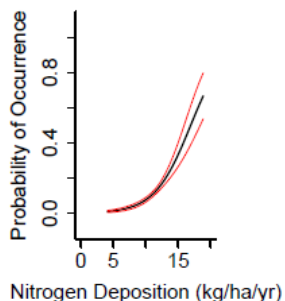
Campanula rotundifolia



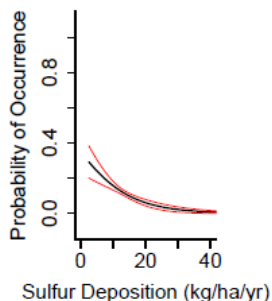
Example species: *Agrostis perennans* (upland bentgrass)

Agrostis perennans

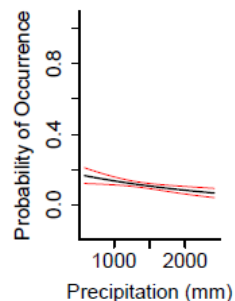
a) N dep main effect



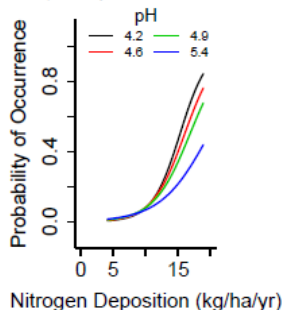
d) S dep main effect



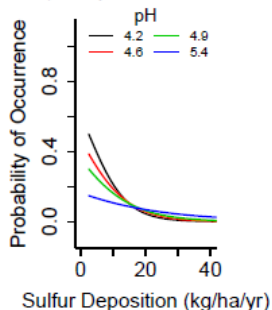
g) Precip. main effect



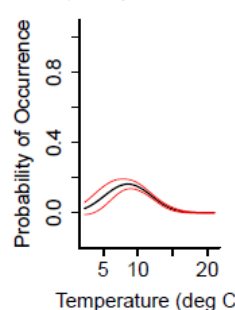
b) N x pH interaction



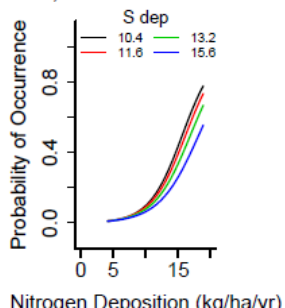
e) S x pH interaction



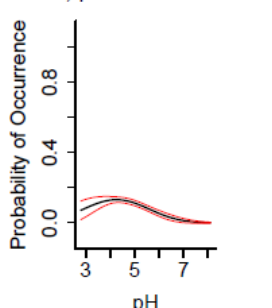
h) Temp. main effect



c) N x S interaction



f) pH main effect



Model diagnostics:

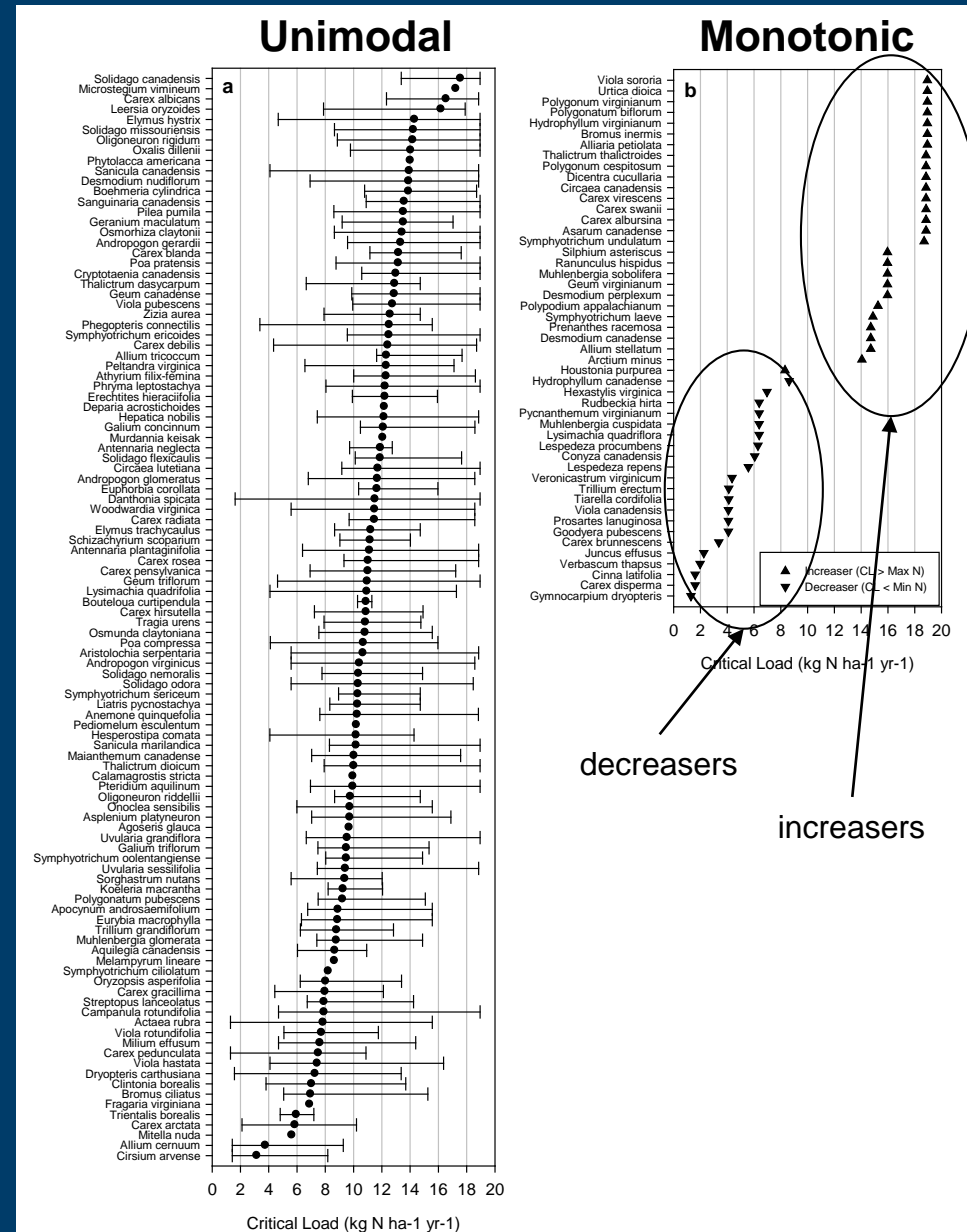
AUC = 0.72
 $R^2 = 0.087$
 $N_{vir} = 2$
 $S_{vir} = 41.6$
 $N \text{ corr. with } S = 0.64$
 $N \text{ CL (kg/ha/yr)} = 18.8$
 $S \text{ CL (kg/ha/yr)} = 2.5$

- Common native grass of the Midwest that does well with moderate fertility on more acidic soils.
- Increases with N, decreases with S.
- Weaker increase with N if S is higher or soil is more alkaline.
- Ok models, N(VIF) good, S(VIF) bad



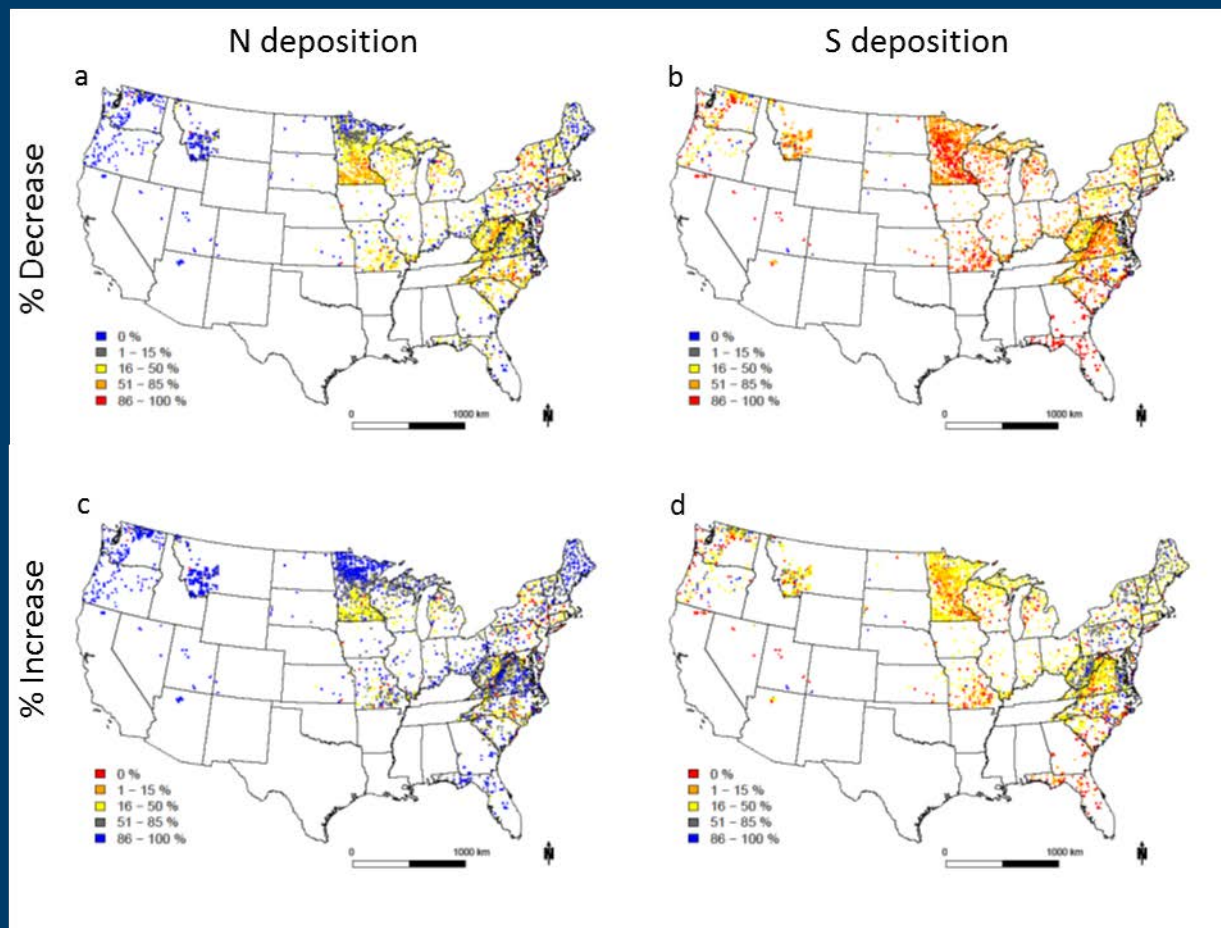
Species level N-CLs

- Large variation within and among species.
- 80% of species at risk to N or S are either moderately or highly valued from a conservation standpoint.
- Lower CLs were correlated with higher floristic value.
- New predictive equations for CLs:
 - Related to leaf Mg and height ($R^2 = 36\%$).
 - Related to leaf N and functional group ($R^2 = 32\%$)



Geographic variability

- More spp. increase than decrease in $\frac{3}{4}$ of plots.
- There are spp. decreasing and increasing almost everywhere



Next Steps

1. What about the other 90% of species?
2. Are there specific species of concern (e.g. T&E or RFSS species)?
3. Integrating this information into decision making processes (e.g. CLAD WG-3, USFS CL Portal) and decision support tools (CL Mapper).

Key points

- 70% of species assessed were negatively affected by N and/or S deposition somewhere in the contiguous U.S.,
- 30 and 139 species, respectively, decreased at all rates of deposition experienced for N and S, and thus are of particular concern.
- Although more species increased than decreased with N deposition, increasers were more likely to be introduced spp., and high value native species tended to be more vulnerable,
- Predictive equations may be useful to assess the other species that we have less information on.



Thanks and questions?

Extra slides