

Estimated losses of plant biodiversity in the United States from historical N deposition (1985–2010)

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Abstract. Although nitrogen (N) deposition is a significant threat to herbaceous plant biodiversity worldwide, it is not a new stressor for many developed regions. Only recently has it become possible to estimate historical impacts nationally for the United States. We used 26 years (1985–2010) of deposition data, with ecosystem-specific functional responses from local field experiments and a national critical loads (CL) database, to generate scenario-based estimates of herbaceous species loss. Here we show that, in scenarios using the low end of the CL range, N deposition exceeded critical loads over 0.38, 6.5, 13.1, 88.6, and 222.1 million ha for the Mediterranean California, North American Desert, Northwestern Forested Mountains, Great Plains, and Eastern Forest ecoregions, respectively, with corresponding species losses ranging from <1% to 30%. When we ran scenarios assuming ecosystems were less sensitive (using a common CL of 10 kg·ha⁻¹·yr⁻¹, and the high end of the CL range) minimal losses were estimated. The large range in projected impacts among scenarios implies uncertainty as to whether current critical loads provide protection to terrestrial plant biodiversity nationally and urge greater research in refining critical loads for U.S. ecosystems.

Key words: biodiversity; critical loads; ecoregion; herbaceous; nitrogen deposition.

INTRODUCTION

The global threat of nitrogen (N) deposition to terrestrial plant biodiversity is increasingly recognized (Sala et al. 2000, Bobbink et al. 2010, Pardo et al. 2011a). Human activities have increased deposition of this key limiting nutrient in many areas by nearly an order of magnitude over historical levels (Galloway et al. 2004). For vascular plants, it is increasingly realized that impacts on biodiversity may be particularly pronounced for herbaceous species, evidenced from large-scale sampling studies across deposition gradients in Europe (Maskell et al. 2010, Stevens et al. 2010), resampling studies comparing past with present community composition (Dupre et al. 2010), and long-term field experiments with low levels of N input in North America, Europe, and Asia (Bowman et al. 2006, Clark and Tilman 2008, Bai et al. 2010). Nonvascular species,

lacking a protective cuticle and experiencing the passive absorption of water over their entire surface, are expected to be even more sensitive (Fenn et al. 2010). Impacts to vascular species are unlikely restricted to grasslands alone, as forest studies indicate that changes in understory and tree species composition may occur as well (Gilliam 2006, Thomas et al. 2010).

Atmospheric deposition of N, however, is not a recent stressor for most of the industrialized world. The activities leading to elevated N deposition such as fossil fuel combustion and fertilizer application for modern agriculture date back to the late 19th century. Networks to monitor N deposition, however, only date back a few decades for the United States and Europe (Galloway et al. 2004). Recently, N deposition has actually been declining over much of northeastern United States, mostly from reductions in oxidized N (Burns et al. 2011, Suddick and Davidson 2012). However, these levels remain high and have been elevated for decades. N deposition from agricultural activities remains high, and total N deposition over much of the rest of the country is actually increasing (Suddick and Davidson 2012).

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TABLE 1. Summary of supporting information for Level I ecoregions and associated field sites examined in this study, including the published range for empirical estimates of critical loads (CL) and saturation points for N-induced species declines.

Level I ecoregion	Associated field site	Empirical CL (kg N·ha ⁻¹ ·yr ⁻¹)†			Saturation point	
		Low	Common	High	N addition rate (kg N·ha ⁻¹ ·yr ⁻¹)	Species decline (%)
Mediterranean California	Jasper Ridge Biological Preserve (JRP)	6	10	33	70	3
North American Deserts	Sevilleta (SEV)	3	10	8.4	100	4
Northwestern Forested Mountains	Niwot Ridge (NWT)	4	10	10	100	1
Great Plains (GP)	Shortgrass Steppe (SGS), Konza Prairie (KNZ), Cedar Creek (CDR)	5	10	18.3	85	30.3
Eastern Forest	Fernow Experimental Forest (FEF)	5	10	17.5	35	25

Notes: All sites except JRP are Long-Term Ecological Research (LTER) sites. Insufficient information was available for five ecoregions, and these were excluded from the analysis (Tropical Wet Forests, Northern Forests, Temperate Sierras, Southern Semi-arid Highlands, and Marine West Coast Forests; gray areas in Fig. 1a). The saturation point for each site was related to the highest fertilization level used in the experiment and the corresponding observed decline in species. The low CL and high CL represent, respectively, the low end of the range for the estimated CL and the high end. The common CL represents a scenario where all systems are assumed to be similarly sensitive.

† Aside from the common CL, all CLs are from Pardo et al. (2011a, b).

Only recently has sufficient information been collected from various, often unrelated, research efforts to enable estimates of possible effects from historical N deposition. Here we combined information from three interrelated sources to generate estimates of potential historical impacts from N deposition: (1) annual total inorganic N deposition over the coterminous United States for the period of record that is available (1985–2010), (2) thresholds or “critical loads” of N deposition for five large ecoregions at which species losses and composition change begins to occur, and (3) functional response curves derived by combining critical loads information with response data from 17 long-term field experiments.

MATERIALS AND METHODS

Three primary analyses were combined to generate hindcasts of impacts on biodiversity from nitrogen deposition. First, we generated maps of total inorganic N deposition in 4-km grid cells over the contiguous United States. We combined total wet inorganic deposition data from the EPA National Atmospheric Deposition Program (NADP), and added to this dry deposition from a previous national effort (Holland et al. 2005) that included aerosol-specific deposition velocities related to land use and other surface characteristics. Because we needed information for a long temporal record, deposition from the Community Multiscale Air Quality model (CMAQ) was not used (only 2002 data were available at the time of our analysis), though we compared our estimates with CMAQ and found reasonable agreement (Spearman correlation, $\rho = 0.850$, $P < 0.0001$; Appendix: Fig. A1). Our estimates were generally biased low largely due to underestimates of dry deposition, especially in urban areas.

Second, we combined these annual N deposition maps with estimates of thresholds or “critical loads” for N-

induced changes in biodiversity from a recent national assessment to determine grid cells in which species declines may have occurred for that year (Table 1, Fig. 1; Pardo et al. 2011a, b). A critical load (CL) is defined as “a quantitative estimate of an 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” (Bobbink et al. 2010). For many ecoregions, there is uncertainty in the critical load and a range is reported (Pardo et al. 2011a); thus, we ran suites of analyses (scenarios) using the lower and upper ends of the CL range (CL_{low}, CL_{high}, respectively). We also included a common critical load (10 kg N·ha⁻¹·yr⁻¹, CL_{com}) for comparison (Table 1).

Third, to determine the impact of a given exceedance on herbaceous biodiversity, we derived functional response curves for each ecoregion. Three pieces of information are needed to define a functional response curve: an x -intercept that defines the point at which changes begin to occur, a saturation point above which no additional impacts occur, and a functional relationship in between (Fig. 1b). CLs define the x -intercept. Experiments that added high levels of N and measured associated levels of biodiversity provide an estimate of the saturation point. For simplicity, we assumed linearity between the CL and the saturation point with zero loss below the CL and no further loss above the saturation point, which fully defined our response functions for these ecoregions (Fig. 1c). We discuss the ramifications of this and other decisions.

Since N deposition is dynamic in time, systems may not lose species immediately, and may have the ability to recover once N deposition declines depending on a range of factors (Fig. 1d; Bakker and Berendse 1999, Clark and Tilman 2008). We explored time lags of 0-, 5-, 10-, and 15-years, and found few differences so long as time lags were less than 15 years (Appendix: Figs. A3–A5). In effect, time lags mean that the responses are calculated

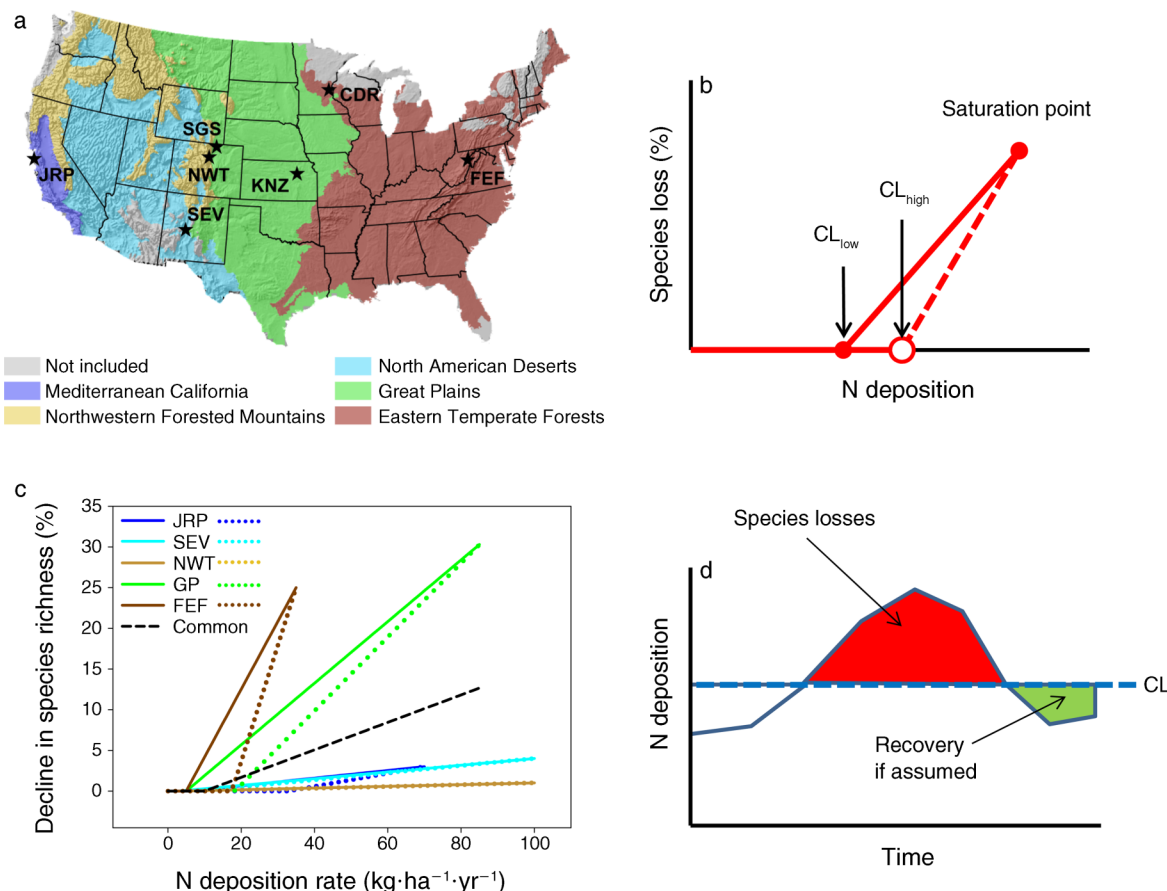


FIG. 1. Map of ecoregions and presentation of functional response curves. (a) Level I ecoregions for the contiguous United States along with locations (stars) for the Long-Term Ecological Research (LTER) sites used in this study (see Table 1 for abbreviations). (b) Illustrative functional response curve constructed using either the low end of the critical load (CL) range (CL_{low}, solid line and solid circles) or the high end (CL_{high}, dashed line and open circle) along with the saturation point from fertilization studies. (c) The full set of functional response curves from Table 1 assuming CL_{low} (solid colored lines), CL_{high} (dotted colored lines), and CL_{com} (a common CL of 10 kg N·ha⁻¹·yr⁻¹ was also examined as a scenario for analysis; dashed black line). Line colors correspond to ecoregion colors in panel (a). (d) Illustration of temporal considerations. Assuming a recovery profile of 0%, the net exceedance is indicated by the red shaded area, while the net exceedance assuming a 100% recovery profile is the difference between the red and green shaded areas (no effect for the early N deposition below the CL).

using prior N deposition information (based on the size of the lag). We present 0-year time lags in the main text for simplicity. We assumed two potential recovery profiles to bracket our projections: 0% and 100% recovery for each year below the CL. Thus, in total, there are six scenarios reported here, two recovery profiles (0% and 100%) crossed with three sets of response functions (CL_{low}, CL_{com}, CL_{high}).

RESULTS AND DISCUSSION

We found a wide range in both the net exceedances of N (Fig. 2) and the estimated impacts on herbaceous biodiversity (Fig. 3) from historical N deposition over the contiguous United States. Using CL_{low} (Figs. 2a, b and 3a, b), many areas in the northeastern United States were predicted to have received cumulative amounts of N in excess of 200 kg N/ha, and to have already reached the saturation point (25%; Table 1). Recovery profile

had little effect for scenarios using CL_{low} because N deposition, although declining, was still above the CL for much of the region (Fig. 4; Appendix: Fig. A2). Much of the southeastern United States was estimated to be greatly impacted by historic N deposition as well, although more southerly regions (e.g., Louisiana, Texas, Alabama, Mississippi, Georgia, and Florida) were estimated to have experienced some recovery under the 100% recovery assumption. In the west, mountainous areas experienced high cumulative exceedances from orographic effects (Fig. 2a, b), though these net exceedances did not translate to large losses of species richness (Fig. 3a, b). Recovery potential had a large effect in the West, with the total area experiencing at least some species loss nearly tripling when comparing 0% recovery to 100% recovery profiles, a difference of almost 40 million ha. High exceedances in the West did not translate to large losses of species richness because the

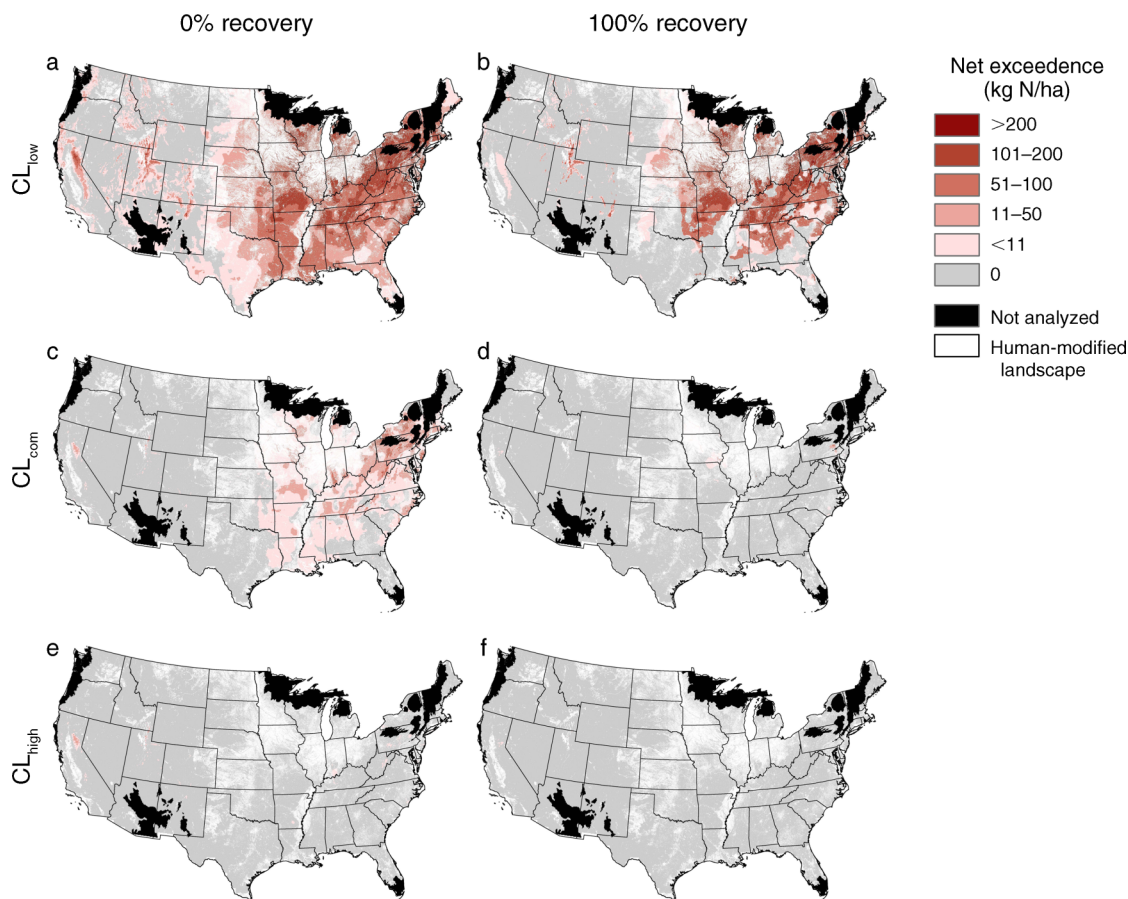


FIG. 2. Spatial pattern of net exceedances of N deposition. Cumulative exceedances of N above the critical load (in kg N/ha) for the six scenarios examined: (a, b) CL_{low}, (c, d) CL_{com} (10 kg N·ha⁻¹·yr⁻¹), and (e, f) CL_{high}. Excluded are the five ecoregions for which a functional response curve could not be derived (shaded black), and grid cells dominated by urban and agricultural activity (shaded white). No recovery (0% Recovery) represents the scenario where species cannot recolonize after they are lost. Full recovery (100% recovery) represents the scenario where for each year and level of N deposition below the critical load, diversity increases at the same rate it was lost when N deposition was above the critical load. These are illustrated in Fig. 1d.

functional response curve peaked at low levels of species losses (1–4%; Table 1), not because N exceedance was low. A low level of species losses, however, does not necessarily imply a low impact from N deposition on biodiversity, because there can be dramatic changes in composition with little change in richness. Indeed, Bowman et al. (2006) found large changes in composition and no change in species richness in different years of the same experiment used here, with much of the change in diversity from increases in the abundance of a single sedge (*Carex rupestris*). Thus, changes in species richness may be a relatively conservative measure of impacts from N deposition, with total effects including compositional changes as substantially larger (Payne et al. 2013). Exceedances and estimated impacts were intermediate in the Midwest, and largely depended on the potential for recovery (see Plate 1). There was a notable transition band across much of the Midwest, with high losses projected in eastern regions and lower losses in western regions. In total, averaging over the 26-

year time period, we found 2.4%, 4.7%, 15.8%, 39.8%, and 90.5% areal exceedance of CL_{low} in the Mediterranean California, Desert, Northwestern Forests, Great Plains, and Eastern Forest ecoregions, respectively, corresponding to 0.38, 6.5, 13.1, 88.6, and 222.1 million ha, respectively (Fig. 4).

A sharply contrasting pattern emerged when examining either CL_{com} (Figs. 2c, d and 3c, d) or CL_{high} (Figs. 2e, f and 3e, f). Using 10 kg N·ha⁻¹·yr⁻¹ as the critical load, we found that only the eastern United States was generally affected. There were a few hotspots in Pennsylvania, West Virginia, and New York where losses approached 10%, though estimated impacts in much of the rest of the ecoregion were lower (<5%), and only under no recovery. The assumed recovery potential had a large effect on the estimated impact, resulting in more than a five-fold increase in impacted area when comparing 100% with 0% recovery (39.6 million and 209.4 million ha, respectively). Using CL_{high}, almost no areas were projected to have been impacted from

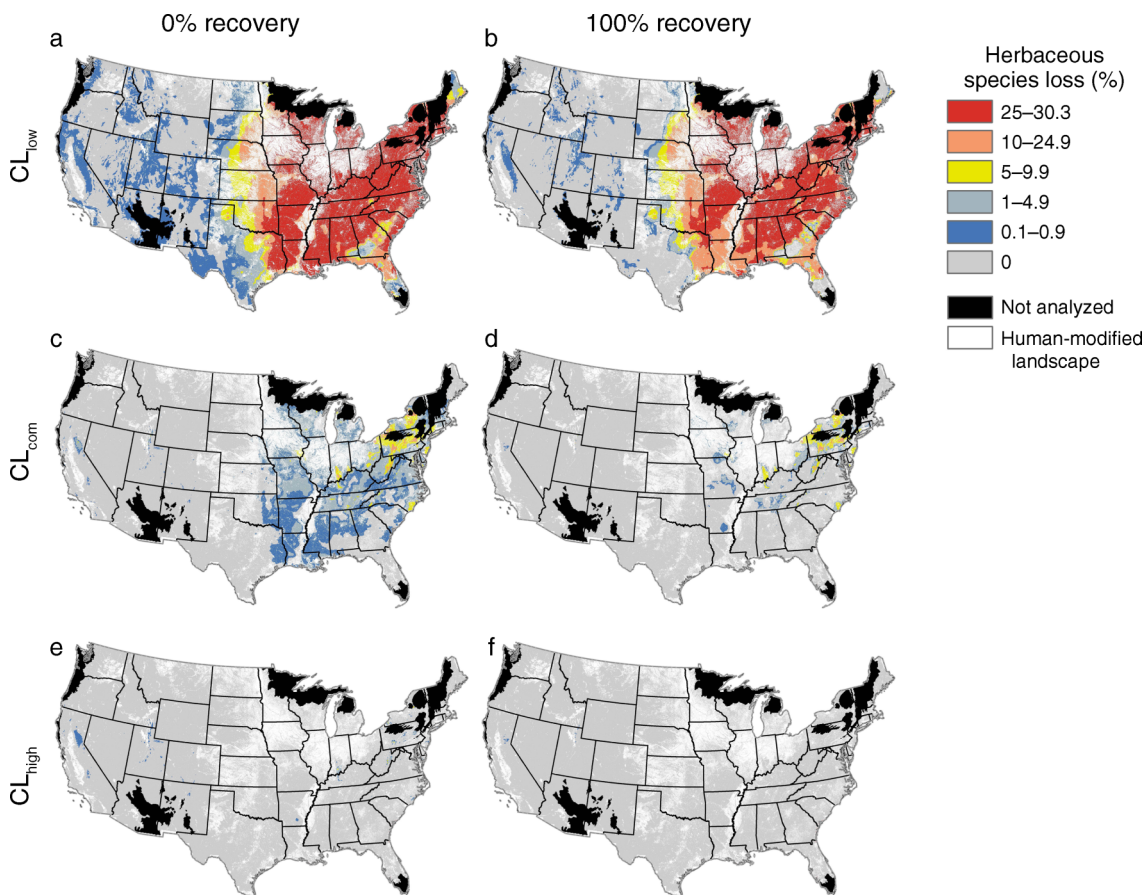


FIG. 3. Spatial pattern of species declines from net exceedances of N. The figure shows projected losses of terrestrial plant biodiversity for the six scenarios examined: (a, b) CL_{low} , (c, d) CL_{com} , and (e, f) CL_{high} . Exclusions are as in Fig. 2.

historical N deposition except for a few hotspots (Figs. 2e, f and 3e, f). However, it should be cautioned that the high CL estimates are included mainly for completeness: They only ensure protection of the least sensitive receptor. Furthermore, comparing initial estimates of empirical CLs from Europe (Bobbink et al. 2003) with revised CLs (Bobbink et al. 2010), suggests that CLs are usually revised downward, not upward, as more information becomes available.

Temporal plots revealed that over the 26-year period N deposition was generally steady through time (Appendix: Fig. A2). An exception was in the East, which showed a decline since 2003 that, if continued, suggested nearly half the ecoregion would be below CL_{low} within a few years. However, it is unknown how readily or quickly biodiversity would recover following reduction of long-term inputs of N, as several soil and demographic factors play a role (Bakker and Berendse 1999, Clark and Tilman 2010). Furthermore, losses of herbaceous species likely occur after other more sensitive ecological impacts (e.g., changes in composition, losses of nonvascular species [Pardo et al. 2011a]). In addition, actual deposition rates may be significantly higher than estimated here if other factors were also

considered, such as organic N deposition, which can constitute 25–35% of the total (Cornell 2011), and cloud and fog deposition, which can dramatically increase deposition in montane areas (Weathers et al. 2006).

Recognizing the high degree of uncertainty and paucity of data at multiple steps of this analysis, we acknowledge these results should serve only as a benchmark for future impact assessments. More research is needed at all stages of the analysis chain (i.e., N deposition estimates, critical loads and exceedance estimates, impacts assessment). However, this is especially true for resolving critical loads and the ecosystem-specific functional responses. Although continued development of atmospheric models to accurately reflect emission, transport, and deposition of N is still critical, we feel that far less is known on the ecological impacts end of the analysis. Even so, our estimates of N deposition are likely biased low (Appendix: Fig. A1) for at least two aforementioned reasons: (1) Several N-species are not measured in the NADP/National Trends Network (NTN) networks (e.g., organic N), and (2) some mechanisms such as cloud deposition are not included. Our comparison with 2002 CMAQ deposition rates indicate our method may be biased low in general

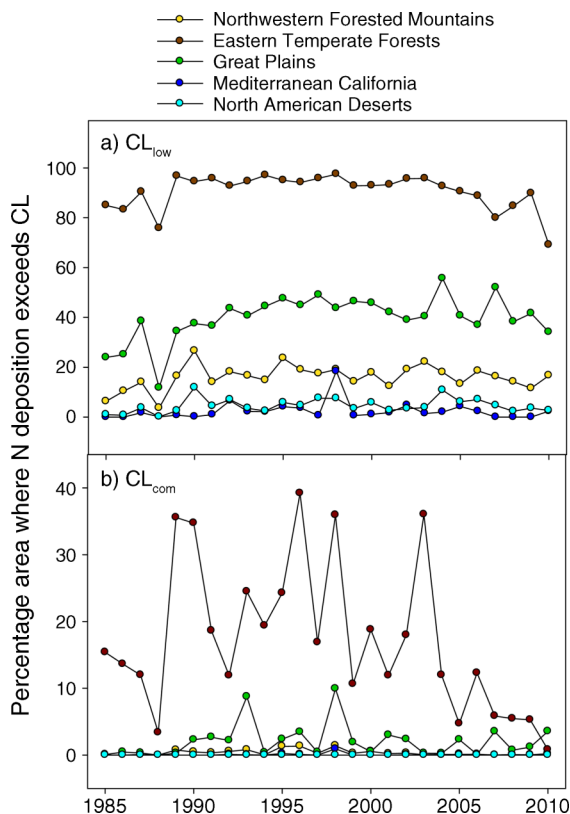


FIG. 4. Areal exceedances through time: percentage area where N deposition exceeded the critical load for the five ecoregions studied, assuming (a) CL_{low} and (b) CL_{com} . There were minimal exceedances for the high CL (not shown).

by ~25%. Use of high N fertilization experiments for the saturation point and the assumption of linearity likely also biases our estimates low rather than high, because the dose–response relationship commonly reported is steeper at lower N input rates (Clark and Tilman 2008, Bai et al. 2010, Bobbink et al. 2010). The higher the fertilization rate (for estimating the saturation point) the greater the underestimation. Thus, our estimates of biodiversity impacts are also likely low because (1) changes in species richness by definition occur after changes in community composition, which may be large or small (Bowman et al. 2006, Bobbink et al. 2010, Payne et al. 2013); (2) our assumption of a linear functional response underestimates impacts at low N deposition (Clark and Tilman 2008); and most importantly (3) N deposition has been occurring long before 1985. We are initiating efforts to address the first issue using the same LTER data set, to examine changes in composition in addition to alpha diversity. For the second issue, very few experiments have added N at multiple rates near and above the CL, thus developing the functionality of the nonlinear response remains a challenge (but see Clark and Tilman 2008, Bai et al. 2010). Coordinated research efforts to add multiple low levels of N could help fill this gap. Additionally, large-

scale gradient analyses like those conducted in Europe (e.g., Stevens et al. 2010) would help in several ways, including refinement of estimated CLs and determination of the linearity of the functional response curves. For the third, hindcasting techniques could be employed to extend our analysis (Baron 2006). On the other hand, our estimates may be biased high because (1) we assumed that any N above the critical load affects species richness up to the saturation point, (2) changes in small-scale species richness used for the saturation point may not translate to changes in large-scale species richness due to species turnover, and (3) low N input rates below the CL may actually increase biodiversity. For the last issue, this increase is predicted from theory as nutrient limitation is relieved for more species (but competitive exclusion has not yet occurred) and has been observed in one site in Colorado (Theodose and Bowman 1997, Sverdrup et al. 2012). However, given that, (1) aside from a few alpine and tundra systems, this increase has not been observed in other systems; (2) other sites in the United States and internationally have reported reductions in diversity at rates lower than those from Colorado (Clark and Tilman 2008, Bai et al. 2010); and (3) large-scale gradient studies have not detected a leading edge of increasing diversity at low N input rates (e.g., Stevens et al. 2010), we concluded that the conservative approach would be to not include this subtlety. Nonetheless, further study is needed to resolve all of the above issues.

Although we assumed no time lag for simplicity, our analyses allow for consideration of any length time lag. In effect, incorporating a time lag means that the species richness impacts are calculated referencing earlier years of net exceedance for longer time lags. As an example, for a five-year time lag, species richness in 2010 references net exceedance in 2005. Experimental evidence suggests a 10-year time lag for N addition at 10 kg N·ha⁻¹·yr⁻¹ to a Minnesota prairie (Clark and Tilman 2008), similar to assumptions in dynamic modeling efforts (Sverdrup et al. 2012), though few other studies have addressed this issue. In this study, results were not qualitatively affected provided the time lag was approximately 15 years or less, and were generally unaffected with time lags of 10 years or less (Appendix: Figs. A3–A5).

This study highlights the importance of resolving with greater precision the three components of the functional response curves (CL, saturation point, curvature), as well as the temporal elements (potential for recovery, time lags). At present, only coarse estimates of the CL are available at the Level 1 ecoregion scale for the United States, some of which are relatively uncertain (Pardo et al. 2011a). High-resolution modeling studies for critical loads over regional areas usually focus on soil acidification rather than eutrophication (Ouinmet et al. 2006), though there have been some small-scale studies in mountainous regions (Sverdrup et al. 2012). Notwithstanding, Pardo et al.'s (2011a, b) estimates repre-



PLATE 1. (Top) High-biodiversity plot from a Minnesota (USA) sand prairie that receives no additional nitrogen amendments, and (bottom) a low-biodiversity plot from the same experiment after receiving high levels of additional nitrogen for several years. Photo credits: G. David Tilman, University of Minnesota.

sent a major step forward for the field, as these are the first estimates nationally for several environmental end points of concern. Uncertainties also remain for the saturation point, primarily: Are species losses caused by high-N fertilization levels a suitable surrogate for estimating impacts at high-N deposition levels? There are many potential discrepancies, including differences in the timing of N input (once at high levels vs. over time at low levels), the form of N input (solid $\text{NO}_3\text{-NH}_4$ pellets vs. wet or dry deposition), as well as others. However, we feel the convergence of research from several different approaches, including fertilization studies (Bowman et al. 2006, Clark and Tilman 2008), observational studies varying across space (Maskell et al. 2010, Stevens et al. 2010) or time (Dupre et al. 2010), and modeling studies (Sverdrup et al. 2012), which each project losses of species with added N, suggest that the same processes are being approximated. Finally, it is likely that the recovery potential varies substantially for different systems depending on the life history of the species of interest, the presence of refuge populations, and a host of other factors (Clark and Tilman 2010). However, several long-term studies to date suggest that recovery over small scales can be slow and require

intervention (Foster et al. 2007, Clark and Tilman 2010, Isbell et al. 2013). Considering anthropogenic N deposition occurs over large spatial scales, making the presence of refugia unlikely, reduction of current N loads is preferred before potentially intensive management options are considered.

N deposition has a long history over most industrialized nations, and it is relatively certain that there have already been, and will likely continue to be, impacts from this global stressor over the foreseeable future. Many national and international policies are in place for addressing the ecological impacts from excess N (e.g., Clean Air Act, Convention on Long-range Transboundary Air Pollution), though they remain under-utilized. Indeed, a recent Science Advisory Board report to the EPA on N (EPA 2010), recommended that greater effort is needed to integrate existing programs within and across agencies, and to develop new programs, to successfully manage the impacts from reactive N on ecosystems nationally.

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SUPPLEMENTAL MATERIAL

Appendix

Detailed description of methodology and supplemental results on time lags ([Ecological Archives E094-129-A1](#)).