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Diversity-dependent soil acidification under nitrogen enrichment constrains biomass productivity

Kaitlin Kimmel[1] | **George N. Furey**[2] | **Sarah E. Hobbie**[2] | **Forest Isbell**[2] | **David Tilman**[2,3] | **Peter B. Reich**[4,5]

[1]Department of Earth and Planetary Sciences, Johns Hopkins University, Baltimore, MD, USA
[2]Department of Ecology, Evolution, and Behavior, University of Minnesota, Minneapolis, MN, USA
[3]Bren School of Environmental Management, UC Santa Barbara, Santa Barbara, CA, USA
[4]Department of Forest Resources, University of Minnesota, Minneapolis, MN, USA
[5]Hawkesbury Institute for the Environment, Western Sydney University, Penrith South, NSW, Australia

Correspondence
Kaitlin Kimmel, Department of Earth and Planetary Sciences, Johns Hopkins University, Baltimore, MD, USA.
Email: kkimmel4@jhu.edu

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Abstract

In most plant communities, the net effect of nitrogen enrichment is an increase in plant productivity. However, nitrogen enrichment also has been shown to decrease species richness and to acidify soils, each of which may diminish the long-term impact of nutrient enrichment on productivity. Here we use a long-term (20 year) grassland plant diversity by nitrogen enrichment experiment in Minnesota, United States (a subexperiment within the BioCON experiment) to quantify the net impacts of nitrogen enrichment on productivity, including its potential indirect effects on productivity via changes in species richness and soil pH over an experimental diversity gradient. Overall, we found that nitrogen enrichment led to an immediate positive increment in productivity, but that this effect became nonsignificant over later years of the experiment, with the difference in productivity between fertilized and unfertilized plots decreasing in proportion to nitrogen addition-dependent declines in soil pH and losses of plant diversity. The net effect of nitrogen enrichment on productivity could have been 14.5% more on average over 20 years in monocultures if not for nitrogen-induced decreases in pH and about 28.5% more on average over 20 years in 16 species communities if not for nitrogen-induced species richness losses. Together, these results suggest that the positive effects of nutrient enrichment on biomass production can diminish in their magnitude over time, especially because of soil acidification in low diversity communities and especially because of plant diversity loss in initially high diversity communities.

KEYWORDS
indirect effects, long-term experiment, nitrogen enrichment, productivity, soil pH, species diversity

1 | INTRODUCTION

The net effects of nitrogen deposition on primary productivity may diminish or accelerate over time if the nitrogen addition also has indirect effects on ecosystem properties that influence productivity. Potential indirect effects of nitrogen addition include declines in biodiversity (Isbell et al., 2013; Komatsu et al., 2019) or changes in abiotic factors like soil pH (Johnston, Goulding, & Poulton, 1986; Lawes & Gilbert, 1880), that then impact productivity. Although the net effects of nitrogen deposition have been reasonably well studied (e.g., Aber et al., 1995; Bobbink et al., 2010; Maskell, Smart, Bullock, Thompson, & Stevens, 2010; Payne et al., 2017; Reich, Hobbie, & Lee, 2014; Stevens et al., 2015), only long-term experiments can document effects of nitrogen addition on other ecosystem properties, like soil pH or species composition, which might be slow to change but that nevertheless might have additional effects on productivity (Smith, Knapp, & Collins, 2009). Such "indirect" effects of nitrogen enrichment on productivity, which are the focus of this paper, may either enhance or constrain the productivity responses of the community.

Over the past 150 years, nitrogen deposition as the result of fossil fuel combustion, fertilizer use, legume crop cultivation, and animal husbandry, has rapidly increased globally and is expected to continue increasing in many places over the next 30 years (Ackerman, Millet, & Chen, 2019; Galloway et al., 2004, 2008; Jia et al., 2016). The amounts, types, and trends of deposition vary by region (Ackerman et al., 2019; Jia et al., 2016), but both dry and total deposition are increasing in the midwestern United States (the location of this study). This large influx of nitrogen into ecosystems can alter ecosystem productivity via both direct fertilizing effects of increased nitrogen availability and several indirect pathways like species losses and soil acidification that are considered here.

Nitrogen deposition has the potential to alter plant community composition through several mechanisms. Even though nitrogen deposition can increase total productivity of the ecosystem (Aber et al., 1995; Borer, Grace, Harpole, MacDougall, & Seabloom, 2017; Reich, Knops, et al., 2001; Xia & Wan, 2008) by increasing the availability of an often limiting resource, it also has the potential to reduce species richness (e.g., Bobbink et al., 2010; Borer et al., 2014; Reich, 2009; Stevens, Dise, Mountford, & Gowing, 2004; Tilman, 1982; Yue et al., 2020). For example, when nitrogen is added to experimental plots, light can become limiting and decreases the richness of the community (Borer et al., 2014; Hautier, Niklaus, & Hector, 2009). Alternatively, plants may have asymmetric access to the higher nitrogen supply or communities may experience reduced soil water availability associated with higher plant growth and evapotranspiration can also cause reduced richness with added nitrogen (Reich, 2009). Reduced species richness may, in turn, constrain the positive effect of nitrogen on productivity given that increasing species richness within a site often has a positive relationship with productivity (O'Connor et al., 2017).

The impact of biodiversity on ecosystem productivity has been extensively studied through experimental manipulations, observational studies, and mathematical theory. Indeed, theoretical models predict that productivity should be higher than the average of the productivities of the two relevant monocultures if the species compete and coexist (Loreau, 2004; Vandermeer, 1981) and that increasing species richness should result in more complete use of available resources leading to higher productivity (Tilman, Lehman, & Thomson, 1997). This positive effect of species richness on productivity has been extensively quantified in experimental settings (Cardinale et al., 2012; O'Connor et al., 2017; Reich et al., 2004; Tilman et al., 2001). Furthermore, this positive impact of species richness on biomass production has been shown to increase through time in experiments (Cardinale et al., 2007; Reich et al., 2012; Tilman, Reich, & Knops, 2006). Thus, diversity loss caused by nitrogen addition could constrain the positive effect of nitrogen enrichment on productivity (Isbell et al., 2013).

Nitrogen addition can decrease soil pH (Johnston et al., 1986; Lawes & Gilbert, 1880; Stevens, Dise, & Gowing, 2009; You et al., 2017) through several mechanisms depending on the source of nitrogen (Tian & Niu, 2015). NO_x pollution leads to the production of nitric acid which is a direct source of acidity to soils. NH_x deposition and ammonium-based fertilizer application lead to higher rates of nitrification (Aber et al., 2003; Booth, Stark, & Rastetter, 2005), and thus, soil acidification. Furthermore, the acidifying potential via plant uptake of nitrogen depends on the relative uptake of ammonium versus nitrate, which can vary among species and ecosystem type (McKane et al., 2002). Excess nitrogen in a system can also lead to nitrate leaching (Aber, Nadelhoffer, Steudler, & Melillo, 1989; Dijkstra, West, Hobbie, Reich, & Trost, 2007; Lu et al., 2011; Matson, Lohse, & Hall, 2002). This process may be particularly important in low diversity systems where nutrient use is less complete (Dijkstra et al., 2007; Hooper & Vitousek, 1998; Niklaus, Wardle, & Tate, 2006; Tilman et al., 1997).

Soil acidification can impact productivity mainly by limiting nutrient availability (e.g., P, K, Ca, Mg; Harpole et al., 2011) under acidic conditions. Nitrogen addition causes acidification along with nitrate leaching that tends to result in the loss of base cations (Ca^{2+}, Mg^{2+}, and K^+; Falkengren-Grerup, Linnermark, & Tyler, 1987, Horswill, O'Sullivan, Phoenix, Lee, & Leake, 2008, Lucas et al., 2011, Tian & Niu, 2015, Wang et al., 2017). Indeed, foliar concentrations of Mg and Ca have been shown to decrease under nitrogen enrichment (Bowman, Cleveland, Halada, Hreško, & Baron, 2008), but the response may be species-specific (Horswill et al., 2008), and impacts on productivity would depend on whether cation availability was or became limiting or co-limiting with other nutrients such as nitrogen or phosphorus. Declines in pH can lead to aluminum toxicity in plants (Goulding & Blake, 1998; Horswill et al., 2008; Stevens et al., 2009) and reduce phosphorus availability. Thus, acidified soils can act as a constraint on productivity under nitrogen enrichment.

In a previous study, nitrogen addition was found to have diminishing returns on productivity through time, partly because it caused plant species loss (Isbell et al., 2013); however, that study did not quantify how soil acidification may also contribute to these diminishing returns, or how the relative importance of species loss or soil acidification may depend on the initial levels of plant diversity. Other studies have found links between nitrogen enrichment, pH declines, and subsequent productivity losses (Clark et al., 2007; Lawes & Gilbert, 1880; Stevens et al., 2004), perhaps because declines in both richness and pH constrained the positive effect of N enrichment on productivity.

Here our objective was to discern whether and how changes in species richness and soil pH altered the positive effect of nitrogen fertilization on productivity. We hypothesized that nitrogen enrichment would stimulate plant productivity but lead to species richness losses and soil acidification. We hypothesized that decreased pH and richness losses would reduce the effect of nitrogen enrichment on productivity. However, the magnitude of these effects over the diversity gradient is unknown. It is likely that the magnitude of the indirect effect of soil acidification and species losses is different over the experimental diversity gradient as monocultures cannot lose diversity whereas initially high diversity communities can (e.g., Vogel et al., 2019). We took advantage of a unique experiment that crossed nitrogen enrichment with plant species diversity treatments. In this experiment, ammonium nitrate (without addition of base cations) was added annually for 20 years to grassland plots planted with 1, 4, 9, or 16 herbaceous perennial species. We then modeled how nitrogen addition, species richness, and soil pH impact productivity and used changes in species richness and soil pH to determine how much these indirect effects constrained biomass production under nitrogen addition.

2 | METHODS

2.1 | Experimental design

The BioCON experiment (Cedar Creek Ecosystem Science Reserve, East Bethel, MN, 45°40′N, 93°18′W) began in 1997 and manipulated **Bio**diversity, **CO**$_2$, and **N**itrogen (Reich et al., 2004). Treatments are applied in a full-factorial split-plot treatment design. In three rings, CO_2 (+180 ppm) was added using free-air enrichment where another three rings did not receive additional CO_2. Within each of these rings, half of the plots received nitrogen (+4 g N m^{-2} $year^{-1}$ as ammonium nitrate), and a species richness gradient was created (one, four, nine, or 16 species) where plots were either randomly (one, nine, 16, and some four-species plots) or non-randomly (additional four-species plots to expand functional group richness) assigned species. The 16 plant species used in this experiment were perennial grassland species from four functional groups which include: C_3 grasses (*Bromus inermis*, *Elymus repens*, *Koeleria cristata*, and *Poa pratensis*), C_4 grasses (*Andropogon gerardii*, *Bouteloua gracilis*, *Schizachyrium scoparium*, and *Sorghastrum nutans*), legumes (*Amorpha canescens*, *Lespedeza capitata*, *Lupinus perennis*, and *Petalostemum villosum*), and non-legume forbs (*Achillea millefolium*, *Anemone cylindrica*, *Asclepias tuberosa*, and *Solidago rigida*). These functional groups have been previously found to explain both differences in productivity among plots planted with different species richness (Reich et al., 2004; Tilman et al., 2001) and how productivity responds to resource addition (Reich, Hobbie, Lee, & Pastore, 2018; Reich, Knops, et al., 2001). These plots were burned every other spring from 2000 to 2012 and every fall starting in 2013. We used data from 163 total plots from control conditions ($n = 82$) and nitrogen addition ($n = 81$) treatments, but none of the plots received elevated CO_2. We used data from the second through the 20th year of the experiment because this was the time period over which productivity, species richness, and pH were all measured. All datasets can be found at https://www.cedarcreek.umn.edu/research/data.

2.2 | Aboveground productivity, species richness, and pH

In August of each year, a 1 m × 0.1 m strip of aboveground biomass was harvested from each plot, sorted to species, then dried. We used these data to determine the total aboveground biomass produced by the originally planted species. We used percent cover data from a 0.5 m^2 section of each plot for each year to calculate observed richness of the originally planted species. pH was measured from in soil from each plot using 1 M KCl solution each year from 1999 to 2017.

2.3 | Overview of analytical approach

We were interested in quantifying the amount of potential biomass lost or gained because of nitrogen-induced shifts in species richness and pH at each level of planted richness (Figure 1). To do this, we first fit a statistical model to quantify how biomass production depended on nitrogen, planted richness, soil pH and year (biomass~N × planted richness × pH × year). This model includes planted richness instead of observed richness to account for the causal relationship between richness and productivity which can be quantified because planted richness was randomized, whereas observed richness was not. Similar results were obtained when observed richness was included instead of planted richness. Next, we fit two more models to determine how nitrogen shifted both observed richness within each level of planted richness and pH (e.g., the ambient point vs. the nitrogen enrichment point in Figure 1). These models took the form of: pH or observed richness~N × planted richness × year. Finally, we combined results from all three models to quantify how shifting pH or observed richness, individually or together, from the nitrogen-enriched to the ambient state impacted biomass production. This allowed us to quantify how biomass was constrained by nitrogen-induced shifts in pH and richness. For example, to estimate how much nitrogen enrichment would have altered biomass production if it had not shifted pH, we used our fitted statistical model to predict biomass by modeling observed species richness at its nitrogen enriched values but shifting pH to its ambient (unfertilized) values. We decided on the aforementioned approach, which relies on the experimental treatments, over structural equation modeling because the planted diversity gradient is not confounded by changes in composition (i.e., because all species are included at all levels of plant diversity), whereas including observed richness in a structural equation model would confound effects of richness, per se, with effects of species composition.

2.4 | Statistical analyses

All statistical analyses were done in R 3.6.0 (R Core Team, 2019). We used the lme function (Pinheiro, Bates, DebRoy, & Sarkar, 2020) to fit a mixed-effects model of biomass with all possible interactions between nitrogen, planted richness (either linear or $\log_2$ transformed), pH, and experiment year (either linear or $\log_2$ transformed) and used Akaike information criterion values to determine the most parsimonious model. We accounted for the random effects of plots nested within three ambient CO_2 rings, and to account for repeated measures through time. We removed the four-way interaction as it was

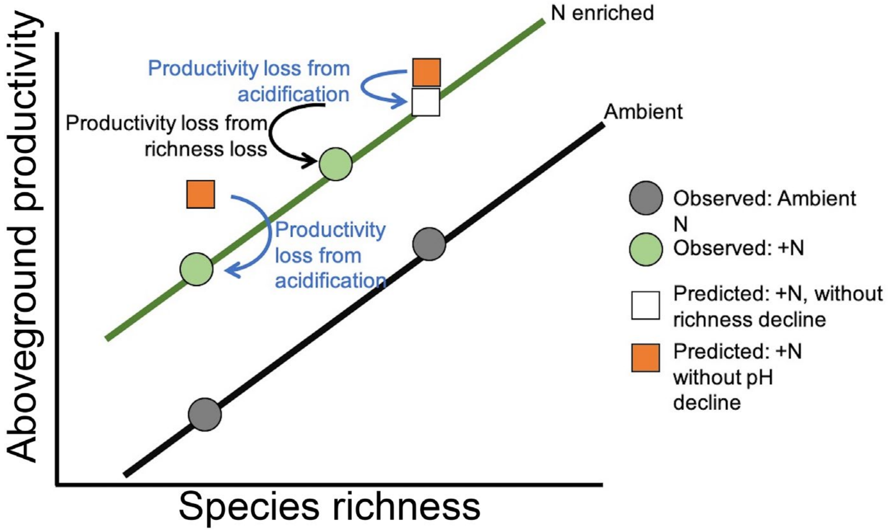


FIGURE 1 Conceptual figure of how nitrogen enrichment can indirectly impact aboveground biomass via shifts in species richness and pH. Here nitrogen enrichment increases aboveground biomass (green points and line vs. gray points and line), but it decreases richness (white vs. green points) and acidifies soils (orange vs. white points). Productivity under nitrogen enrichment is still greater than in ambient conditions, but these gains are less than expected (green) because of the indirect effects of nitrogen enrichment on richness and pH. In high diversity communities (circles), richness losses mainly decrease the amount of productivity gained from nitrogen enrichment, and in low diversity communities (squares), soil acidification decreases the amount of productivity gained under nitrogen enrichment [Colour figure can be viewed at wileyonlinelibrary.com]

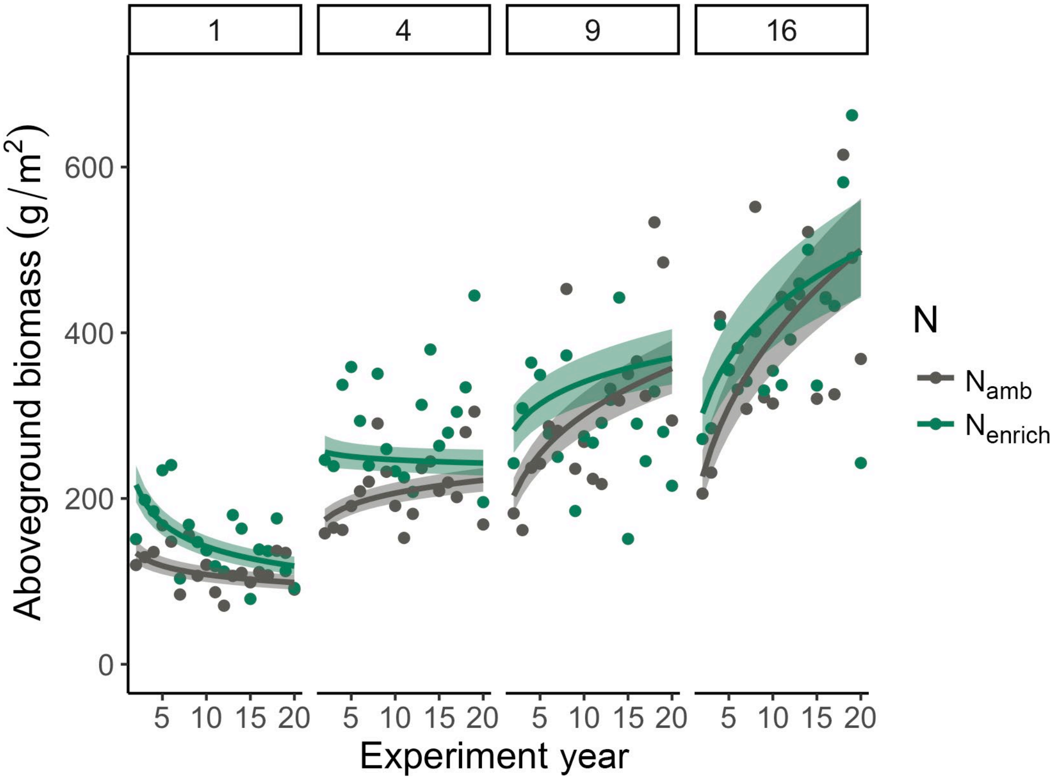


FIGURE 2 Net effects of nitrogen enrichment on biomass production over time in four different planted species richness treatments (panels). The difference between green and gray lines diminishes through time for all levels of planted richness. Lines are the predicted output from the best fitting model of biomass through time, colored bands are ±1 *SE*, and points are observed averages across all plots in nitrogen-enriched (green) and ambient (gray) conditions. For full model details, see Table 1 and Table S1 [Colour figure can be viewed at wileyonlinelibrary.com]

not significant and any other non-significant three-way interactions to simplify the model. Next, we fit mixed effects models with the same random effects structure to determine how observed richness and pH were impacted by nitrogen depending on planted richness through time. As before, we tested if models fit better with linear or $\log_2$ transformed richness and experiment year. Lastly, we determined how nitrogen-induced shifts in richness, pH, and the combination of both altered biomass production. To determine how species losses alone impacted biomass production, we took nitrogen-enriched values for pH but ambient values for observed richness for each time point in the four levels of planted richness. We then predicted the potential biomass from our model of biomass. The same approach was used to determine the impact of pH shifts alone and richness and pH together on potential biomass production. The code for all analyses is provided at github.com/kaitkimmel/BioCONpH.

3 | RESULTS

We found diminishing returns of productivity from nitrogen fertilization through time across all levels of planted richness (Figure 2; Tables 1 and 2). In early years of the experiment, there was a significant effect of nitrogen enrichment on productivity that was not seen in later years of the experiment (Figure 2; Table 2). Nitrogen-enriched plots produced about 38% more aboveground biomass than ambient plots on average between years 2 and 4 of the experiment but did not significantly increase aboveground biomass between years 18 and 20 (Figure 2; Table 2).

The impact of nitrogen enrichment on observed richness through time was dependent on planted richness (Figure 3a; Table 1). Nitrogen enrichment tended to decrease species richness within the first 2 years of treatment in high diversity plots, and these plots continued to lose species through time. Nine species plots lost about 1.5 species and 16 species plots lost about seven species by year 2 and lost an additional 37% each by year 20. Ambient plots also lost species through time, such that by year 20, 9-, and 16 species plots lost about 35.6% and 48% of species respectively in ambient plots compared to year 2. By year 20, there was no discernible effect of nitrogen enrichment on the plant species richness of the nine- and 16 species treatments.

The impact of nitrogen enrichment on pH through time was also dependent on planted richness (Figure 3b; Table 1). In monocultures, nitrogen enrichment decreased pH linearly though time, whereas in high diversity plots, there was less soil acidification as indicated by the significant positive three-way interaction between nitrogen enrichment, planted richness, and time. By year 20 on average, monocultures under nitrogen enrichment had a pH of 5.0 compared to 5.7 in ambient plots, whereas 16 species plots under nitrogen enrichment had a pH of 6.2 compared to 6.3 in ambient plots. Planted species richness had an increasingly positive effect on pH through time. Unfertilized monocultures had an average pH of approximately 5.6 that did not significantly change throughout the experiment, but in 16-species plots, the average pH increased from about 5.2 in year two to about 6.2 in year 20 (Figure 3b; Table 1). Thus, high species richness not only increased pH through time in unfertilized plots, it also ameliorated the acidifying effects of nitrogen enrichment.

Biomass production was greater at higher planted species richness (Figure 4). While there was not a significant three-way

TABLE 2 Impact of nitrogen addition on aboveground biomass in early years (years 2 through 4) and in late years (years 18 through 20) in the BioCON experiment

Predictor	Early years Estimate (*SE*)	Late years Estimate (*SE*)
Intercept	4.91 (0.09)***	4.87 (0.12)***
N	0.45 (0.13)***	0.18 (0.16)
ln(SR)	0.24 (0.06)***	0.52 (0.08)***
N × ln(SR)	−0.05 (0.09)	−0.06 (0.11)

*$p < .1$, **$p < .05$, ***$p < .01$.

TABLE 1 Results from the best-fitting mixed-effects models of aboveground biomass, observed species richness changes, or pH changes in the BioCON experiment through time. SR as a predictor refers to planted species richness. See Table S1 for *df* and *t* values

	ln(aboveground biomass)	Observed richness	pH
Predictor	Estimate (*SE*)	Estimate (*SE*)	Estimate (*SE*)
Intercept	5.25 (0.59)***	−3.69 (0.45) ***	5.51 (0.07)***
N	0.54 (0.34)	2.59 (0.64)***	0.19 (0.07)**
ln(SR)	0.50 (0.18) ***	5.64 (0.24)***	0.002 (0.03)
pH	−0.05 (0.10)	–	–
Year[a]	−0.52 (0.21) **	1.22 (0.15)***	−0.005 (0.003)
N × Year	−0.11 (0.04) **	−1.64 (0.33)***	−0.04 (0.004)***
N × ln(SR)	−0.09 (0.08)	−1.59 (0.34)***	−0.03 (0.05)
N × pH	0.003 (0.06)	–	–
ln(SR) × Year	0.16 (0.02)***	−1.15 (0.08)***	0.02 (0.002)***
ln(SR) × pH	−0.07 (0.03)**	–	–
pH × Year	0.07 (0.04)*	–	–
N × ln(SR) × Year	–	0.61 (0.12)***	0.01 (0.003)***

[a] Year is $\log_2$ transformed experiment year for biomass and richness models, but linear for pH model.

*$p < .1$; **$p < .05$; ***$p < .01$.

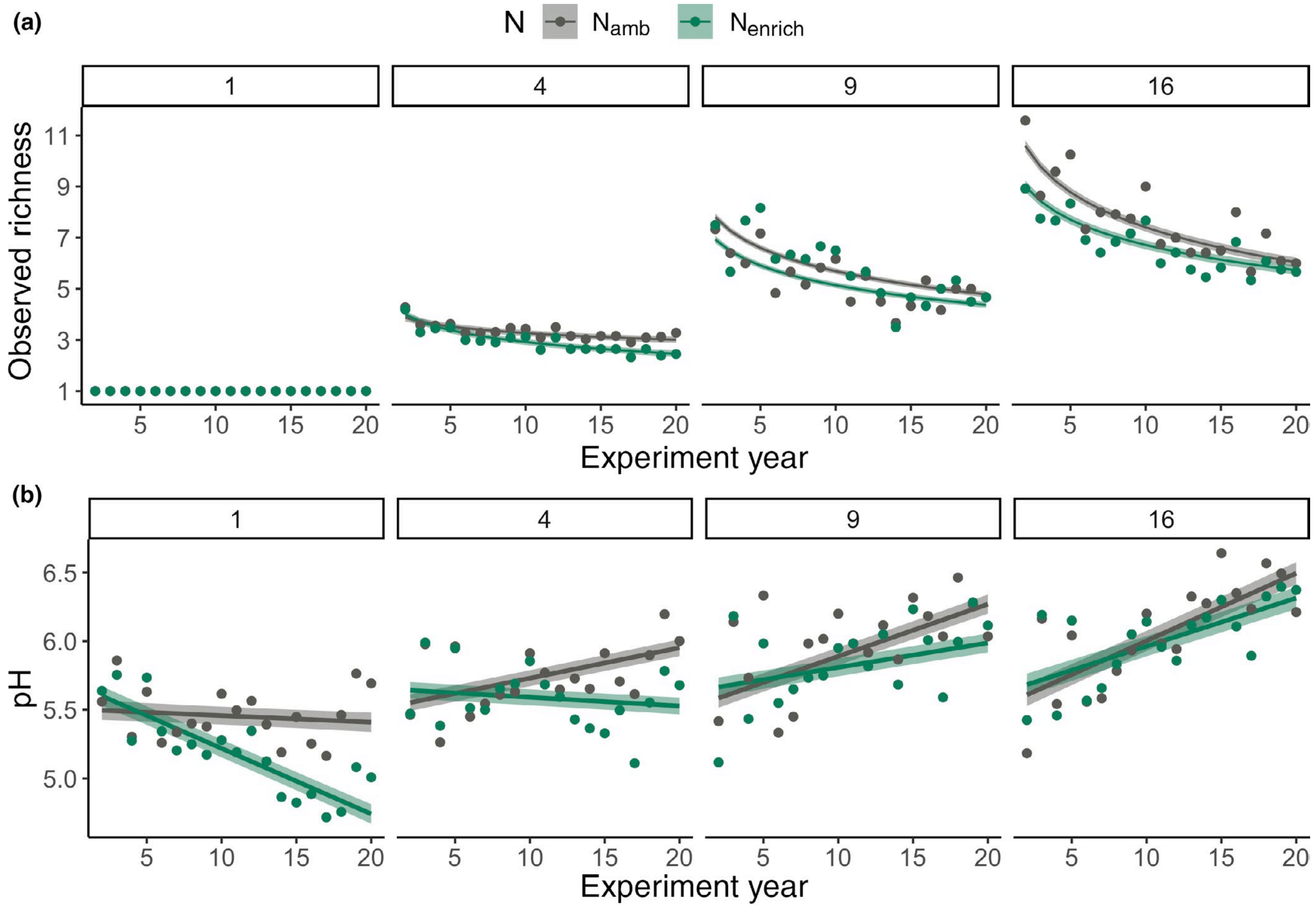
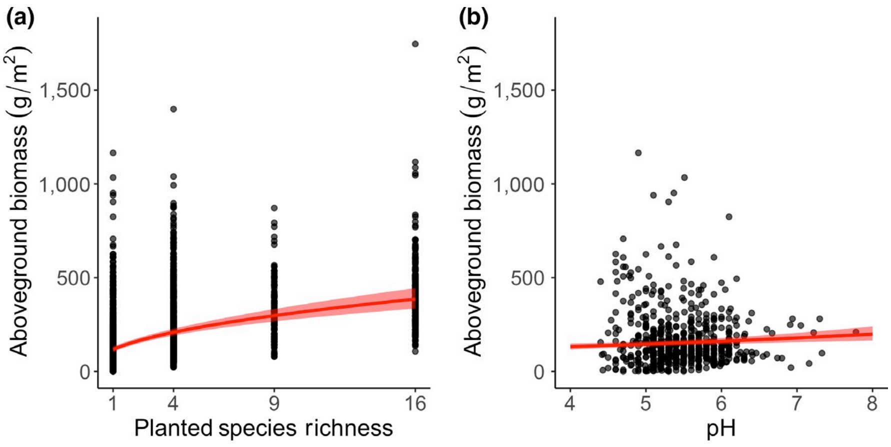


FIGURE 3 Effects of nitrogen enrichment on observed plant species richness (a) and pH (b) in four different planted species richness treatments (panels). High diversity plots tended to rapidly lose richness under nitrogen enrichment. Nitrogen enrichment also decreased pH through time in low diversity plots, whereas this effect was not as prominent in high diversity plots. Lines are fitted using mixed effects models (see Table 1), bands are ±1 *SE*, and points are observed annual averages across all plots in nitrogen-enriched (green) and ambient (black) conditions [Colour figure can be viewed at wileyonlinelibrary.com]

FIGURE 4 The relationship between (a) planted species richness treatment and aboveground biomass for all diversity treatments, and (b) pH and the aboveground biomass of just monoculture plots. For simplicity, both panels show the response averaged over time in ambient nitrogen treatments. Points are the observed values of each plot in each year. Lines are fitted (see Table 1 for model details) and bands are the *SE* of fitted line [Colour figure can be viewed at wileyonlinelibrary.com]



interaction between richness, pH and N, there was a significant interaction between richness and pH. The effect of pH on biomass production was dependent on species richness such that across monocultures, productivity was positively related to pH (Figure 4), but this relationship was not apparent at higher levels of richness (Table 1). Together, this suggests that both decreasing pH in monocultures and depressed richness in speciose plots constrained the amount of biomass produced under nitrogen enrichment over time. Biomass increased by about 20% on average between ambient and nitrogen-enriched plots over all levels of richness and across all years. However, according to our statistical model, the net effect of nitrogen on productivity could have been 14.5% greater over

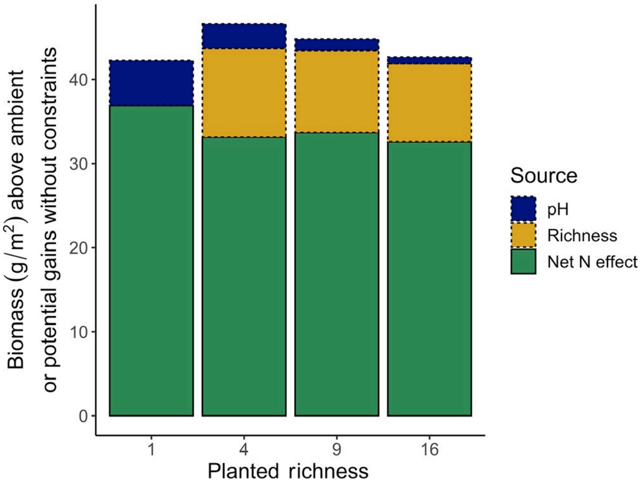


FIGURE 5 Average aboveground biomass across all 20 years under nitrogen enrichment (green) and further potential biomass that might have otherwise been gained under nitrogen enrichment, if not for shifts in pH (blue) or species richness (yellow) associated with nitrogen enrichment for each of the levels of planted species richness. Portions of the bars with solid outline are the net observed nitrogen effect and dotted outlines are the potential gross N effect. In low diversity communities, the increase in biomass caused by nitrogen enrichment could have been greater if not for changes in pH, whereas in high diversity communities, it could have been greater if not for losses of plant species. Nitrogen enrichment bars are the average aboveground biomass gained from nitrogen enrichment averaged across all years. pH and richness sections are the amounts of biomass gained on average if each variable was shifted toward its higher ambient value [Colour figure can be viewed at wileyonlinelibrary.com]

20 years for monocultures if not for nitrogen-induced decreases in pH and about 28.5% greater on average over 20 years for 16 species communities if not for nitrogen-induced richness losses (Figure 5). However, the magnitude of these indirect impacts of pH and richness were dependent on experiment duration (Figure S1) such that in later years, the net nitrogen effect could have been about 93% more in monocultures and 52% more in 16 species communities.

4 | DISCUSSION

On average across all 20 years of this experiment, our results showed that annual nitrogen enrichment had diminishing productivity returns through time, with species losses driving these diminishing returns in high diversity communities and soil acidification driving them in monocultures. Here we consider nitrogen-dependent constraints imposed by declines in plant richness and by soil acidification, but there may be other indirect effects of nitrogen enrichment like species composition changes or competition with weedy invaders. Like other studies, we found that species richness increased productivity (O'Connor et al., 2017) and soil acidification decreased productivity (Dodd, Silvertown, McConway, Potts, & Crawley, 1994). These effects were not directly modified by nitrogen addition as nitrogen addition did not significantly modify the main effects of pH or species richness either (Table 1). Instead productivity was impacted via the indirect routes of nitrogen's effects on richness and soil pH. Productivity response to nitrogen enrichment in high diversity communities was constrained because of an initial rapid decrease in species richness, as found previously in this experiment and in naturally assembled grassland communities (Isbell et al., 2013). Here we additionally found that the addition of ammonium nitrate tended to acidify low diversity plots, whereas this effect was much smaller in higher diversity plots. However, the effect of this acidification on productivity was small relative to the direct impacts of nitrogen fertilization and the nitrogen-dependent losses in planted richness on average over 20 years of the experiment. Higher species richness ameliorated the impacts of nitrogen enrichment on soil acidification and subsequent declines in productivity. Thus, over longer timescales in initially diverse grasslands, nitrogen enrichment may first drive declines in species richness and then, after diversity becomes sufficiently low, cause soil acidification, both of which could contribute to diminishing returns of productivity from nitrogen enrichment.

Lower-diversity communities tend to have less complete nutrient use compared to their more speciose counterparts (Hooper & Vitousek, 1998; Mueller, Hobbie, Tilman, & Reich, 2013; Tilman, Wedin, & Knops, 1996) which may explain both the diversity-dependent soil acidification effect and its constraint on productivity. Nitrogen addition tends to increase soil nitrate more in low diversity communities compared to species rich mixtures (Mueller et al., 2013; Reich, Knops, et al., 2001; Reich, Tilman, et al., 2001). At the study site, monocultures tend to leach more dissolved inorganic nitrogen than species-rich plots (Dijkstra et al., 2007). If this leaching is accompanied by base cation leaching, productivity may become limited by base cations (Aber et al., 1995; Gilliam, 2006). Furthermore, at low enough soil pH, P can become insoluble and toxic metals can become available. These two factors may also constrain the productivity of the community under acidic soil conditions. Furthermore, the accumulation of nitrate and loss of base cations could also contribute to creating more acidic soils in low diversity communities. However, the extent of this acidification and its constraint on productivity will depend on the soil's buffering capacity (Clark et al., 2007; Matson et al., 2002). Soils which are more able to buffer this acidification will likely take more time to see the impact of nitrogen enrichment on soil acidification.

The positive effect of biodiversity on soil pH may result from a diversity-dependent increase in total soil C and soil N (Cardinale et al., 2012; Dybzinski, Fargione, Zak, Fornara, & Tilman, 2008; Fornara & Tilman, 2008; Lange et al., 2015; Yang, Tilman, Furey, & Lehman, 2019). In addition, plants can modify the rhizosphere by taking up more anions relative to cations, which increases soil pH around their roots (Bagayoko, Alvey, Neumann, & Buerkert, 2000); higher root biomass in more speciose communities (Reich, Knops, et al., 2001; Reich et al., 2004) suggests that plant communities with higher diversity likely have more root mass and surface area which can lead to increased pH through time. The long-term trend of soil pH in ambient conditions are likely site-specific but highly dependent on species richness and could be the result of changing background nitrogen deposition rates, the experimental set-up, or other edaphic factors. However, species-rich communities likely have both a higher capacity to increase soil pH and maintain that pH under nitrogen enrichment than monocultures.

Our results suggest that under nitrogen enrichment via fertilization or deposition, liming of low diversity agroecosystems may reduce the negative impacts of soil acidification on productivity, whereas maintaining high diversity in more speciose systems may help ensure productivity returns. It has long been realized that continual inputs of nitrogen can lead to diminishing returns on productivity in natural and agricultural ecosystems (Huang, Zhang, Yu, & Huang, 2010; Jie, Jing-zhang, Man-zhi, & Zi-tong, 2002; Lawes & Gilbert, 1880; Matsuyama et al., 2005). Liming is a common practice to combat the negative impacts of nitrogen enrichment on soil pH leading to many of these declines. Indeed, liming has been shown not only to neutralize soil pH (Blake, Goulding, Mott, & Johnston, 1999; Goulding, 2016) but also to decrease nutrient leaching (Gibbons et al., 2014) and increase root colonization by mycorrhizal fungi (Johnson, Leake, & Read, 2005). Our results suggest that high diversity ecosystems, on the other hand, may be less vulnerable to soil acidification; and that productivity in these systems may instead be constrained by species losses from nitrogen enrichment. Furthemorer, if formerly high diversity systems stay in these low diversity states long enough, they may become vulnerable to soil acidification. In this case, maintaining richness may help to both sustain productivity and maintain soil pH.

Overall, we show a diversity-dependent impact of nitrogen enrichment on the indirect drivers of diminishing productivity returns from nitrogen addition. Specifically, soil acidification from nitrogen enrichment leads to diminishing returns of fertilization on biomass through time, but this effect is greatest at low diversity because higher plant diversity ameliorates the acidifying effect of nitrogen addition. In more speciose communities, losses of biodiversity have the potential to decrease future productivity of grassland ecosystems under chronic nitrogen deposition. It is now necessary to understand if our results relate to temporal dynamics over longer timescales than the current study; in initially high diversity systems under nitrogen enrichment, do species losses happen rapidly and without much effect on pH, but over longer timescales, does staying in this low diversity state then allow for declines in pH such that the temporal dynamics of the indirect effects of nitrogen enrichment shift through time? Overall, these results suggest that maintaining biodiversity may be a key component to ensuring highly productive grasslands impacted by nitrogen deposition.

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DATA AVAILABILITY STATEMENT

All data are publicly available at https://www.cedarcreek.umn.edu/research/experiments/e141. Code for analyses is available at github.com/kaitkimmel/BioCONpH.

ORCID

Kaitlin Kimmel https://orcid.org/0000-0003-3261-5248

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SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section.

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