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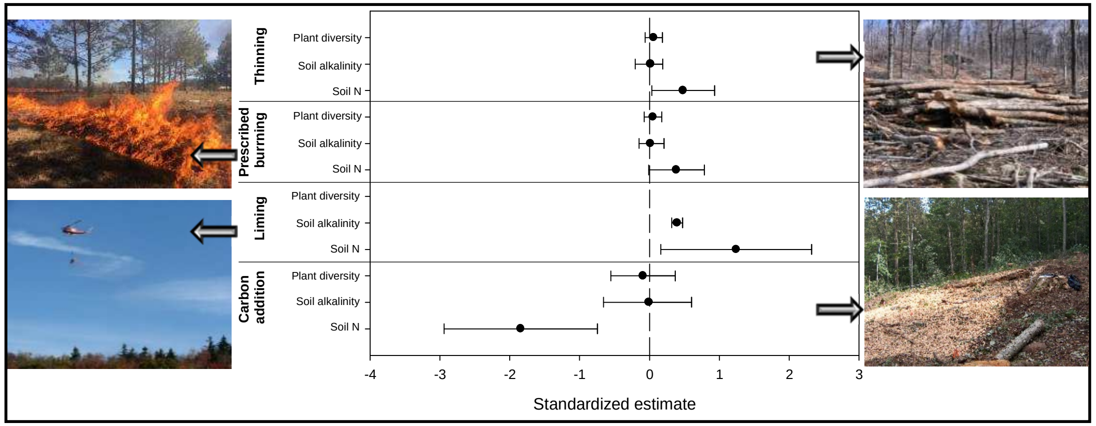

Title Page

Title: A synthesis of ecosystem management strategies for forests in the face of chronic nitrogen deposition

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Abstract

Total nitrogen (N) deposition has declined in many parts of the U.S. and Europe since the 1990s. Even so, it appears that decreased N deposition alone may be insufficient to induce recovery from the impacts of decades of elevated deposition, suggesting that management interventions may be necessary to promote recovery. Here we review the effectiveness of four remediation approaches (prescribed burning, thinning, liming, carbon addition) on three indicators of recovery from N deposition (decreased soil N availability, increased soil alkalinity, increased plant diversity), focusing on literature from the U.S. We reviewed papers indexed in the Web of Science since 1996 using specific key words, extracted data on the responses to treatment along with ancillary data, and conducted a meta-analysis using a three-level variance model structure. We found 72 publications (and 2158 responses) that focused on one of these remediation treatments in the context of N deposition, but only 31 publications (and 408 responses) reported results appropriate for our meta-analysis. We found that carbon addition was the only treatment that decreased N availability (effect size: -1.6 to -1.8), while liming, thinning, and prescribed burning all tended to increase N availability (effect sizes: +0.2 to +1.1). Only liming had a significant positive effect on soil alkalinity (+10% to 80% across metrics). Only prescribed burning and thinning affected plant diversity, but with opposing and often statistically marginal effects across metrics (i.e., increased richness, decreased Shannon or Simpson diversity). Thus, it appears that no single treatment is effective in promoting recovery from N deposition, and combinations of treatments should be explored. These conclusions are based on the limited published data available, underscoring the need for more studies in forested areas and more consistent reporting suitable for meta-analyses across studies.

Capsule: Combinations of interventions in forests may be necessary to remediate soil N status, soil acidity, and plant community diversity from the effects of long-term N deposition.

Keywords: nitrogen deposition, soil nitrogen availability, soil acidity, plant diversity, forest management

Introduction

Enhanced atmospheric nitrogen (N) deposition remains one of the major stressors to terrestrial ecosystems globally (Bobbink et al., 2010; Sala et al., 2000). In forests, N deposition can lead to increased soil N availability (Aber et al., 1998), alterations in soil carbon and biogeochemical cycling (Cheng et al., 2019; Tian et al., 2018), increased primary production (Du and de Vries, 2018; Vitousek and Howarth, 1991), increases or decreases in tree growth and mortality (De Vries et al., 2014; Du and de Vries, 2018; Horn et al., 2018; Thomas et al., 2010), changes in tree nutrient status and vitality (De Vries et al., 2014), and increased N leaching to downstream aquatic habitats (Driscoll et al., 2003a). Elevated N deposition, along with sulphur (S) deposition, can also result in soil acidification, which can lead to nutrient imbalances, cation and nitrate losses, reduced nutrient health of trees, and reduced rates of regeneration (Carter et al., 2017; Driscoll et al., 2003b; Sullivan et al., 2013; Tian et al., 2018). Increased production and aboveground biomass resulting from higher N availability can lead to decreased plant diversity and/or shift species composition of understory community (Bobbink et al., 2010; Du, 2017; Hautier et al., 2009; Simkin et al., 2016; Verheyen et al., 2012). Long term N deposition may even shift ecosystems away from typical N limitation (Vitousek and Howarth, 1991), and toward limitation by other nutrients like phosphorus (P) (Goswami et al., 2018). The numerous effects that N deposition can have on ecosystems, crossing environmental media (e.g., land, air and water) as well as administrative jurisdictions, make the management of this environmental stressor particularly challenging (EPA, 2010; Sutton et al., 2011).

There are many parts of the world where atmospheric N deposition is either unchanging or continuing to increase, including the western U.S. (Houlton et al., 2013), industrializing parts of Africa (Vet et al., 2014), and in most parts of south and eastern Asia (Duan et al., 2016; Itahashi et al., 2018; Liu et al., 2011; Liu et al., 2013). Furthermore, emissions and deposition of reduced N are not decreasing in many countries and may be increasing globally (Li et al., 2016; Vet et al., 2014). On the other hand, deposition of total N and S have been declining in many countries in Europe and in eastern North America after national and international air quality policies were enacted to combat acid rain and ozone (Burns et al., 2011; Clark, 2018; Du et al., 2014). Many of the air quality policies enacted to address these issues generally reduced S more than N due to the focus on acidification. Thus, the role of N deposition (esp. reduced N) is increasingly important now and into the future.

It is unclear whether decreasing N deposition alone is sufficient to promote forest recovery (Gilliam et al., 2018; Schmitz et al., 2018; Stevens, 2016). Results from forests are mixed, and demonstrate that some biogeochemical and physiological responses (e.g., nitrate leaching, tissue N concentrations) may recover fairly quickly (Boxman et al., 1998b; Boxman et al., 1995), while others (e.g., soil N, understory vegetation) may not (Boxman et al., 1998a; Van Dobben and de Vries, 2017). Recovery from acidification appears to be beginning in some forests in the eastern US (Lawrence et al., 2015) and Europe (Boxman et al., 2008; Johnson et al., 2018; Verstraeten et al., 2012). However, not all forests or indicators show signs of recovery (Gilliam et al., 2018; Lawrence et al., 2015; Verstraeten et al., 2017). Furthermore, recovery may lead to other environmental issues such as the mobilization of soil carbon, N and possibly P that may impact water quality downstream (Evans et al., 2012; Johnson et al., 2018; Monteith et al., 2007; Oulehle et al., 2011; Oulehle et al., 2018; Stoddard et al., 2016). Regardless, because of the increasing concern that ecosystems may not recover on their own, or may recover but only over fairly long time scales (Johnson et al., 2018; Stevens, 2016), it is increasingly apparent that management intervention may be required to assist forest recovery from decades of elevated N deposition.

There are several remediation approaches that have been proposed or adopted to reduce the effects of chronic N deposition and support ecosystem recovery. These include prescribed burning, carbon addition, thinning, liming, litter or topsoil removal, mowing, grazing, planting and harvesting of plant biomass, and replanting desired target species either as seed, seedlings, or adults (Jones et al., 2016). Carbon addition involves the addition of a carbon source that is either labile (e.g., sucrose) or more recalcitrant (e.g., sawdust) to induce microbial immobilization of N and thereby reduce N availability to plants (Blumenthal et al., 2003; Morgan, 1994; Torok, 2000). All of these approaches affect one or more processes that influence recovery. Some approaches reduce soil N availability, either by enhancing soil microbial immobilization (carbon addition, thinning with slash left onsite; Clark and Tilman, 2010; Eschen et al., 2006; Torok, 2000; Wolk and Rocca, 2009), or by direct removal of either soil N (prescribed burning, litter/topsoil removal, planting and harvesting: Boerner et al., 2008; Jones et al., 2016; Boxman and Roelofs, 2006), or of aboveground N (prescribed burning, mowing, grazing, planting and harvesting, thinning with slash removal: Boerner et al., 2008; Boxman and Roelofs, 2006; Jones et al., 2016). Other approaches reduce the acidity of the soil whether from N or S (primarily liming: Błońska et al., 2015; Driscoll et al., 2001; Huang et al., 2014; Lawrence et al., 1999; Lawrence et al., 2016; Likens et al., 1996). Other approaches make habitats more suitable by either increasing light levels at the soil surface and opening germination sites for colonization (prescribed burn, thinning, mowing, grazing: Ares et al., 2010; Wolk and Rocca, 2009), or reintroduce propagules that may either be dormant in a deep seed bank or locally extirpated (litter/topsoil removal, replanting: Bakker and Berendse, 1999; Jones et al., 2016; Wolk and Rocca, 2009).

The effectiveness of remediation approaches for recovery from N deposition has recently been assessed in European grasslands, heathlands, coastal habitats, bogs and fens (Jones et al., 2016). While many approaches improved habitat suitability, most did little to slow or reduce the accumulation of N in soils at current deposition rates. No parallel analysis has yet been conducted for forests. We fill this key knowledge gap, and review the effects of four remediation approaches in forests (i.e., prescribed burning, thinning, liming, and carbon addition) on three indicators of recovery (i.e., reduction in soil N availability, increases in soil alkalinity, and increases in understory plant diversity). Mowing, grazing, planting and harvesting, and replanting of desired target species, are more common approaches in herb-dominated communities (e.g., grasslands) than in forests, the focus of this study. We focus on literature in the U.S. because of the intended focus on remediation from deposition in the U.S., but include seminal literature from Canada, Europe, and other areas to fill key gaps and provide context.

Methods

Literature and data collection

We used a meta-analysis approach in this study (Borenstein et al., 2011; Gurevitch et al., 2001; Hedges et al., 1999), because it facilitates the combination of results from multiple independent studies in order to effectively increase sample size for a given research question. We searched literature databases using Web of Knowledge, Google Scholar, and journal articles directly provided by co-authors (~60) and from scientists at the U.S. Environmental Protection Agency (EPA), U.S. National Park Service (NPS), U.S. Department of Agriculture Forest Service (USFS), and U.S. Geological Survey (USGS). Keywords for searches included combinations of habitat (e.g., “Forest”, “Deciduous forest”, etc.), nitrogen and nitrogen effects (e.g., “nitrogen,” “eutrophication,” “acidification”), and four management techniques of interest (e.g., “liming,” “prescribed burnning,” “carbon addition,” “thinning,” etc.) (Table S1). We explored topsoil removal, mowing, and grazing, but these were not commonly found in forests and thus were not included. We also included various synonyms of the core terms listed above (Table S1).

From the studies identified through literature searches, we selected those where remediation from N deposition or improving N cycling was considered as part of the intention of treatment. Because of the requirement of a focus on N, general studies that looked at these treatments for other reasons and that did not discuss N in context were not included. We feel this is appropriate because we wanted to focus on recovery from N deposition, rather than on the remediation approaches themselves, because remediation approaches could be applied for reasons not pertinent to recovery from N deposition (e.g., clearing slash following forest dieback from drought, pests, or hurricanes; mine reclamation, etc.). Results were further narrowed in Web of Science by publication years (1996 – present), countries (North American and EU countries), and titles were reviewed to exclude papers that were not relevant. These filtering steps reduced the number of publications from over 7000 to 72. Only a subset of these focused on soil N availability, soil alkalinity, or plant community diversity (many addressed total biomass or other end points), which further narrowed the literature set to 46.

Because we were using a meta-analytic approach, we required reporting of six parameters in tabular form: (1) sample size of the treatment and control, (2) mean of the treatment and control, (3) standard deviation/error of the treatment and control. This reduced the number of papers from 46 to 29, because many papers did not publish all six required parameters, with the standard deviation/error lacking most frequently. Some papers were excluded because they only published partial information in the main text (e.g., means without standard deviations). We did not explore additional data mining software due to time and resource constraints. Eleven of the 29 studies included were from the USFS Fire and Fire Surrogates (FFS) program. These were treated as separate publications for each of the 11 locations across the country where the FFS study design was implemented (McIver et al., 2012; McIver et al., 2016).

Data processing

For the 29 studies used in the meta-analysis (Table S2), we identified records within the database with control and treatment group mean, variance and sample size for three categories of response: soil N availability, soil alkalinity, and plant community diversity. Each of these categories of response had several metrics used in the literature to represent them. There were 10 for soil N availability (ammonium, nitrate, nitrate N, inorganic N, net ammonification, N mineralization, net N mineralization, nitrification, net nitrification, and mineralizable N), five for soil alkalinity (soil pH, base saturation, and base cation exchangeable Ca, K, and Mg), and three for plant community diversity (species richness, Simpson diversity index, Shannon diversity index) (Table 1). For the plant response category, non-native species richness and diversity records were excluded where species origin information was available. We used Simpson diversity where necessary to ensure increases in the metric were associated with increases in diversity. For the soil N availability category, we excluded total soil N from the analysis for several reasons: (1) we were interested in N availability rather than the total soil N pool, (2) total soil N is a slowly changing variable that is likely not responsive over the study period for most studies (<5 years), and (3) including "slow variables" and "fast variables" in a meta-analysis can complicate the portioning of variance and interpretation of results. For both the soil available N and alkalinity categories, mineral and organic soil layers were included. All outcome measures were selected so that responses were unidirectional within each system response (i.e., for soil N higher values indicated higher soil N availability; for soil alkalinity higher values indicate greater alkalinity; for plant biodiversity higher values indicate increased plant community diversity). Different studies reported multiple effect categories, and/or multiple metrics within an effect category.

Overview of the literature surveyed

In total from the 29 publications included in the meta-analysis there were 408 effects reported combining study, management method, and response metric for forests (Table 1, Table S2 and S3). Most studies focused on the treatments of prescribed burning (17 studies and 152 effects) and thinning (13 studies and 143 effects) (Table 2). Effects of these treatments were reasonably well distributed across U.S. forests (Figure 1) and response categories owing to a common origin from the FFS (Table 2). However, there was a notable absence of representative forests from Utah, Wyoming, and Idaho. Liming was less intensively studied in the context of N deposition (9 studies and 101 effects), and almost entirely focused on soil alkalinity (93 of 101 effects) and in the east (Figure 1). No studies reported the effects of liming on plant diversity and only one on soil N availability. Most liming studies in the full database of 72 references that examined the plant community assessed other responses such as plant growth and tissue contents (e.g., N, Ca, P, etc.), rather than on biodiversity (Table S3). There were only two carbon addition studies in forests (12 effects), and only one from the U.S. (Figure 1).

Statistical Analysis

Unique effect sizes were calculated for the 408 response records using a log transformed ratio of means (Eqn. 1) (Hedges et al., 1999).

$$\ln RR = \ln\left(\frac{\overline{X}_T}{\overline{X}_C}\right) \qquad (1)$$

and its variance as:

$$V_{\ln RR} = S_{pooled}^2\left(\frac{1}{n_T(X_T)^2}\right) + \left(\frac{1}{n_C(X_C)^2}\right) \qquad (2)$$

with

$$S_{pooled} = \sqrt{\frac{(n_T-1)s_N^2+(n_C-1)s_C^2}{n_T+n_C-2}} \qquad (3)$$

Where RR is the response ratio of treatment mean ($\overline{x_T}$) divided by the control mean ($\overline{x_C}$), S_{pooled} is the pooled standard deviation, n_T and n_C are the number of replicates for the treatment and the control, and s_N and s_C are the sample standard deviations for the treatment and the control, respectively. Log transformations are generally used in meta-analyses such as this because values generally follow a log-normal distribution (Borenstein et al., 2011).

Because selected outcome measures for soil N availability included zero and negative values (nitrate, net nitrification, and net N mineralization), the log transformed ratio of means is not applicable. Thus, soil N effect sizes were calculated using standardized mean difference (SMD), which is standard for responses that can be negative or positive (Eqn. 4).

$$SMD = \overline{X}_T - \overline{X}_C \qquad (4)$$

Thus, SMD was used for soil N availability, and log response ratios (lnRR) were used for the soil alkalinity and plant responses. Effect sizes for SMD were measured in units of standard deviations, while for lnRR, effect sizes were back transformed to percent changes. A small constant was added to metrics with zeroes (i.e., soil nitrate).

A meta-analytic mixed-effects linear model was then fit to the data for each system response. All meta-analytic models were specified using the "metafor" package (Viechtbauer, 2010) in the statistical software program R (R Core Team, 2016). A three-level model structure was used to account for different sources of variance in our database, including: (1) sampling variance, (2) among-study variance, and (3) within-study variance for studies with multiple response metrics. In addition, moderator variables representing all reported management practices were included in the model structure. This modeling framework allows us to report estimates for each individual management action in the dataset.

Meta-analyses were generally conducted at the effect category level (i.e., combining individual metrics within the three response categories). Where there were sufficient data at finer levels of detail (e.g., for individual metrics or subsets of metrics), additional separate meta-analyses were conducted. This included two separate analyses within soil N availability (i.e., extractable N, net nitrification/mineralization), two within soil alkalinity (i.e., soil pH, base cations [including base saturation, exchangeable Ca, K, and Mg]), and two within plant diversity (i.e., species richness, diversity). The binning of individual metrics into response subsets is shown in Table S4.

Results

Soil nitrogen availability response

Soil N availability (Figure 2, Table 3) was strongly reduced by carbon addition whether examining all metrics (P<0.001) or extractable N separately (P=0.002). Prescribed burning tended to increase soil N availability (all metrics, P=0.053) through increased extractable N (P=0.024), but had no effect on rates of mineralization/nitrification. Liming and thinning had similar effects to one another, increasing soil N availability (all metrics, P=0.021 and P=0.031, respectively), and tended to increase extractable N though not at conventionally significant levels (i.e., P=0.073 and P=0.137 for liming and thinning, respectively, Table S5).

Soil alkalinity response

As expected, soil alkalinity (Figure 3, Table 3) strongly and significantly increased with liming (all metrics, +48.6%, P<0.001). Individual response sets showed strong responses as well, with base cation concentrations increasing by 82.2% (P<0.001) and pH by 10.5% (P<0.001). There were no other treatment effects on combined or individual metrics for soil alkalinity (Table 3, Table S5).

Plant community response

Species richness tended to increase and diversity tended to decrease with either prescribed burning or thinning (Figure 4, Table 3), though not at conventionally significant levels (Table 3). Carbon addition had no effect on aggregated or individual diversity measures, and the variation of effects was wide owing to the small number of studies in forests. Effects from liming on plant diversity were not examined.

Discussion

Effectiveness of carbon addition to mitigate negative effects of nitrogen deposition

We found that carbon addition only improved one of the three indicators of recovery examined (i.e., decreased soil N availability). However, there were very few studies on the effects of carbon in forests (N=5) and only two that reported results compatible for our meta-analysis. Cassidy et al. (2004) added sawdust and sucrose (in addition to a separate lime treatment) to an upland forest in west-central Massachusetts to test whether the invasiveness of Japanese barberry (*Berberis thunbergii*) was limited by soil acidity or N availability. They found that carbon addition significantly reduced soil ammonium by 32-37%, and reduced N mineralization by 48-69%, though the latter result was not conventionally significant ($P < 0.05$). Koorem et al. (2012) adjusted site fertility (i.e., increased with fertilizer addition and decreased with sucrose addition) to an Estonian forest dominated by Norway spruce (*Picea abies*) and common hazel (*Corylus avellana*). They found soil available N was relatively unchanged with sucrose addition, though soil nitrate was not assessed and the plant community did show signs of decreased shoots and species richness with sucrose addition. The three other studies not included in the meta-analysis because of insufficient reporting had mixed results. Chapman et al. (2015) found that carbon addition to a secondary oak forest in Pennsylvania led to reductions in nitrate and ammonium, but only during certain times of the growing season, and Hunt et al. (1998) found little effect from carbon addition to a mesic pine meadow site in Wyoming. This diversity of responses within years and across precipitation gradients suggest covariation with climate as reported in grassland studies, with larger reductions under drier rather than wetter conditions (Blumenthal, 2009).

Thus, although less studied in forests, there may be a growing body of literature suggesting that carbon addition may have a remediation effect on reducing soil N availability (Blumenthal et al., 2003; Cassidy et al., 2004; Clark and Tilman, 2010; Koorem et al., 2012; Morgan, 1994). The addition of a carbon-rich source, whether labile (e.g., sucrose) or more recalcitrant (e.g., sawdust), induces the soil microbial community to immobilize soil N, which reduces the available N in the soil to support plant growth (Torok, 2000). There is much more literature from grasslands as opposed to forests on this effect. Thus, even though the biogeochemical mechanisms are likely similar in forests, more work is needed to better understand the efficacy of this approach for reducing soil N availability in forests, and how soil water and climate affect the efficacy of treatment.

It is unknown whether carbon addition in forests has direct or indirect effects on soil alkalinity. There may be direct effects through the alkalinity of the carbon source added, when added as wood chips (contains base cations) as opposed to sucrose (i.e., no base cations). However, these are likely minor relative to base cations in the mineral soil. Indeed, only Cassidy et al. (2004) and Chapman et al. (2015) reported the effect of carbon addition on soil pH, and neither found a significant effect. There could be indirect effects through the plant community through changes in plant growth and increases in root:shoot biomass and root exudates to offset lower N availability (Eschen et al., 2006; Walker et al., 2003), but these are likely minor.

In terms of the ultimate effects on the plant community, the results from the meta-analysis are inconclusive because of small sample sizes (Table 1, Figure 4). However, closer inspection of the literature suggest carbon addition may be a useful strategy. Koorem et al. (2012) found that the growth of an understory forest specialist species (*Oxalis acetosella*) was enhanced with carbon addition, provided the arbuscular mycorrhizal fungal community was not disturbed, while the growth of a generalist species (*Prunella vulgaris*) was not significantly affected. Furthermore, Cassidy et al. (2004) found that the growth of the forest invasive shrub Japanese barberry (*Berberis thunbergii*) was reduced in the carbon addition treatment after accounting for initial biomass. These differential effects on target species is often the goal of restoration approaches, where treatment is intended to reduce invasive species and promote native species (Blumenthal et al., 2003). Both responses in Koorem et al. (2012)

and Cassidy et al. (2014) were associated with the effects of carbon addition on reducing soil available N. These responses, however, were not large enough to significantly affect plant community diversity in Koorem et al. (2012), and effects on diversity were not assessed in Cassidy et al. (2004).

These few studies for forests can be compared with a much larger number of studies on carbon addition in grasslands (Blumenthal, 2009; Blumenthal et al., 2003; Clark and Tilman, 2010; Eschen et al., 2006; Eschen et al., 2007; Paschke et al., 2000). Controlled greenhouse experiments show that carbon addition reduces the growth of annual species and grass species more than perennial and leguminous species, because the former group is more sensitive to soil N availability (Eschen et al., 2006). However, results from field experiments are sometimes mixed. Reductions in total plant growth are consistently reported in field experiments (Blumenthal, 2009; Blumenthal et al., 2003; Clark and Tilman, 2010; Eschen et al., 2007; Paschke et al., 2000). However, species- and functional-group-specific results consistent with predicted recovery (i.e., decreased cover of grasses, increased cover of forbs legumes, and increased diversity) are not consistently found, and the restorative effect in some cases depends on climate, or an initial disturbance to till in the carbon and/or stimulate the extant seed bank (Blumenthal et al., 2009; Clark and Tilman, 2010; Eschen et al., 2007).

Carbon addition may promote the recovery of the desired plant community following N enrichment through species- and functional-group-specific responses to reduced soil N availability, but there are many uncertainties that remain. First, more studies are needed in forests, and for longer periods, across a broad range of forest types and climates. Second, it is unclear whether the short-term effects observed from carbon addition studies, whether as labile or more recalcitrant forms, are sustained over long enough periods to induce permanent shifts in the plant community. Third, although it is hypothesized that nutrient-demanding invasive species will be more hindered by carbon addition than nutrient-efficient species, the results from field studies are mixed and may require additional treatments in combination or an initial tillage to incorporate the carbon more fully into the soil. Fourth, because there is no evidence of a direct or indirect effect of carbon addition improving soil alkalinity, a combination of treatments may be required to restore soil alkalinity in addition to soil N and the plant community. Finally, the efficacy of carbon addition is not only restricted to its ecological effectiveness, but also cost and ease of application over a wide area. Lower cost carbon sources (e.g., sawdust or wood chips over sucrose) may have the added benefit of longer lasting effects, though the magnitude of effect may be lower than observed for more labile forms.

Effectiveness of liming to mitigate negative effects of nitrogen deposition

We found that liming had countervailing remediation effects, increasing soil alkalinity, but also increasing soil N availability (all metrics). No study in the meta-analysis or the larger database examined the effect of liming on plant diversity (Table 2). Those studies that did include plant end points focused on other end points (e.g., tissue N, Ca, Mn, Mg; total biomass, etc., Table 3). Thus, most of the available information focused on the effect of liming on soil alkalinity (and in the eastern U.S.), with other direct or indirect effects on the ecosystem much less studied.

Liming has been well studied for decades as a treatment for mitigating the acidifying effects from N and S deposition in the U.S. (Driscoll et al., 2001; Lawrence et al., 2016; Lawrence et al., 1999; Likens et al., 1996), Europe (Błońska et al., 2015; Frank and Stuanes, 2003), and China (Huang et al., 2014; Li et al., 2014). Given the historically high N and S deposition in the eastern U.S. and associated acidification effects, the geographic emphasis in our study makes sense, though clearly areas in the west also deserve attention. The application of lime restores nutrient and buffering base cations to the soil, enhances base saturation on soil exchange sites, reduces the mobility of aluminum (Al) which is phytotoxic to plants, and improves plant growth, health and recruitment. Our results of increased alkalinity are similar to a much larger global meta-analysis focused on recovery from N and S acidification (Reid and Watmough, 2014). Because both N and S deposition can acidify soils (and N increasingly so as S deposition decreases) lessons from Reid and Watmough (2014) and the associated literature are relevant. Reid and Watmough (2014) found in their meta-analysis of 110 peer-reviewed publications, that six of the seven end points evaluated had large significant and positive responses to liming and wood ash addition in forests (i.e., soil pH, base saturation, tree foliar Ca, tree growth, ectomycorrhizal fungi root colonization, and microbial indices), and only one did not have a significant response (soil C:N). They also found that base cation addition had a larger effect on increasing soil pH in the organic soil layer than in the mineral soil layer, consistent with the higher mineral content and slower responsiveness of the mineral layer to surficial applied treatments. Reid and Watmough (2014) also found greater effects with larger treatment magnitudes (e.g., with addition of lime over wood-ash, with the former having more base cations per unit mass than the latter), in more acidic soils, and in the organic layer of younger stands. Thus, as with other studies, liming is consistently shown to be an effective remediation treatment for soil acidification whether from N or S deposition.

Soil N availability was not examined in Reid and Watmough (2014), and their finding of no significant effect on soil C:N is not inconsistent with our results, as soil C:N changes much more slowly than soil available N (Booth et al., 2005). Furthermore, our finding of an increase in soil N availability is consistent with their reported increase in tree growth, even though increased tree growth could have been induced by other factors as well (e.g., reduced Al mobility, increased base cation availability). Our results on liming effects on soil N availability were only based on a single study (Cassidy et al., 2004), which added lime, N, and sawdust-sugar to an upland forest in Massachusetts. They reported an increase in nitrification and mineralization in the lime and N-addition plots relative to the sawdust-sugar, with the controls in between. An increasing body of literature on recovery from acid deposition suggests that increased N availability may be an unintended consequence of improvements in soil pH from reductions in S deposition (Evans et al., 2012; Johnson et al., 2018; Monteith et al., 2007; Oulehle et al., 2011). In more acidic soil, organic matter is more tightly retained in complexes with Al (de Wit et al., 1999), which reduces solubility (Clark et al., 2006). Thus, with increases in pH induced either by liming or recovery from acid deposition, more organic matter is available for mineralization that may then be measured in the extractable pools (Evans et al., 2012). This has been observed in forested watersheds and in downstream water bodies recovering from acidification, where organic losses from the forest floor leads to N leaching to downstream waterways (Johnson et al., 2018; Monteith et al., 2007; Oulehle et al., 2011).

It was somewhat surprising that no studies reported the effects of liming on plant biodiversity, given that most forest diversity is in the understory herb layer (Gilliam et al., 2006;Gilliam, 2014). This could reflect a historical bias for terrestrial liming studies to focus on acidification and soil or tree responses, our filtering process that required a focus on N, or both. The intersection of these two sub disciplines deserves more attention. Simkin et al. (2016) found that in more alkaline forested soils, N deposition tended to monotonically increase understory species richness, and that in acidic forest soils N deposition tended to increase then decrease understory species richness. Since liming is typically only applied to acidified soils, liming may end up reducing plant diversity if the subsequent increase in N availability induces competitive exclusion (Simkin et al., 2016). This may come at an additional loss of soil available N to adjacent waterways during the process of recovery if the plant community cannot take up the additional N. Increased N leaching can last a decade or longer (Oulehle et al., 2011), which could impact downstream ecosystems until leaching levels decline to some new equilibrium. Oulehle et al. (2011) found that decreases in S deposition in the Czech Republic between 1995 and 2009 (50 to 11 kg S ha^{-1} yr^{-1}; no changes in N deposition), reduced N leaching from high levels (13 kg N ha^{-1} yr^{-1}) to almost no leaching (<0.2 kg N ha^{-1} yr^{-1}) after 2006. Of this, net uptake by trees only accounted for 12.6%, leaching losses for 23.9% and mineral soil N accumulation for 64.3% (Oulehle et al., 2011). A number of studies from eastern North America also suggest a common pattern of declining nitrate leaching, as N deposition decreases, but these patterns may vary due to legacy effects from historical acid deposition, snow-pack dynamics, and other catchment-scale factors (Goodale et al., 2003; Judd et al., 2011; Kothawala et al., 2011). Thus, elevated N leaching, though transient, may be a negative and unintended consequence of liming forested soils.

Increases in soil N availability and leaching to waterways is not the indented outcome of remediation efforts from exposure to N deposition. However, if acidification is the dominant effect, (whether from N, S, or both), these effects may be inevitable without combining liming with other treatments. Only one study in the meta-analysis (Cassidy et al., 2004) and two in the full database (plus Cleavitt et al., 2011) had both carbon addition and liming as treatments, and neither of these examined them in combination. Acidified areas often have suppressed plant growth (Carter et al., 2017; Schaberg et al., 2002), and it may be difficult to synchronize the increased growth of desired plant species with increased soil N availability that occurs once recovery from acidification begins. These desirable plant species may not be present in the local community, and/or their growth may be sufficiently reduced to preclude their ability to respond. However, combinations of liming and carbon addition with or without seed addition may be a promising area for additional study. If the target plant community is still extant and healthy, then perhaps liming alone might be sufficient to induce recovery. If not, then liming alone may lead to either losses of N to waterways, or to sequestration of newly available N in undesirable plant species, further inhibiting recovery. Either way, there may be a lag period between the recovery of soil conditions and the ability of the plant community to respond, suggesting carbon addition as a temporary measure to sequester N locally in the microbial pool. This sequestered N may then be taken up by a recovering plant community. Thus, a careful diagnosis of the plant community, in addition to soil nutrient and acidity status, is needed to determine a remediation plan for an affected area.

There are several uncertainties that remain regarding the efficacy of liming to mitigate the effects of N deposition. First, more work is needed on endpoints other than soil alkalinity, including the processes that control the rate and duration of increased soil N availability (Oulehle et al., 2011; Oulehle et al., 2013), and whether these have positive or negative effects on plant community diversity. Second, a deeper understanding is needed on how the type of base cation source, the magnitude of treatment, and forest type and condition influence the soil alkalinity response (Reid and Watmough, 2014).

Effectiveness of prescribed burning to mitigate negative effects of nitrogen deposition

We found that prescribed burning had little utility in remediating the effects from N deposition, tending to increase soil N availability over the short term, have no effect on long-term soil N availability or soil alkalinity, and having countervailing effects on plant diversity. Prescribed burning is typically used to reduce fuel loads in order to protect human settlements, minimize the spread of insects, disease, and unwanted plant species, and promote the growth of desired plant species (Boerner et al., 2008; Ganzlin et al., 2016; Stephens et al., 2009). In the context of recovery from N deposition, prescribed burning is hypothesized to reduce the stocks of N in plant biomass and the upper soil horizon, reduce overall N availability and promote the establishment of diverse assemblages of native species over invasive species that may have come to dominate (Brockway, 1998; Cavender-Bares and Reich, 2012; Tilman, 1993). Prescribed burning also may increase light availability to the forest floor, create open sites for new propagules, or trigger seed release and germination in fire-adapted species, thereby promoting the establishment of new species that may have been locally extirpated (Tilman, 1993). On the other hand, prescribed burning also directly removes plant cover, which reduces plant uptake of available N and can lead to an increase in soil available N, N leaching, and/or erosion to nearby water bodies (Schoch and Binkley, 1986). The effect of fire also depends on the frequency and intensity of events, with intense events often damaging viable seeds and frequent events preventing their establishment. Overall, the effect of prescribed burning on soil N availability likely depends on the duration of study. Over the short term there are often observed net increases in soil N availability, from reduced plant uptake, increased mineralization and nitrification, or N released from fuels (Ficken and Wright, 2017; Gundale et al., 2005;

Schoch and Binkley, 1986), which may transition to net decreases or no change in soil N availability as a new equilibrium is established (Boerner et al., 2008; Ganzlin et al., 2016).

The short time duration of the FFS study (1-4 years), which made up the bulk of the prescribed burning effects in our database (Table S2), can partly explain our reported increase in soil available N. The only longer-duration study in the full database was Ganzlin et al. (2016) that re-measured soil N dynamics in one of the FFS sites after 11 years (Lubrecht Experimental Forest in Montana, USA). Ganzlin et al. (2016) found that the initial pulse in N availability after 1-4 years (Gundale et al., 2005), was not sustained after 11 years. Indeed, they found that all seven end points were not different from controls (O Horizon: NH_4^+, NO_3^-; Mineral soil: NH_4^+, NO_3^-, net ammonification, net nitrification, net N mineralization). This is consistent with the larger but shorter-duration meta-analysis of soil and vegetation N from the FFS study (Boerner et al., 2008), which found that although total soil and vegetation N decreased with burning after one year (due to direct removal by fire), these decreases relative to controls disappeared after years 2-5. Additionally, other research suggests that fire removes only a small fraction of the large mineral soil N reservoir and removal of soil N occurs only in the most severe wildfires (Johnson et al., 2008). Only two other studies included in the meta-analysis also examined prescribed burning and soil N availability. Ficken and Wright (2017) found from a study of three longleaf pine savanna sites in North Carolina that the initial pulse in soil extractable N following a burn was short lived to only a few weeks. Furthermore, only one of the three sites examined had sustained levels of higher soil extractable ammonium, and that was in the site where the understory vegetation had not returned (Ficken and Wright, 2017).

Prescribed burning was not found to affect any of the soil alkalinity. This lack of effect was reported after 1-3 years (Boener et al. 2008) and 11 years (Ganzlin et al. 2016). Thus, even though ash is typically alkaline, prescribed burns are lower-intensity fires that do not volatilize minerals (Boerner et al., 2008; Gundale et al., 2005) and thus do not lead to long term changes in soil alkalinity. Shorter-term studies have found increases in alkalinity following burning (Stephens et al. 2009), but these appear to be short-lived responses.

Prescribed burning did lead to subtle and countervailing changes in the plant community, with increases in species richness (P=0.054) and decreases in diversity indices (P=0.079) (Table 3, Figure 4). These results, though statistically weak, suggest that although the total numbers of species may increase, the communities become more and more dominated by fewer species. These trends are contradictory to the goals of remediating the effects of N deposition – i.e., increases in both native richness *and* diversity. We hypothesize that the decrease in diversity measures is likely due to increased growth of extant native species that were not removed by fire, and that were able to capitalize on increased soil available N. Whether this is a favored outcome is dependent on the desirability of the native species. Either way, given the short duration of the FFS study, (and that Ganzlin et al., 2016 did not assess the plant community), it is unknown whether these changes persist over time. There was only one other study in our dataset that assessed the effect of prescribed burning on plant diversity in forests (Brockway and Lewis, 1997), though many assessed the effect of prescribed burning on other plant responses. Brockway and Lewis (1997) found that although prescribed burning had little impact on overstory pines, cover of grasses increased significantly by up to 2500% and Galberry shrub (*Ilex glabra*) declined 33%. In a modeling study, Gimeno et al. (2009) concluded that only periodic prescribed burning, such as a burn interval of every 15 years, is needed to remediate N-saturated forest soils. However, in some situations burning too frequently can reduce ecosystem nutrient stocks resulting in decreased productivity (Johnson et al., 2009; Raison et al., 2009).

Thus, it appears that prescribed burning is not an effective treatment for remediating soil N conditions from chronic N addition, as: (1) short term losses from the fire itself or from the pulse in available N and subsequent leaching merely redirects the eutrophication problem to other terrestrial or aquatic ecosystems, (2) levels of total soil N are either not affected by fire, or are only affected short-term, and

(3) long term reductions in available soil N are not observed. Prescribed burning may be effective in inducing plant community recovery, but this remains uncertain due to the short-term nature of most studies included in our analysis. There are other goals that are clearly met with prescribed burning, including reducing risk and severity of future wildfires (Fiedler et al., 2010; Stephens et al., 2009), improved soil water status (Sala et al., 2005; Skov et al., 2004), and increased tree growth and photosynthetic rates (Sala et al., 2005). Thus, prescribed burning is still a very useful management practice for meeting other goals; however, remediation of long term N deposition may not generally be one of them.

Prescribed burning was the most studied treatment in our assessment, with 17 studies and 152 effect sizes across end points (Table 1). Nevertheless, significant uncertainties remain. Most of the information was from the FFS study; and, although this is a very robust national study examining many factors across forested areas in the U.S., it only ran for 4 years aside from individual site-specific follow up studies. More work generally is needed on the effect of fire severity and frequency. Forest type also clearly matters, as the ability of the target community to regenerate varies among forests.

Effectiveness of thinning to mitigate negative effects of nitrogen deposition

We found that thinning, like prescribed burning, had little utility in remediating the effects from N deposition, tending to increase soil N availability over the short term, with no long-term effect on soil N availability, and no or countervailing effects on the other two end points. Thinning is an approach that along with prescribed burning, is utilized to reduce fuel loads to protect human settlements and other factors not directly associated with N deposition (Boerner et al., 2008; Ganzlin et al., 2016). It has many of the same ecological effects as prescribed burning (opening new sites, increasing light availability, reduced plant N update), but with a few key differences. Thinning usually removes biomass in a patchy manner, and this slash may or may not be removed from the site. Prescribed burns affect an area more homogenously, and more of the biomass is volatilized compared with ash left on site. Thinning tends to remove more aboveground biomass carbon and N while prescribed burning removes more total biomass carbon and N because of the much larger removal of ground vegetation (Boerner et al., 2008). These differences can lead to subtle differences in effects. If slash from thinning is left onsite, either as fallen logs or chipped (Glitzenstein et al., 2016; Wolk and Rocca, 2009), then there is an abundant carbon-rich material, which may lead to enhanced soil N immobilization by microbes relative to prescribed burning.

We found that thinning had all the same directional effects as prescribed burning (Table 3, Figures 2-4). Extractable N increased less and non-significantly for thinning (+0.4 units, P=0.137) compared with prescribed burning that had a larger effect (+0.71, P=0.053). This likely occurred because burning removed more total biomass and thus reduced plant uptake more than thinning (Boerner et al., 2008). A weaker effect on extractable N from thinning compared with burning was probably not driven by increased immobilization in thinned plots from carbon-rich slash left behind, as mineralization increased though not significantly with thinning (P=0.134, Figure 2). The lack of a long-term effect on soil N cycling from prescribed burning was also found for thinning (Ganzlin et al., 2016). Similarly, the lack of a long-term effect from prescribed burning on forest floor and vegetation N was also found for thinning (Boerner et al., 2008).

Thinning also increased plant richness and decreased diversity, though less than prescribed burning and non-significantly (Table 3). The reason for these differences is unclear, but are likely driven by similar processes as with burning, and the weaker effect is also likely driven by the weaker increase in soil available N with thinning compared with burning. The only studies in our meta-analysis additional to the FFS that focused on thinning effects on the plant community were Ares et al. (2010) and Wolk and Rocca (2009). Wolk and Rocca treated a ponderosa pine site in Boulder CO, USA to thinning (with biomass removal if feasible), and thinning with chipping where the wood chips were re-distributed onto the site.

They found that total understory cover increased only slightly with any treatment, and this was mostly of non-native species. Treatment with- versus without-chippings responded differently in some instances, with the chippings increasing the litter layer and reducing native and non-native plant growth. Other studies mostly from grasslands have underscored the important influence that the litter layer can have on the plant community, reducing germination and biodiversity because of lower light levels (Clark and Tilman, 2010; Facelli and Pickett, 1991). In other ponderosa pine forests, thinning has been found to increase the abundance and species richness of herbaceous understory vegetation (Laughlin et al., 2006; Metlen and Fiedler, 2006), but not always (Metlen et al., 2004). On the other hand, Ares et al. (2010) reported results from the western Oregon Cascades that were more consistent with the FFS and our analysis, with increases in both native and introduced richness and cover, much more so from natives than introduced species. Ares et al (2010) found that, comparing control with plots thinned to both high density and medium density, early seral species increased by 3-15% in cover and 5-6 in richness, while introduced species only increased by 0.6-0.8% in cover and 1.1-1.2 in richness. The difference between these appears to be due to the degree to which the slash is removed (affecting the buildup of litter and availability of germination sites), the initial cover of the plant community, and the availability of local propagules of natives (affecting the ability to fill those new germination sites) (Ares et al., 2010; Wolk and Rocca, 2009). Thinning seems to have little or no effect on understory vegetation in forests growing at high latitudes or with understory plant communities having relatively low diversity (Ares et al., 2010). Thinning is a form of disturbance, and weedy often non-native species are often early colonizers to a disturbed site if they are locally present.

Thinning has also been applied and studied as an approach to minimize the large export of nitrate observed to occur following clearcutting at sites with a history of elevated atmospheric N deposition (Bormann et al., 1974; Burns and Murdoch, 2005). Studies have shown that thinning harvests can result in either no change (Kastendick et al., 2012) or slight increases in export of nitrate (Clinton, 2011), but where large increases have been measured, they have generally been much less than those that follow clearcutting (Wang et al. 2006). Evidence suggests that there may be a harvesting intensity threshold above which the relation between basal area removal and nitrate export steepens (Siemion et al., 2011; Wang et al., 2006). Many factors such as the evenness of the harvest, tree species composition, atmospheric N deposition levels, climate, soil drainage properties, and others affect the response of the N cycle to thinning harvests (Gundersen et al., 2006). As found in prescribed burning studies, application of a carbon source can maximize immobilization and minimize nitrate leaching following thinning (Homyak et al., 2008).

Thus, overall thinning does not appear to be an effective approach for reducing the elevated N status of forests from long term N enrichment for the same reasons as prescribed burning, but it may help in some forests recover forest biodiversity depending on the type of forest and initial conditions of the site. Although leaching was not specifically examined in this meta-analysis, forest thinning may be a promising approach to reduce nitrate leaching over the long term as the forest regrows (though not over the short term) as opposed to more intensive harvesting in areas of active forestry (Siemion et al., 2011; Wang et al., 2006).

There are several uncertainties that remain with respect to the efficacy of thinning as a remediation approach. Many of these are shared with prescribed burning discussed above (e.g., dependence on the FFS, short time durations, frequency and severity of thinning, different types of forest types, soil, and climate, etc.). However, some are unique to thinning and worth elaborating upon briefly. Removing versus not removing slash was found to have significant effects on several aspects of community recovery in Wolk and Rocca (2009). It appears that leaving slash on site may be better for soil health and in some cases the plant community. However, the slash often is a merchantable product that creates tradeoffs for decision makers in how to apply treatments. Either way, thinning is often more time consuming and costly than prescribed burning, with costs as high as $1000 per acre as opposed to as little as $86 per acre for prescribed burns. Thus, thinning is usually utilized when fire is not possible due to hazardous burn conditions (Wolk and Rocca, 2009), and even then, its utility to remediate the effects of N deposition may be limited. Nevertheless, as with prescribed burning, there are other management goals that decision makers much weigh that thinning may meet when prescribed burning is not an attractive option.

Conclusions

The relative global importance of N deposition as a stressor is likely to increase in the future, as N deposition increases in Asia and Africa, and as N deposition declines less than S deposition in Europe, the U.S., and Canada. Management interventions may be necessary to promote recovery, as these ecosystems have been exposed to elevated N deposition for many decades (Clark et al., 2018), and decreased deposition alone may not be sufficient to induce recovery over timescales desired by decision makers (see Gilliam et al. 2019, Schmitz et al, 2019). Here we found that no single treatment was effective in promoting recovery from N deposition for all three responses of interest (i.e., decreased soil available N, increased soil alkalinity, increased plant biodiversity), suggesting combinations of treatments should be explored, especially for situations where both acidification and eutrophication impacts occur. In particular, the combination of carbon addition and liming may hold promise, with carbon addition reducing N availability and liming increasing alkalinity. Our conclusions on the efficacy of carbon addition in forests are largely inferential from the large body of work in grasslands and deserves more attention in forests. Both liming and carbon addition may promote the recovery of the plant community, but many uncertainties remain due to low numbers of studies of carbon addition in forests overall, and low numbers of liming studies examining impacts on plant biodiversity.

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[1] Permanent url generated following acceptance.

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Tables and Table Captions

Table 1: Response categories and individual metrics.

Response category	Individual metrics
Soil N availability	Ammonium, inorganic N, mineralizable N, N mineralization, net ammonification, nitrate, nitrate N, nitrification, net nitrification, net N mineralization
Soil alkalinity	pH, base saturation, exchangeable Ca, K, or Mg
Plant community diversity	species richness, Shannon diversity index, Simpson diversity index

Table 2: Summary of the literature included in the meta-analysis. Shown below are the number of studies out of 29 (and individual effects out of 408 in parentheses) that examined the effect of each treatment on each category of response (note one study could use multiple treatment levels, as well as address multiple response categories, and/or multiple metrics within a response category).

	Studies (effects)			
	Overall	Soil N availability	Soil alkalinity	Plant Diversity
Carbon addition	2 (12)	1 (8)	1 (2)	1 (2)
Liming	9 (101)	1 (8)	9 (93)	0 (0)
Prescribed burning	17 (152)	13 (46)	12 (40)	10 (66)
Thinning	13 (143)	10 (35)	9 (22)	10 (86)

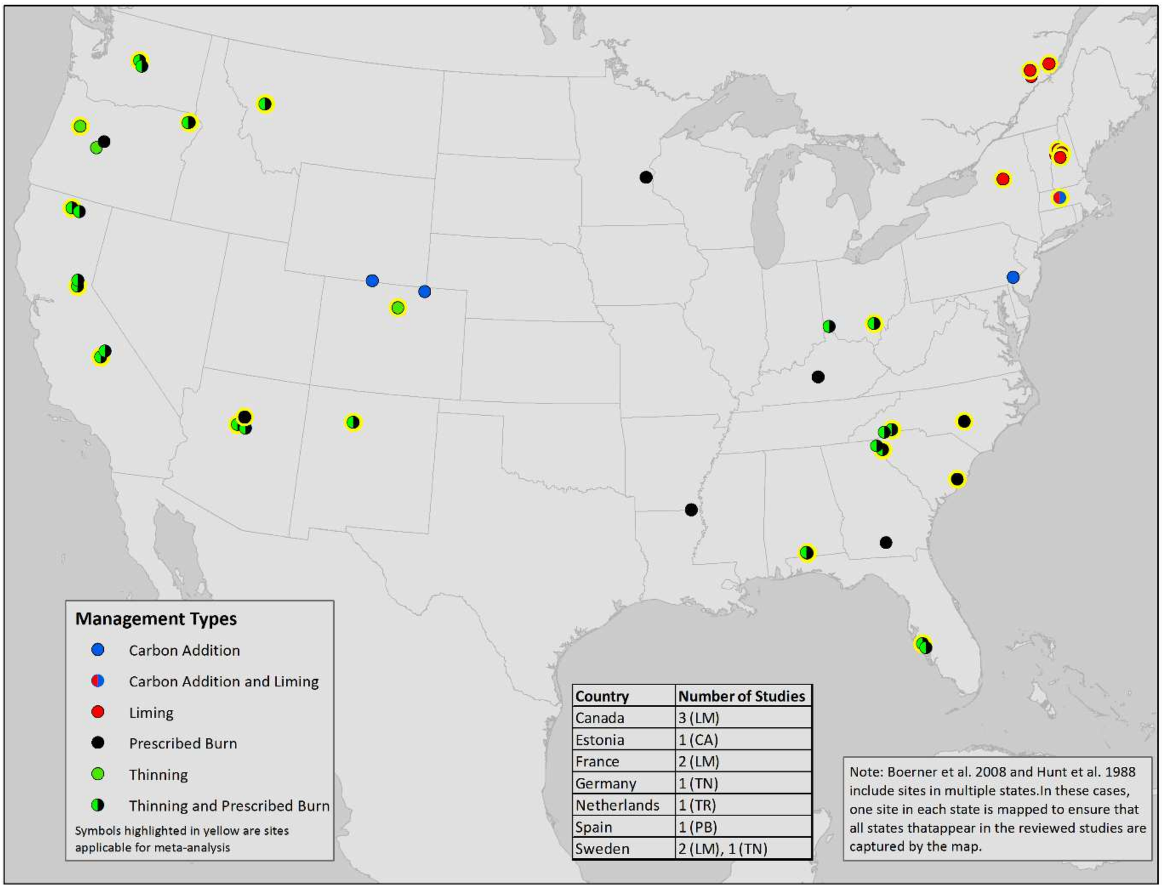
Table 3: Summary of statistical results from the meta-analysis. Shown below are the standard mean differences (SMDs) for soil N availability and back-transformed % difference (soil alkalinity and plant diversity for each of three responses for each of four treatments .

Response category	Metric(s)	Carbon addition	Liming	Prescribed burning	Thinning
Soil N availability (SMDs)	All	-1.8***	1.2*	0.4†	0.5*
	Extractable N	-1.8**	1.0†	0.7**	0.4
	Net Nitrification /Mineralization	NA	NA	0.1	0.4
Soil alkalinity (RR)	All	-2.7	48.6***	2.9	-0.9
	pH	-3.8	10.5***	2.8	-2.5
	Base cations	NA	82.2***	4.1	2.1
Plant Diversity (RR)	All	-8.9	NA	5.0	6.1
	Species richness	-6.6	NA	18.1†	12.6
	Diversity	-11.1	NA	-7.9†	-4.0

†, P<0.1; *, P<0.05; **, P<0.01; ***, P<0.001. NA indicates that this combination of treatment and effect was not present in the database.

Figures and Legends

Figure 1: Map of study locations and treatments. Shown are the locations of the 46 studies included in the full database for the U.S. and Canada (other studies outside the map domain in the table inset), with the subset of 29 highlighted in yellow with sufficient reporting that were used in the meta-analysis.



Country	Number of Studies
Canada	3 (LM)
Estonia	1 (CA)
France	2 (LM)
Germany	1 (TN)
Netherlands	1 (TR)
Spain	1 (PB)
Sweden	2 (LM), 1 (TN)

Figure 2: Soil N responses. Shown are the treatment effects (and 95% CIs) in standard deviation units for each of the four treatments relative to controls from the Standardized Mean Difference analysis. Responses include all soil N availability metrics combined (blue), extractable N (green), and net rates of mineralization or nitrification (red). Metrics associated with each analysis are shown in Table S4 and effects from individual studies are shown in Figure S1.

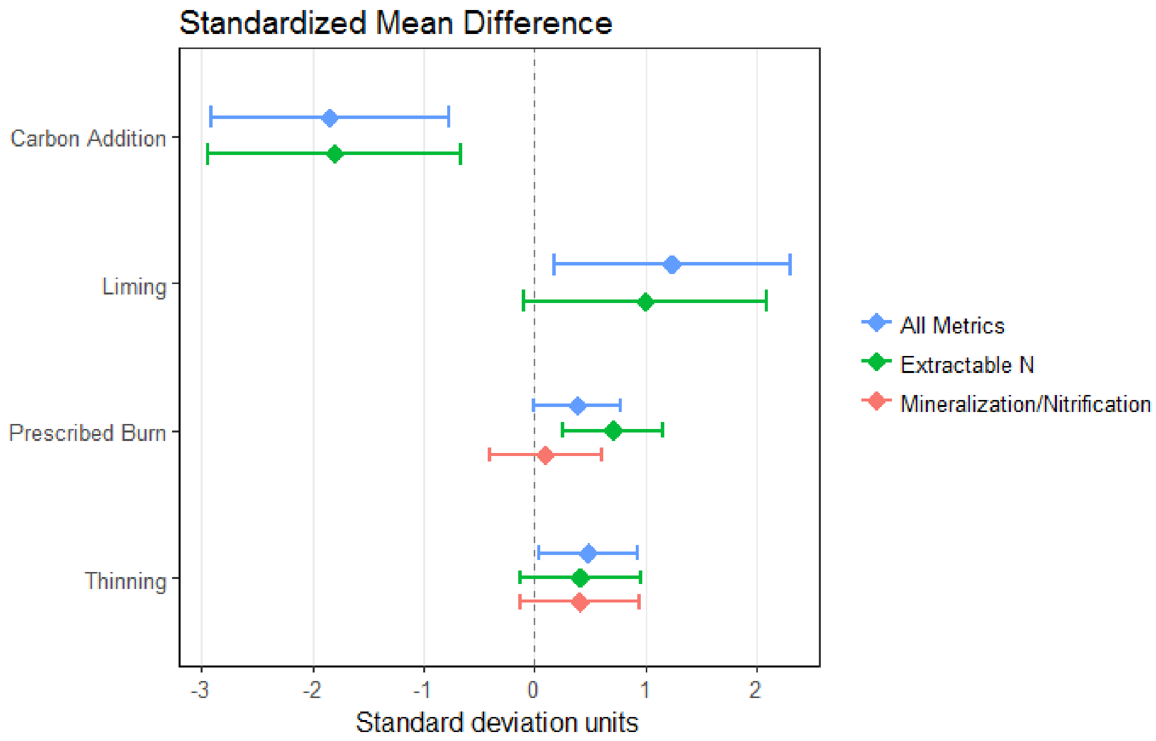


Figure 3: Soil alkalinity responses. Shown are the back-transformed percent differences (and 95% CIs) for each of the four treatments relative to controls from the response ratio meta-analysis. Responses include all soil alkalinity metrics combined (blue), base cations (green), and soil pH (red). Metrics associated with each analysis are shown in Table S4 and effects from individual studies are shown in Figure S2. Note that 95% CIs on back-transformed variables may not represent significance accurately, see Table 2 for statistical tests.

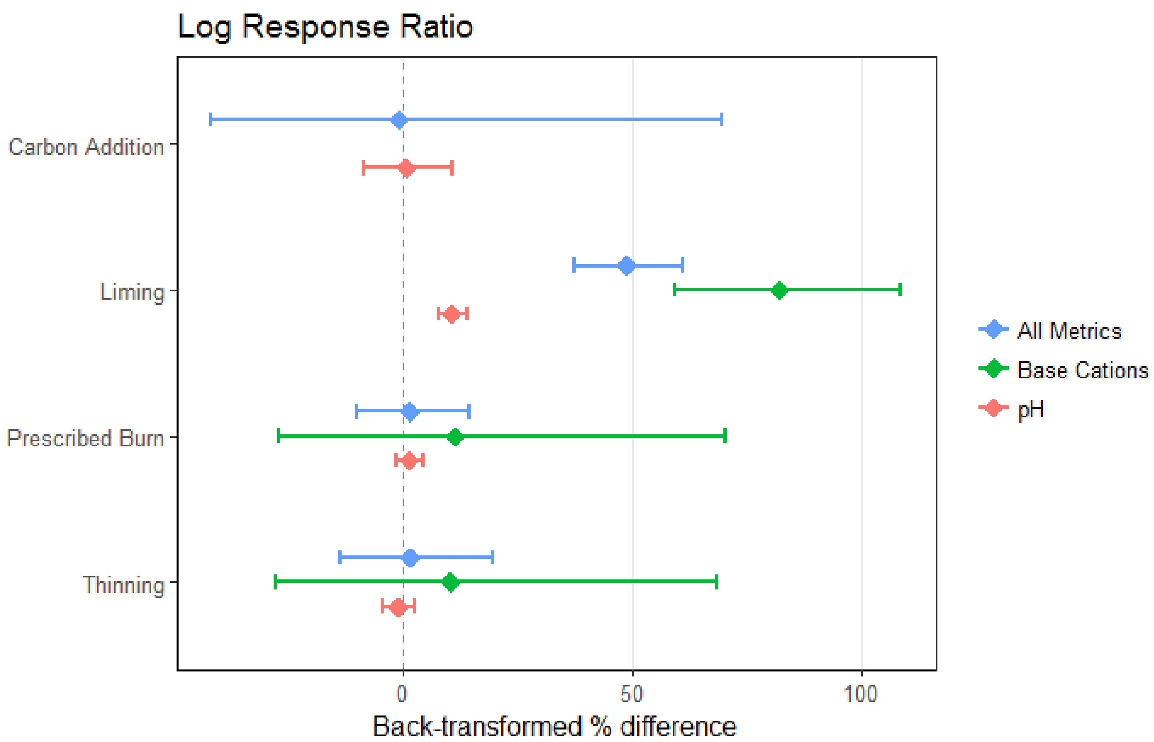
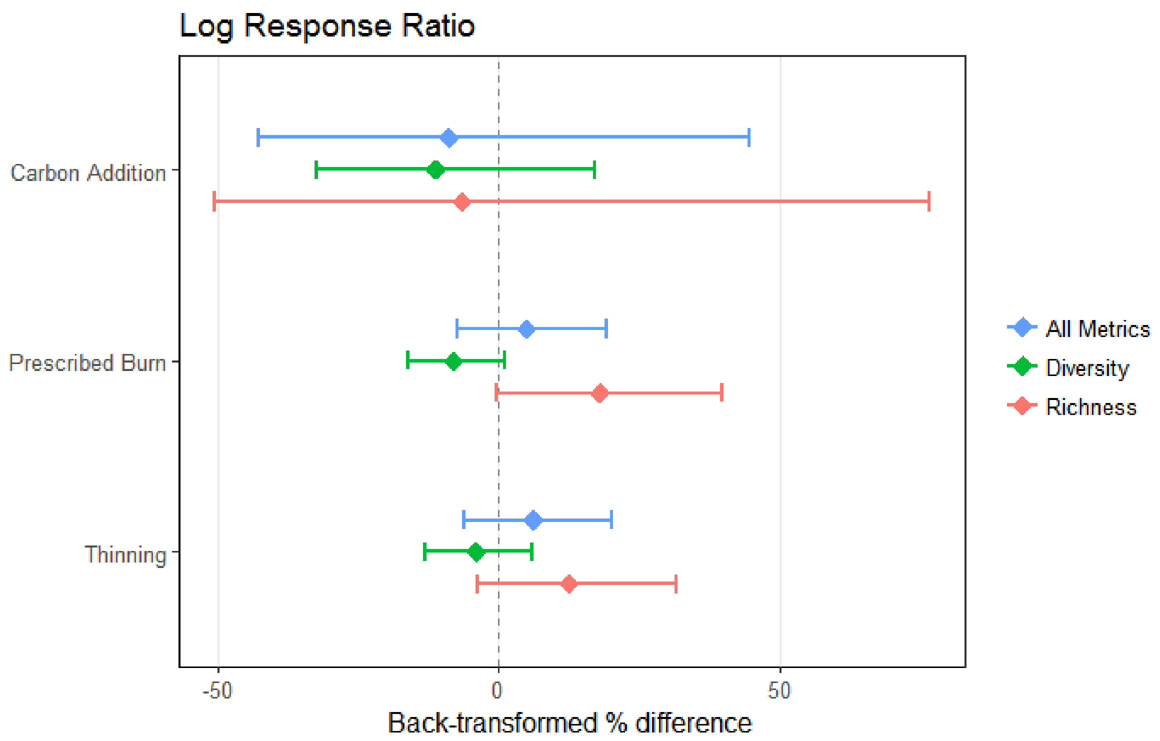


Figure 4: Tree-plot of treatment effects for plant community response metrics. Shown are the back-transformed percent differences (and 95% Cis) for each of the three treatments relative to controls from the response ratio meta-analysis. Responses include all plant biodiversity metrics combined (blue), diversity metrics (green: Simpson and Shannon), and species richness (red). Metrics associated with each analysis are shown in Table S4 and effects from individual studies are shown in Figure S3. There were no liming studies that examined plant biodiversity. Note that 95% CIs on back-transformed variables may not represent significance accurately, see Table 2 for statistical tests.



Supplementary Material

Supplemental Tables

Supplemental Table 1: Keywords used. All combinations of the keywords below were searched using Web of Science (October 2017). The query had to include one entry from each category (i.e., management type, ecosystem type, nutrient). The titles of these were then read for relevance.

MANAGEMENT METHOD +	ECOSYSTEM TYPE +	NUTRIENT
Burn	Forest	Nitrogen
C addition		Acidification
Carbon Addition, C addition		Eutrophication
Cutting		
Fire		
Grazing		
Harvest		
Liming		
Management		
Mitigation		
Mowing		
Recovery		
Remediation		
Restoration		
Seed Addition		
Sod Removal		
Topsoil Removal		
Turf Stripping		

Supplemental Table S2: Summary of the 29 references used in the meta-analysis. An "X" indicates that either that treatment or response category was examined.

		Treatment				Response category			
Reference	Study Area	Carbon addition	Liming	Prescribed burning	Thinning	Soil N	Alkalinity	Plant Biodiversity	Effect sizes
Alcaniz et al. 2016	Montgrí Massif, Catalonia, Spain			X			X		3
Ares et al. 2010	Keel Mountain, Oregon, USA				X			X	30
Binkley et al. 1992	Francis Marion National Forest, South Carolina, USA			X			X		16
Cassidy et al. 2004	Quabbin Reservoir, Massachusetts, USA	X	X			X	X		20
McIver et al. 2016	Blue Mountains, Oregon, USA			X	X	X	X		12
McIver et al. 2016	Central Appalachian Plateau, Ohio, USA			X	X	X	X	X	20
McIver et al. 2016	Central Sierra Nevada, California, USA			X	X	X	X		10
McIver et al. 2016	Florida Coastal Plain, Florida, USA			X				X	4
McIver et al. 2016	Gulf Coastal Plain, Alabama, USA			X	X	X	X	X	24
McIver et al. 2016	Northeastern Cascades, Washington, USA			X	X			X	12
McIver et al. 2016	Northern Rocky Mountains, Montana, USA			X	X	X	X	X	40
McIver et al. 2016	Southeastern Piedmont, South Carolina, USA			X	X	X	X	X	28
McIver et al.	Southern Appalachian Mts.,			X	X	X	X	X	17

2016	North Carolina, USA								
McIver et al. 2016	Southern Cascades, California, USA			X	X	X	X	X	21
McIver et al. 2016	Southern Sierra Nevada, California, USA			X		X	X	X	19
McIver et al. 2016	Southwestern Plateau, Arizona, USA			X	X	X	X	X	12
Ficken and Wright 2017	Fort Bragg Military Reservation, North Carolina, USA			X		X			6
Fisk et al. 2006	Hubbard Brook Experimental Forest, New Hampshire, USA		X				X		4
Ganzlin et al. 2016	Lubrecht Experimental Forest, Montana, USA			X	X	X			14
Hawley et al. 2006	Hubbard Brook Experimental Forest, New Hampshire, USA		X				X		1
Homan et al. 2016	Honnedaga Lake, New York, USA		X				X		4
Johnson et al. 2014	Hubbard Brook Experimental Forest, New Hampshire, USA		X				X		36
Koorem et al. 2012	Koeru, Estonia	X						X	2
Lofgren et al. 2009	Bråtängsbäcken, Gårdsjön IM, Lommabäcken, and Ringsmobäcken, Sweden		X				X		8
Ouimet and Moore 2015	Montmorency Experimental Forest, Quebec, Canada		X				X		30
Ouimet et al. 2017	Duchesnay, Quebec, Canada		X				X		4
Rizvi et al. 2012	Vosges Mountains, France		X				X		4
Wolk and Rocca 2009	Heil Valley Ranch, Colorado, USA				X			X	4
Wright and Hart 1997	Fort Valley Experimental Forest, Arizona, USA			X		X			3
	Sum	2	9	17	13	14	21	13	408

Supplemental Table S3: Full Data Table. See EPA’s Environmental Data Gateway for the full dataset (https://edg.epa.gov).

Supplemental Table S4: Binning of individual metrics into different analyses.

		Soil N Availability			Soil alkalinity			Plant Community Diversity		
Response category	Metric	All	Extractable N	Net nitrification /mineralization	All	pH	Base cations	All	Species richness	Plant diversity
Soil N availability	Ammonium	X	X							
	inorganic N	X	X							
	mineralizable N	X								
	N mineralization	X		X						
	net ammonification	X		X						
	nitrate	X	X							
	nitrate N	X	X							
	nitrification	X		X						
	net nitrification	X		X						
	net N mineralization	X		X						
Soil alkalinity	pH				X	X				
	base saturation				X		X			
	exchangeable Ca				X		X			
	exchangeable K				X		X			
	exchangeable Mg				X		X			
	Ca:Al				X		X			
Plant community diversity	species richness							X	X	
	shannon diversity							X		X
	simpson diversity							X		X

Supplemental Table 5: Full statistical results (see separate file).

Supplemental Figures

Figure S1: Tree-diagram of soil nitrogen availability responses to carbon addition (CA), liming (LM), prescribed burning (PB) and thinning (TN) using standardized mean difference (SMD). Points to the right indicate more soil available N relative to controls. Shown below are the effect metric means (points) and standard deviation (bars), from each study, and the overall effect of each treatment.

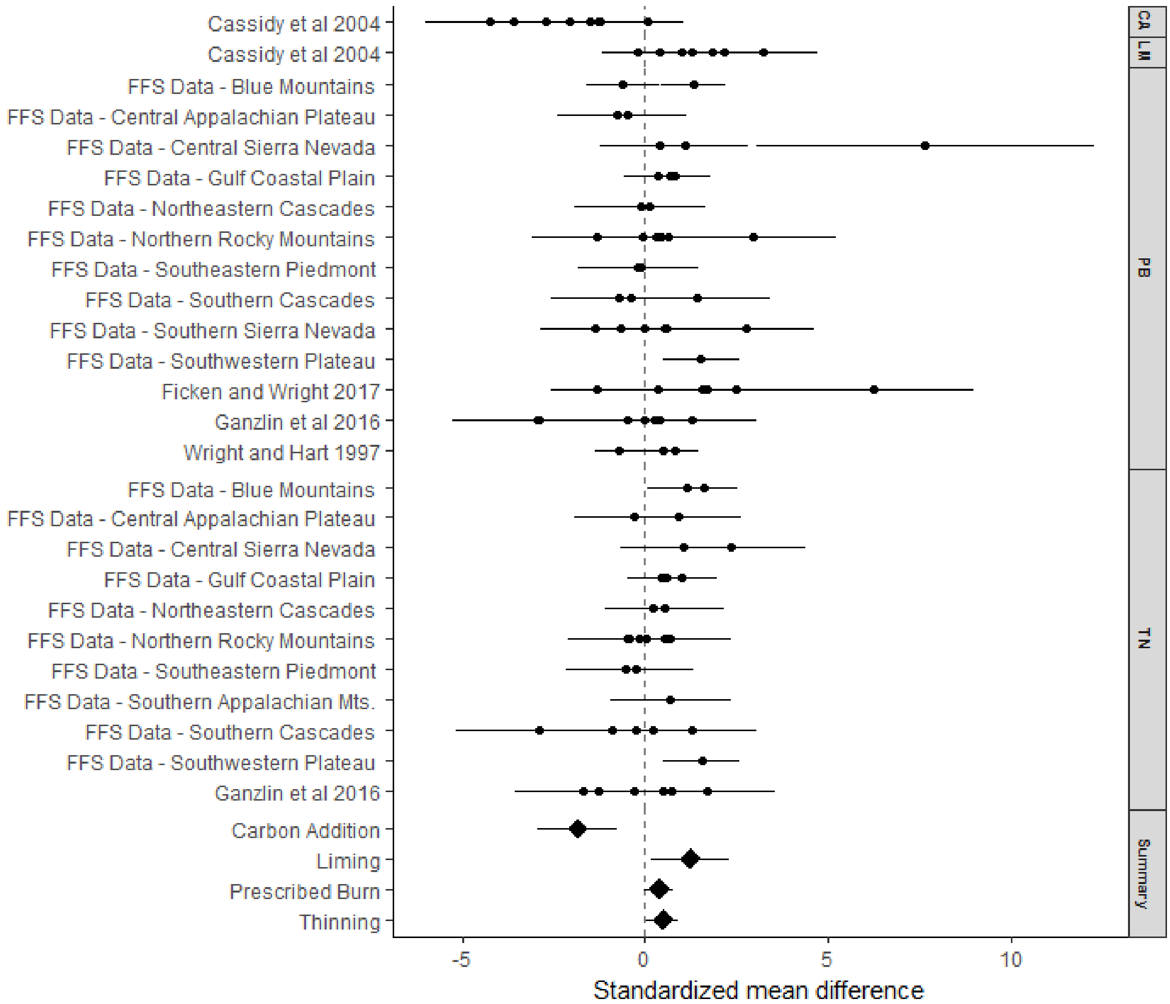


Figure S2: Tree-diagram of soil alkalinity responses to carbon addition (CA), liming (LM), prescribed burning (PB) and thinning (TN) using log-transformed response ratios. Points to the right indicate more soil alkalinity relative to controls. Shown below are the effect metric means (points) and standard deviation (bars), from each study, and the overall effect of each treatment.

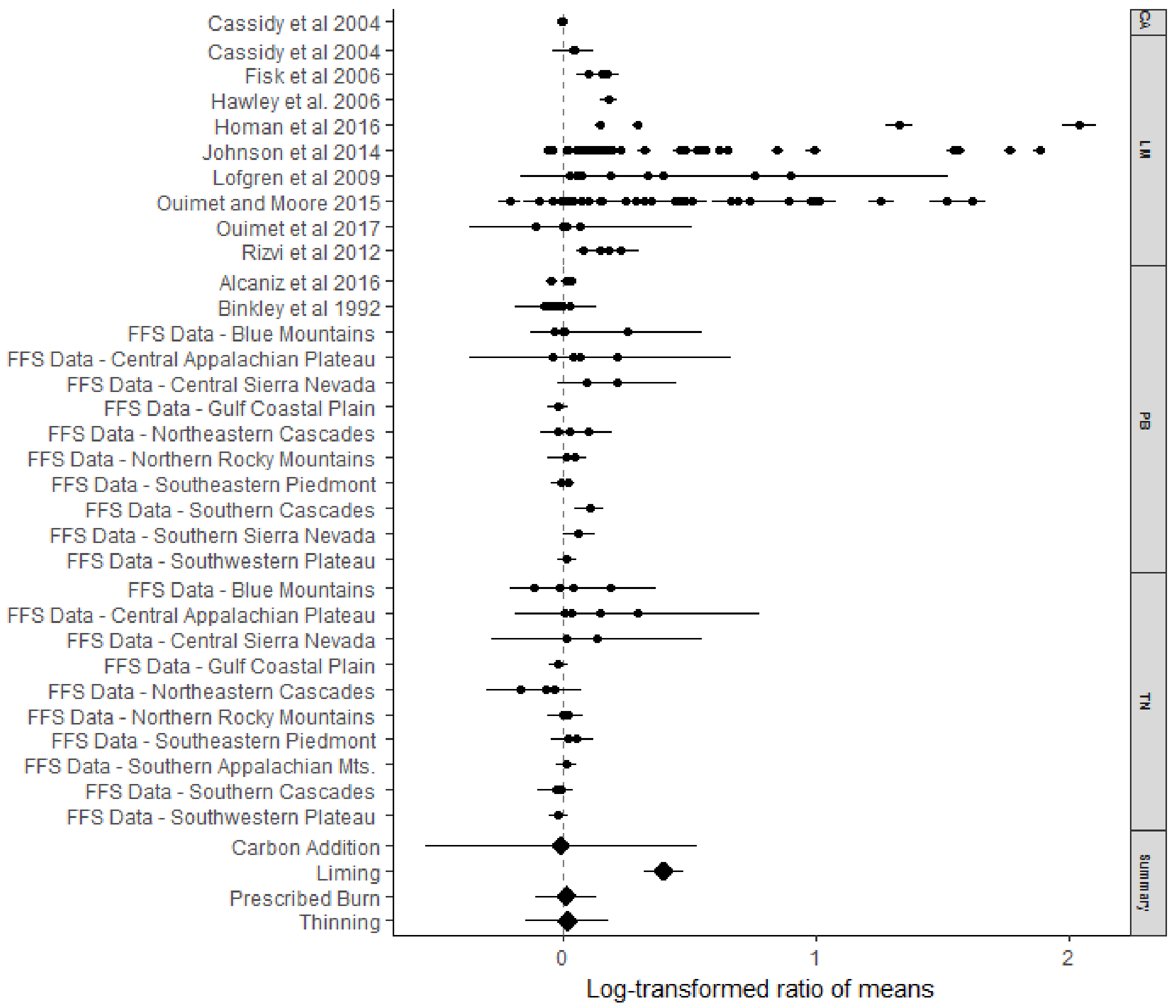
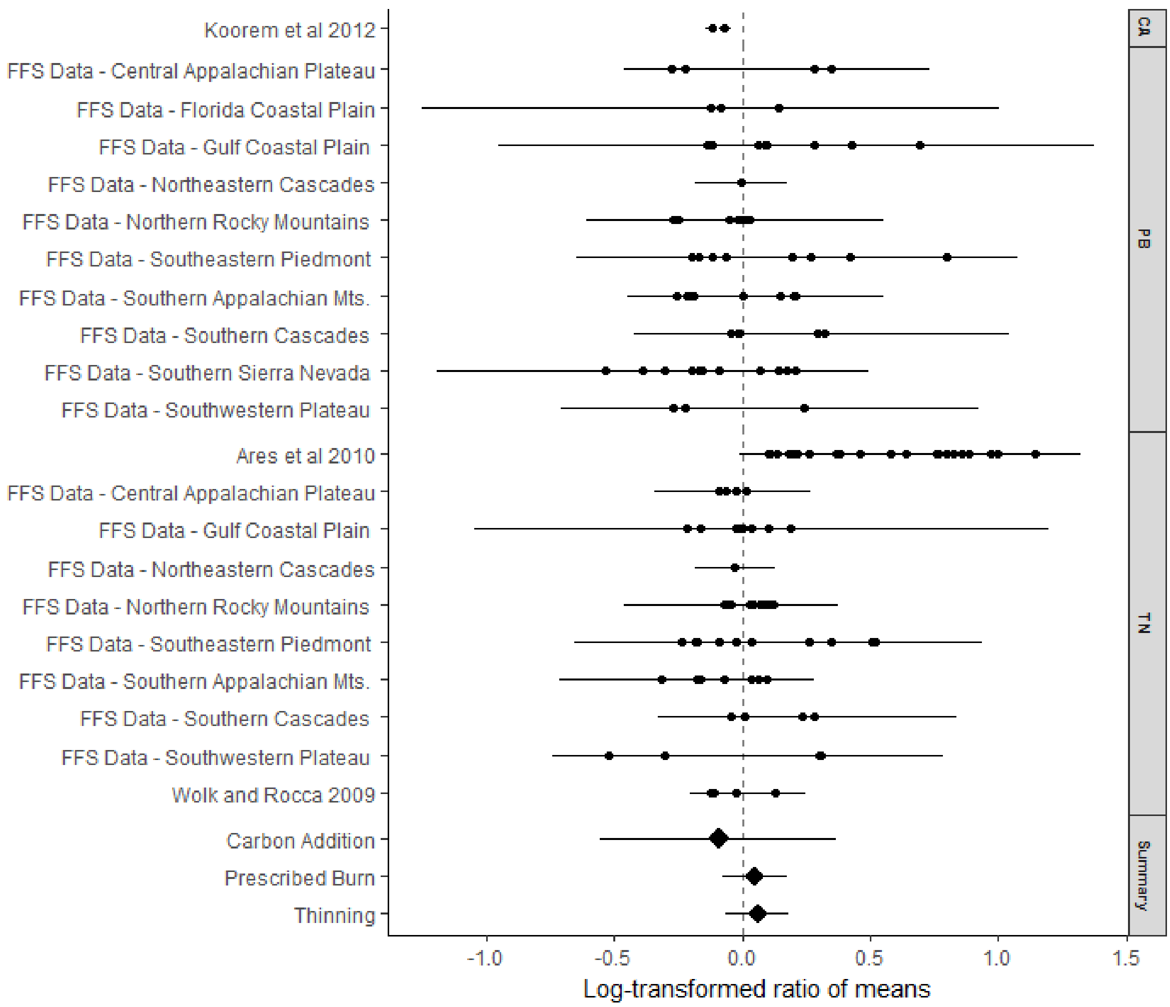


Figure S3: Tree-diagram of plant community diversity responses to carbon addition (CA), prescribed burning (PB) and thinning (TN) using log-transformed response ratios. Points to the right indicate more plant biodiversity relative to controls. Shown below are the effect metric means (points) and standard deviation (bars), from each study, and the overall effect of each treatment.



Highlights:

- No single factor improved forest soil N availability, alkalinity, and biodiversity.
- Only carbon addition reduced N availability, only liming increased alkalinity.
- Prescribed burning and thinning had weak or undesirable effects on responses.
- Results are not consistently reported in the literature to support meta-analysis.
- Several treatments may be needed to promote forest recovery from N deposition.