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Review

Response of Temperate Forest Ecosystems under Decreased Nitrogen Deposition: Research Challenges and Opportunities

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Abstract: Although past increases in emissions and atmospheric deposition of reactive nitrogen (N_r) provided the impetus for extensive research investigating the effects of excess N in terrestrial and aquatic ecosystems, the Clean Air Act and associated rules have led to decreases in emissions and deposition of oxidized N, especially in the eastern U.S., but also in other regions of the world. Thus, research in the near future must address the mechanisms and processes of recovery for impacted forests as they experience chronically less N in atmospheric depositions. Recently, a hysteretic model was proposed to predict this recovery. By definition, hysteresis is any phenomenon in which the state of a property depends on its history and lags behind changes in the effect causing it. Long-term whole-watershed additions of N at the Fernow Experimental Forest allow for tests of the ascending limb of the hysteretic model and provide an opportunity to assess the projected changes following cessation of these additions. A review of 10 studies published in the peer-reviewed literature indicate there was a lag time of 3–6 years before responses to N treatments became apparent. Consistent with the model, I predict significant lag times for recovery of this temperate hardwood ecosystem following decreases in N deposition.

Keywords: decreased N deposition; forest recovery; hysteresis; temperate hardwood forests; Fernow Experimental Forest

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1. Introduction

Historic increases in atmospheric deposition of reactive nitrogen (N_r, primarily NH_4^+ and NO_3^-, but including numerous other reactive species [1]), and modeled projections for future increases on a global scale, have led to a proliferation of studies on the effects of excess N on aquatic and terrestrial ecosystems over the past several decades. Galloway et al. [2] estimated that the total global atmospheric deposition of NH_4^+ and NO_3^- in terrestrial ecosystems increased from 17 Tg N yr^{-1} in 1860 to 64 Tg N yr^{-1} in the early 1990s. They also projected further increases to 125 Tg N yr^{-1} by 2050, a >7-fold increase during this time period. Bobbink et al. [3] predicted similar increases in N deposition by 2030. Although most terrestrial ecosystems studied were initially herb- and grass-dominated [4,5], recent decades have witnessed an expansion of studies in forest ecosystems [6–13]. Seminal papers on then-new perspectives of N biogeochemistry, e.g., [14–16], changed our views of N in forest ecosystems from a predominantly growth-limiting nutrient to one whose excess could threaten the structure and function of forests, including net primary productivity and biodiversity, a phenomenon called N saturation [17].

Understanding the general responses of temperate forests to changes in N biogeochemistry is of particular importance because of their (1) global distribution (Figure 1), (2) high biodiversity, and (3) close proximity to high densities of human populations [18]. Early predictions for temperate forests in response to increasing N deposition included increased nitrification leading to leaching of NO_3^- and the associated loss of nutrient cations (Ca^{2+}, Mg^{2+}, K^+) [16,17]. Although most of these predictions were initially—and continue to be—tested and refined via field N manipulation studies, e.g., [19], enhanced NO_3^- and cation leaching was also observed on the long-term untreated reference watershed (WS4) at Fernow Experimental Forest (FEF), West Virginia, based on stream chemistry data from 1969 to 1990 [20]. Peterjohn et al. [20] further identified seven symptoms of N saturation at FEF, including high relative rates of net nitrification, relatively high concentrations of NO_3^- in soil solution, low seasonal variability in stream NO_3^- concentrations, high loss of NO_3^- from an aggrading forest, a rapid increase in NO_3^- loss following fertilization from an aggrading forest, and low retention of inorganic N compared to other forested sites. They concluded that untreated watersheds at FEF were perhaps the best example of a temperate forest that had undergone N saturation via ambient deposition of N.

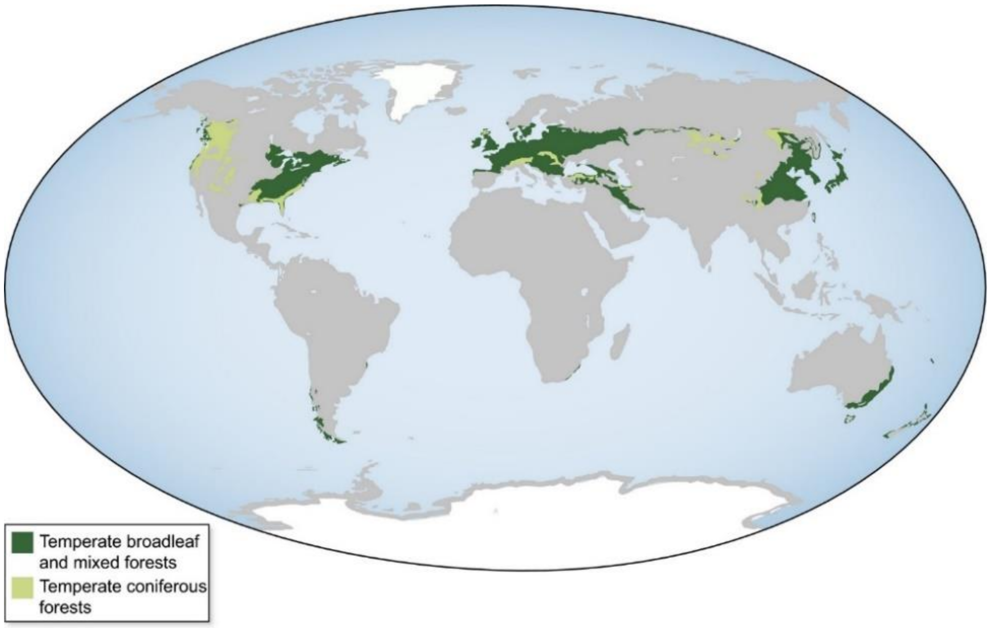

Figure 1. The distribution of temperate forests. Reprinted with permission from ref. [18]. Copyright 2016 Gilliam.

Other research in temperate forests has examined the effects of excess N on plant biodiversity, microbial communities, and forest health. In general, chronic increases in N inputs have decreased the diversity of the herbaceous layer [3,11,21], altered the structure and composition of soil microbial communities [22], and the threatened the growth and vitality of some temperate forests [23]. How these ecosystem properties will respond in the future, however, remains an open, and important, question.

The Clean Air Act (CAA) of 1970 in the U.S. and similar environmental regulations worldwide have been exemplars of environmental legislation, leading to global-scale improvements in many facets of environmental health, including lower human mortality rates in the U.S. [24]. Initially targeting anthropogenic emissions of sulfur, subsequent rules addressed emissions of N, leading to reductions of >50% from vehicles and power plants in the U.S. [25]. On the other hand, the focus of the CAA has been on N oxides, rather than reduced forms of N, such that temporal trends of N deposition vary between oxidized versus reduced N (Figure 2). Thus, although total deposition of NO_3^- peaked in the mid-1990s and is currently declining throughout most of the U.S. [25,26], total deposition of NH_4^+ has either increased of remained stable [27,28].

This recent trend in atmospheric deposition of N, at least for NO_3^-, challenges some of the earlier models predicting future increases in N deposition, e.g., [2,3], and alters the way N biogeochemists must think about N-impacted ecosystems in the future. Recent papers have hypothesized several future scenarios for changes in terrestrial ecosystems in response to reduced levels of atmospheric N input [29–33]. Gilliam et al. [28] proposed a hysteretic model to predict future changes in forests of eastern North America, given current patterns of declines in atmospheric deposition of N (Figure 3). Hysteresis is a phenomenon in which the state of a property depends on its history and lags behind changes in the effect causing it. Thus, it is a system property wherein output is not a strict function of corresponding input, resulting in a response to decreasing inputs that exhibits a different trajectory than the response to increasing inputs.

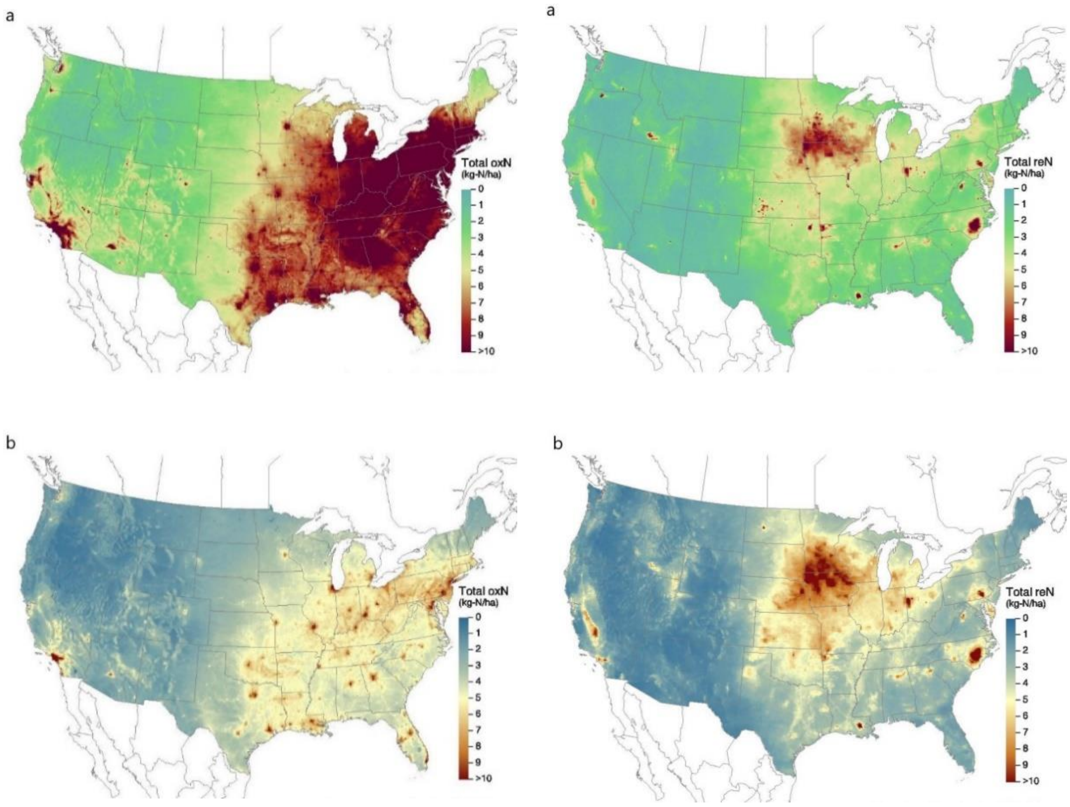

Figure 2. Total oxidized N and total reduced N deposition. Figures marked (**a**) are from 2000; figures marked (**b**) are from 2014. Reprinted with permission from ref. [28]. Copyright 2019 Gilliam et al.

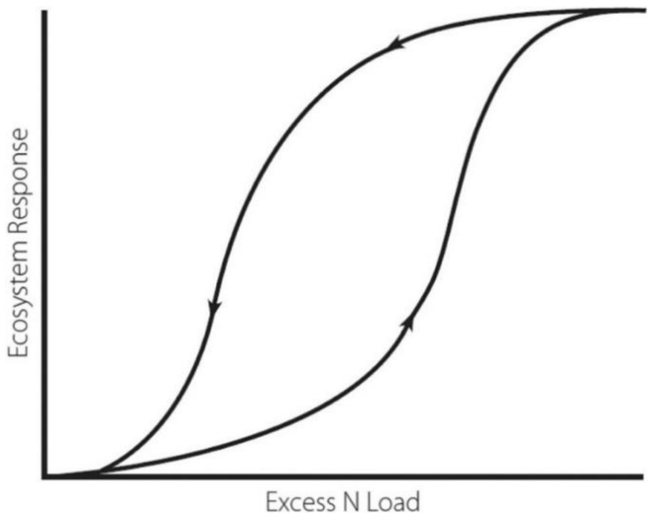

Figure 3. Hysteretic model for responses of terrestrial ecosystems to atmospheric deposition of N. Note lack of units and variables, as this is a conceptual model, with variables and units varying by ecosystem process and N status of the ecosystem. Reprinted with permission from ref. [28]. Copyright 2019 Gilliam et al.

With this in mind, the curvilinear nature of the hysteretic model when applied to important ecosystem responses at FEF (e.g., plant diversity and soil nutrient availability) suggests that initial effects may have been buffered and slow to occur after experimental increases in N deposition. Following declines in atmospheric N inputs, the hysteretic model predicts varying lag times in the recovery of virtually all components of temperate forest ecosystems, including soil nutrients and microbial communities, plant biodiversity, and surface water chemistry toward conditions prior to N saturation as deposition of N continues to decline.

The purpose of this paper is to use results from a long-term experiment at FEF to assess the hysteretic model of ecosystem response for a forest during a time of elevated N inputs, and to consider its implications for the recovery of forest ecosystem processes during a period of declining N inputs. First, I describe FEF as a study site, along with a general overview of field design and sampling associated with numerous investigations over the past three decades on the effects of whole-watershed additions of N. Next, I summarize the findings of those studies in the context of the hysteretic model. Finally, I describe future directions for work at FEF and elsewhere as N biogeochemists address this relatively new paradigm of decreasing N deposition, especially in the context of climate change.

2. Research at Fernow Experimental Forest

2.1. Background

Forest ecological research at FEF has a long, productive history [34], with many efforts initially focused on silvicultural practices [35]. The collection of hydrochemical data for the long-term reference watershed (WS4) began in 1951. Investigations into the effects of acid deposition were initiated via the Fernow Watershed Acidification Study (WAS), beginning as a now-terminated pilot study in 1987 on a watershed adjacent to FEF. The study was established on FEF watersheds in 1989 and remains on-going. A notable characteristic of the WAS is that it employs a whole-watershed application of simulated acid deposition via three aerial additions of $(NH_4)_2SO_4$ per year as a solid powder by fixed- and variable-wing aircraft, representing a total N addition of 35 kg N ha^{-1} yr^{-1}, and it was one of few studies utilizing watershed-scale simulations of atmospheric deposition. After three decades, the $(NH_4)_2SO_4$ additions were discontinued in 2019, creating the unique opportunity to examine experimentally the recovery of a temperate hardwood forest ecosystem following a significant decrease in N inputs [34].

2.2. Site Description

FEF comprises approximately 1900 ha of the Allegheny Mountain section of the unglaciated Allegheny Plateau near Parsons, West Virginia (39°03′16″ N, 79°41′0″ W). Mean annual precipitation is approximately 1430 mm yr^{-1}. Concentrations of acid ions in wet deposition (i.e., H^+, $SO_4^=$, and NO_3^-) were once among the highest in North America. Soils of the experimental watersheds are coarse-textured Inceptisols (loamy-skeletal, mixed mesic Typic Dystrochrept) of the Berks and Calvin series sandy loams largely derived from sandstone [34].

Forest stands of FEF watersheds are composed of mixed hardwood species generally varying with age. Young watersheds support early-successional species, such as black birch (*Betula lenta* L.), black cherry (*Prunus serotina* Ehrh.), and yellow-poplar (*Liriodendron tulipifera* L.), whereas older watersheds support late-successional species, such as sugar maple (*Acer saccharum* Marshall) and northern red oak (*Q. rubra* L.) [34]. Herbaceous layer communities initially exhibited less age-related variation, and included wood-nettle (*Laportea canadensis* (L.) Wedd.), violets (*Viola* spp.), and several ferns [36].

2.3. Field Design

Although FEF has numerous experimental watersheds that have been, and continue to be, studied in a variety of contexts, the WAS focused on three watersheds (Figure 4). WS4 supports >100 yr-old even-aged stands and has served as the long-time reference watershed at FEF, whereas WS7 supports >40 yr-old even-age stands, and both are used as untreated watersheds of contrasting stand ages. WS3 supports an approximately 40 yr-old even-age stand and serves as the treatment watershed, receiving three aerial applications of $(NH_4)_2SO_4$ yr^{-1}, beginning in 1989 and extending to 2019. March (or sometimes April) and November applications were approximately 7.1 kg N ha^{-1}; July applications were approximately 21.2 kg N ha^{-1} [34].

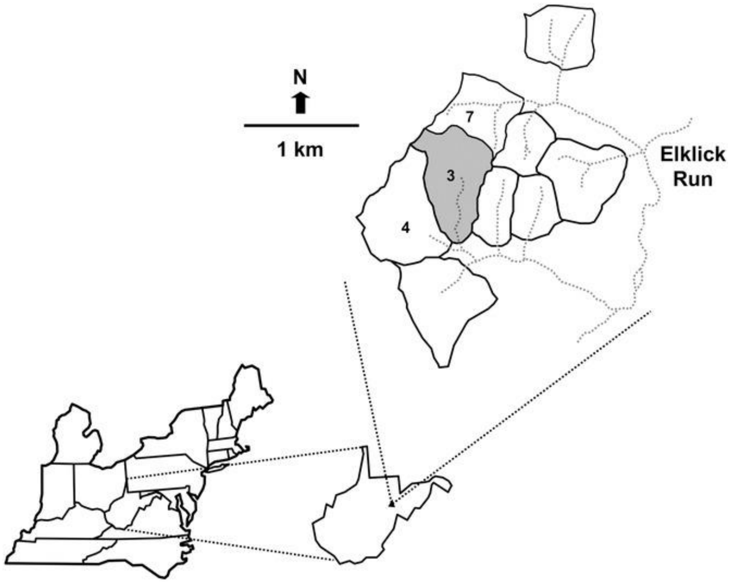

Figure 4. Map depicting watersheds of the Fernow Experimental Forest, West Virginia, USA. WS4 is the long-term reference watershed, WS3 is the treated watershed as part of the Watershed Acidification Study, and WS7 is an additional reference watershed of stand age similar to that of WS3.

2.4. Findings

A notable number of investigations have been carried out within the design of the WAS, including several Master's theses and Ph.D. dissertations from multiple institutions, such as Marshall University, the Pennsylvania State University, the University of Pittsburgh, and West Virginia University. To date, these have resulted in ~130 publications, mostly articles in the peer-reviewed ecological literature, but also books, e.g., [34,37,38], symposia proceedings, book and proceedings chapters, and USDA Forest Service research publications. To assess the findings of the WAS in the context of the hysteretic model, I have summarized 10 studies from among these publications using three main criteria. First, each must have been published in the peer-reviewed literature, thus excluding books, proceedings, chapters, and USDA Forest Service publications. Second, each must represent a specific study with a particular sampling within WAS watersheds, thus excluding review articles (with the exception of Peterjohn et al. [20], a historically important synthesis placing WAS watersheds in the context of N saturation). A good example of an excluded peer-reviewed paper would be Gilliam [21], which used extensive results from the WAS, but did so only in the context of general responses of forest herb communities to excess N deposition, including studies from throughout Europe and North America. Third, studies should represent largely continuous measurements of variables (e.g., herb communities, soil fertility, stream chemistry) over time.

These studies are summarized in Table 1 and placed in order according to the cumulative number of years that $(NH_4)_2SO_4$ had been added to WS3 when the study was conducted. Since several studies used multiple sampling periods (e.g., stream chemistry), the number of years listed represents the latest sampling included in the paper. Although many, perhaps most, studies were multifaceted in their scope, for brevity only the main focus and findings are summarized. All told, these studies comprise a sample period that extends from three years [39] to 30 years of treatment [12].

Table 1. A brief summary of 10 studies published in the peer-reviewed literature. Yr indicates the number of years of treatment on WS3 represented by latest year of sampling of a given study. Many studies were multi-focused with multiple findings. For brevity, only the principle areas of focus and findings are summarized herein.

Study	Yr	Focus	Findings
Gilliam et al. (1994) [39]	3	herb layer/soil nutrients	no significant differences between WS3, WS4, and WS7
Gilliam et al. (1996) [40]	4	N mineralization, foliar nutrients	no differences for N mineralization
Peterjohn et al. (1996) [20]	4	symptoms of N saturation	clear evidence of N saturation on untreated WS4
Gilliam et al. (2006) [36]	5	herb layer communities	no differences in composition and diversity
Edwards et al. (2002) [41]	8	soil solution chemistry	higher NO_3^- and cation concentrations on WS3
Edwards et al. (2002) [42]	8	stream chemistry	increases in NO_3^-, cations, and acidity, following ~2 yr lag
Gilliam et al. (2016) [11]	25	herb layer composition/diversity	N alters herb layer composition, decreases species diversity
Gilliam et al. (2018) [43]	25	soil N mineralization/nitrification	no watershed differences, increased homogeneity on WS3
Gilliam et al. (2020) [44]	25	soil fertility	significant decreases in base cations and soil pH
Eastman et al. (2021) [12]	30	long-term carbon and N budgets	added N leads to greater C storage in vegetation and soil

The timeline generated by these summarized results generally follows the trajectory depicted in the hysteretic model (Figure 3). Early on, most studies reported minimal effects of added N to WS3. After 3 yr of treatment, there were no treatment-related differences in either soil or herb foliar nutrients [39], but 25 yr of treatment yielded numerous effects [44]. Following even as many as five years of treatment, Gilliam et al. [36] reported no significant differences between WS3 and WS4 in species composition and diversity in forest herb communities, yet 25 yr of treatment greatly altered composition and decreased diversity [11]. By 8–10 years of treatment, Edwards et al. [41,42] reported higher concentrations of NO_3^- and base cations in both streamflow and soil solution, but also demonstrated a time lag of 2–3 years before responses became apparent, also consistent with the model and confirmed more recently by Gilliam et al. [44]. Essentially all studies after this period reported significant treatment effects on WS3.

It should be noted that many studies within the WAS were not carried out in ways that allow direct assessment with the hysteretic model. On the other hand, the complete body of published work merits summarization of the effects of excess N at FEF.

Following a lag period of 3–5 years, excess N elicited several responses in a temperate hardwood forest ecosystem. It decreased rates of decomposition of organic matter [45], likely through the alteration of microbial communities and extracellular enzymes [46]. Excess N increased NO_3^- mobility, accompanied by the leaching of base cations [41,42] and leading to decreases in soil fertility [44], increased Al mobility [47], increased NO and NO_2 emissions [48,49], and limitation by P [50]. Several of these responses are also evidenced in both tree and herb tissues [19,51]. Although there was an initial effect of fertilizer added on tree growth, decreased soil fertility has led to slower growth of prominent tree species [52–54]. There was, however, a high degree of interspecific variability in such a response. Despite slower tree growth, excess N has led to greater storage of C in soil and vegetation [12]. Finally, there has been a pronounced shift in herb layer composition that arose from increases in a nitrophilic species, blackberry (*Rubus allegheniensis* Porter) (hereafter, *Rubus*) [55], that competitively eliminated numerous N-efficient herbaceous species, resulting in a loss of plant diversity [11]. The observed increase in cover of *Rubus* at FEF in response to increasing deposition of N, as both a function of time and N loading, is consistent with the ascending limb of the hysteretic model (Figure 5).

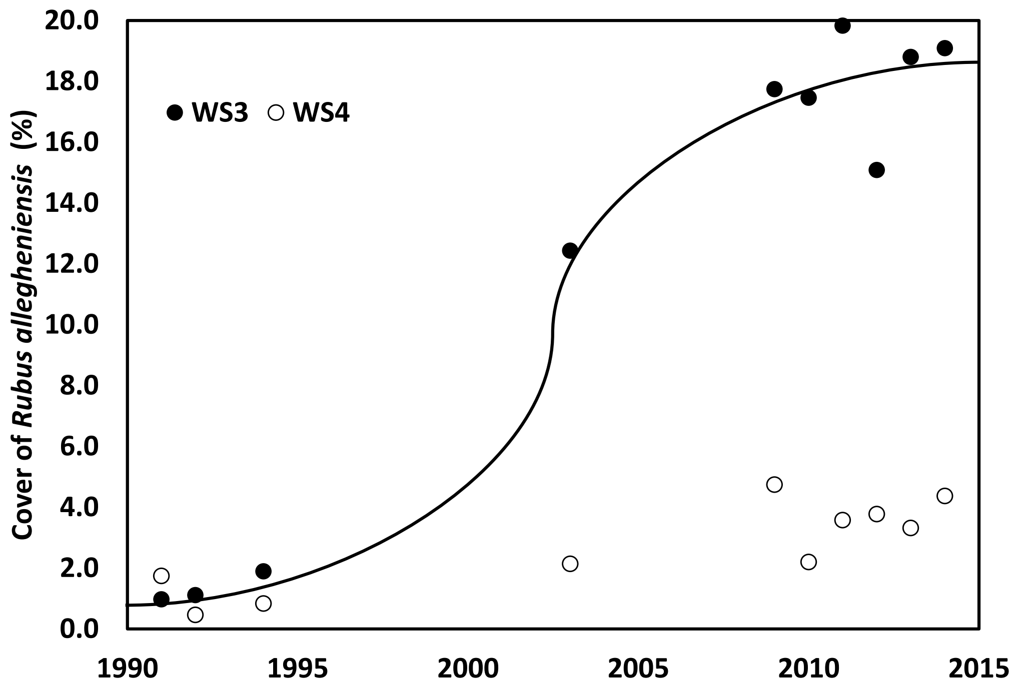

Figure 5. Changes in cover of *Rubus allegheniensis* in response to a quarter century of N additions at Fernow Experimental Forest, West Virginia. Data taken from Gilliam et al. [11].

3. Response of Terrestrial Ecosystems to Decreased N Deposition

Relative to temporal patterns of increases in Nr on a global scale, decreased N deposition is a somewhat novel phenomenon. As a result, few studies have directly assessed how terrestrial ecosystems respond to such decreases. Using whole-watershed additions of $(NH_4)_2SO_4$ (same as the WAS at FEF) from 1989 to 2016 at Bear Brook Watershed in Maine, Patel et al. [13] found relatively rapid recovery (within one year) of stream NO_3^- outputs following cessation of treatment. They concluded, however, that the pattern for base cation loss distinctly followed the predictions of the hysteretic model [13].

Earlier studies on potential recovery for forest herb communities following decreased N deposition were all carried out in Europe, including the NITREX roof experiments [56] and forest fertilization studies, e.g., [57]. In the 1990s, NITREX comprised a network of sites throughout Europe that, among several integrated investigations, used roofs to experimentally decrease high ambient N deposition. They found that nitrophilous plant species, all of which had increased under high N deposition, declined over a 5-yr period in plots under the roofs, suggesting a relatively rapid recovery [56]. By contrast, Strengbom et al. [57] addressed what they called 'legacy effects' of excess N in forests of northern Sweden by examining forest herbs 9 yr after cessation of 20 yr of N fertilization. They found that N-mediated declines in ericaceous species and increases in a nitrophilous grass, wavy hairgrass—*Deschampsia flexuosa* [(L.) Trin.]—persisted after this period of nearly a decade, concluding that the effects of excess N can be long-lived for forest herbs. As with biogeochemical responses, these sharply contrasting results highlight both the research challenges and opportunities for the temperate forest sites in the eastern U.S.

Stevens [31] reviewed evidence from long-term experiments in grasslands, forests, heathlands, and wetlands experiencing lower N inputs, primarily from cessation of experimental additions of N. She concluded that plant species composition and soil microbial communities may be slow in recovery, whereas soil N dynamics may respond more rapidly. Based primarily on long-term research at Hubbard Brook Experimental Forest, New Hampshire, USA, Groffman et al. [32] observed declines in the atmospheric deposition of N over a half century from 1964–2014 and referred to ecosystem responses to this as *N oligotrophication*. They suggested that this phenomenon is driven via increased C flux from the atmosphere to soils in ways that stimulate microbial immobilization of N, decreasing the plant's available N pool, a response further exacerbated by climate change, including lengthening of the growing season. Similar to patterns reported for North America [26], Schmitz et al. [33] reported declines in N deposition throughout Europe since the 1990s. They reviewed both observational (generally using deposition gradients) and experimental studies for changes in soil acidification and eutrophication, understory vegetation, tree foliar nutrients, and tree growth and vitality. In contrast to trajectories for the U.S., they predicted that further declines in N deposition will be minimal, but also affirmed the hysteretic model for forests of Europe.

4. Future Directions

With the cessation of whole-watershed additions of $(NH_4)_2SO_4$ at FEF in 2019 following 30 years of continuous treatment, the WAS at FEF is uniquely positioned to provide empirical documentation of the recovery of a temperate hardwood forest following decreases in N deposition. Some of these investigations are already in place and are currently of a monitoring nature. Plots to assess the response of the forest herb layer community were established in 1991 and were sampled at various time intervals until 2009, after which they have been sampled annually in early July [11]. Beginning in 1993, in situ incubations of mineral soil were made monthly during the growing seasons of several years until 2007, after which they have received monthly growing season sampling every year [43]. In addition, personnel of the Timber and Watershed Laboratory, Parsons, West Virginia—which manages the FEF—take weekly grab samples of stream water at calibrated weirs for complete chemical analysis. As previously suggested, temporal patterns of stream chemistry for treatment WS3 are consistent with the ascending curve of the hysteretic model, exhibiting a lag time for the response of pH, NO_3^-, and $SO_4^=$ of ~3 yr (Figure 6). The extension of all such investigations will provide a continuous timeline for potential changes under conditions of decreased N deposition.

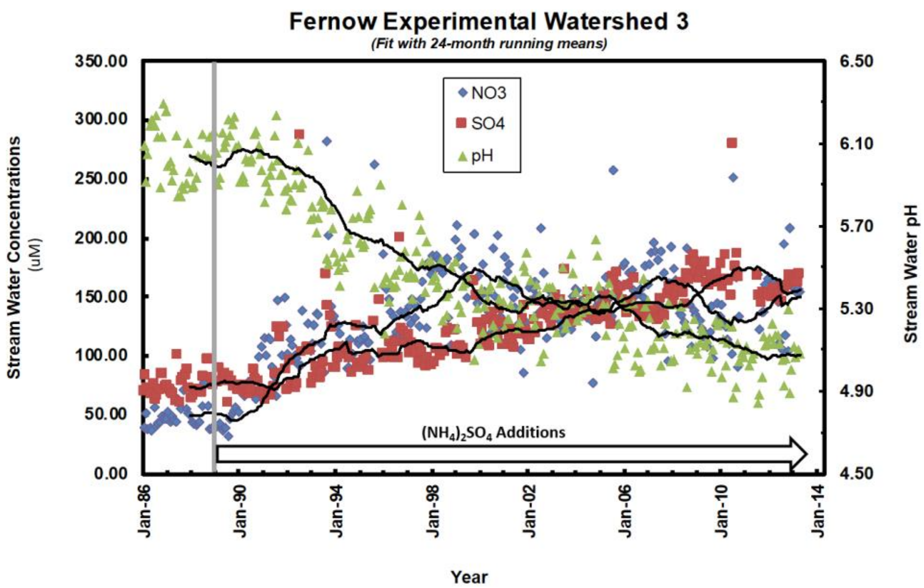

Figure 6. Monthly mean stream water pH and concentrations of NO_3^- and $SO_4^=$ for treated WS3 from 1986 to 2014.

It is indeed likely that the temporal patterns of recovery will be as varied and nonlinear as the responses to 30 years of treatment. It is reasonable to hypothesize that most ecosystem processes will display lag times as predicted by the hysteretic model (Figure 3), but that the length of this period will vary considerably among processes. Once again, Patel et al. [13] reported an immediate decline in stream NO_3^- output at Bear Brook Watershed, Maine, following cessation of whole-watershed additions identical to those at FEF. Base cations, however, exhibited the hysteretic pattern. It is likely that the NO_3^- response at FEF will be less immediate than in Maine because of the higher conifer component of stands at Bear Brook Watershed, Maine [58], especially at higher elevations [13].

Of particular interest will be the response of forest herb communities on WS3. Once again, other studies have exhibited conflicting results. A reasonable hypothesis for FEF in particular is that there will be a very pronounced lag time in the response of herb community composition and diversity. The major change in response to N additions on WS3 has been the increased dominance of a single nitrophilous species that was once only a minor component—*Rubus* (Figure 5). Among the many effects this increase has had on the biotic and abiotic environment of the forest understory is that it is has effectively redistributed high, possibly phytotoxic, levels of Mn from deep soil to surface horizons [50]. Because *Rubus* accumulates Mn in pre-senescent leaves and further concentrates Mn in post-senescent leaves [59], this effect may persistent for several years.

Finally, regarding future directions, perhaps the greatest challenge is the 'moving target' represented by climate change. Consider that total inorganic deposition in the U.S. declined by nearly 25% from a maximum in 1995 to 2012, at which time it equaled the deposition in 1985 [26]. Mean annual temperature in the U.S., however, was 10.7 C in 1985, increasing to 13.2 C in 2012. More importantly, CO_2 concentrations for those two years in the Northern Hemisphere were 346 and 395 ppm, respectively, an increase of >1% over that 30-yr period. Accordingly, whereas it is certain that N deposition will decline to previous levels, it is equally certain that ambient temperature and CO_2 will not.

5. Conclusions

In conclusion, the Clean Air Act in the U.S. and similar environmental regulations worldwide have exhibited a high degree of efficacy with respect to decreasing emissions of pollutants, including and especially N_r. As a result, atmospheric deposition of N has declined over the past few decades on a global scale, including North America [59], Europe [33], and China [60], representing a challenge to the way N biogeochemists have thought and carried out research over this period of time. Moving forward, such challenges lead to new research opportunities and directions.

The hysteretic model proposed by Gilliam et al. (2019) has received support in the literature in predicting a non-linear response of forest ecosystems to declines in atmospheric deposition of N_r, coupled with time lags of varying duration, depending on specific conditions for a particular site [13,61,62]. Studies over the past three decades at the Fernow Experimental Forest, West Virginia, generally support the ascending limb of the hysteretic model during which time aerial applications were added to an entire watershed. Cessation of this treatment in 2019 now allows for further empirical testing of the model via ongoing studies of several components of this hardwood forest ecosystem, including biogeochemical cycling and dynamics of the forest herbaceous layer.

Author Contributions: F.S.G. wrote the manuscript. The author has read and agreed to the published version of the manuscript.

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