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Nitrogen oligotrophication in northern hardwood forests

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Abstract While much research over the past 30 years has focused on the deleterious effects of excess N on forests and associated aquatic ecosystems, recent declines in atmospheric N deposition and unexplained declines in N export from these ecosystems have raised new concerns about N oligotrophication, limitations of forest productivity, and the capacity for forests to respond dynamically to disturbance and environmental change. Here we show multiple data streams from long-term ecological research at the Hubbard Brook Experimental Forest in New Hampshire, USA suggesting that N oligotrophication in forest soils is driven by increased carbon flow from the atmosphere through soils that stimulates microbial immobilization of N and decreases available N for plants. Decreased available N in soils can result in increased N resorption by trees, which reduces litterfall N input to soils, further limiting available N supply and leading to further declines in soil N availability. Moreover, N oligotrophication has been likely exacerbated by changes in climate that increase the length of the growing

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season and decrease production of available N by mineralization during both winter and spring. These results suggest a need to re-evaluate the nature and extent of N cycling in temperate forests and assess how changing conditions will influence forest ecosystem response to multiple, dynamic stresses of global environmental change.

Keywords Climate change · Carbon · Dissolved organic carbon · Hubbard Brook Experimental Forest · Nitrogen

Introduction

In most temperate forest ecosystems, N is a limiting nutrient that constrains net primary production (LeBauer and Treseder 2008; Vitousek and Howarth 1991). However, in excess, N can contribute to environmental problems, such as acidification, eutrophication, and loss of biodiversity (Davidson et al. 2012). In recent decades, much research has focused on anthropogenic activities that increase inputs of "reactive" N to forests through increases in emissions and atmospheric deposition (Galloway et al. 2008) and the ability of these inputs to accelerate forests toward a condition of N saturation, with adverse consequences on soils, plant growth, and aquatic ecosystems (Aber et al. 1989, 2003; Stoddard 1994). However, atmospheric N deposition is now declining over large areas of North America (Eshleman et al. 2013; Lloret and Valiela 2016) and there have been remarkable declines in N export from non-aggrading northern hardwood forests that cannot be explained by declines in atmospheric deposition alone (Bernal et al. 2012; Bernhardt et al. 2005; Driscoll et al. 2016; Fuss et al. 2015; Goodale et al. 2003; Likens 2013; Martin et al. 2000; McLauchlan et al. 2007; Rosi-Marshall et al. 2016; Yanai et al. 2013). Now, concerns about N saturation and over supply are being replaced with concerns about N oligotrophication causing N limitation of forest productivity and diminished capacity of ecosystems to dynamically respond to disturbance and environmental change (Durán et al. 2016; Elmore et al. 2016).

We refer to the changing state of N limitation in temperate forests as "oligotrophication," borrowing a term from aquatic sciences (Hutchinson 1973). While we cannot define specific nutrient concentrations associated with various trophic conditions (e.g., oligotrophic, mesotrophic, eutrophic) for terrestrial ecosystems, we can examine quantitative changes in multiple measures of N flux and availability that serve as symptoms or indices of oligotrophication. Similar analyses have long been done to evaluate N richness in different ecosystem types (Pastor et al. 1984; Vitousek et al. 1979) or in response to changes in atmospheric CO_2 manipulations (Zak et al. 2003). We hope that this examination begins a discussion of specific classifications of trophic state for terrestrial systems as these have been very useful in aquatic systems and terrestrial ecosystems around the world are in a dynamic state of increasing or decreasing N richness (Battye et al. 2017).

The great challenge posed by the emergence of N oligotrophication is understanding how ecosystems are responding to decreases in anthropogenic reactive N deposition and the availability of key nutrients such as N, while simultaneously experiencing changes in atmospheric chemistry (e.g., sulfur deposition, elevated concentrations of carbon dioxide (CO_2), ozone), climate, and community composition (pests, pathogens, invasive species) (Groffman et al. 2013; Holmes and Likens 2016; Keenan et al. 2014; Loehle et al. 2016; Niu et al. 2016; Rosi-Marshall et al. 2016; Xu et al. 2016). For example, recent findings suggest that environmental "deacidification" is catalyzing marked increases in decomposition of forest soil organic horizons (forest floor) and the flow of C to soil microbial populations responsible for production and consumption of reactive N (Johnson et al. 2014; Oulehle et al. 2011, 2017). Further challenges come from the manipulative nature of most research focused on understanding the effects of global changes on forest nutrient cycling. For example, while studies in diverse ecosystems have demonstrated that changing climate can substantially alter C and N cycles and budgets (Hofmockel et al. 2011; Luo et al. 2011; Melillo et al. 2011; Pendall et al. 2008; Phillips et al. 2011), most of this research has emerged from manipulation experiments (i.e., Free-Air Carbon dioxide Enrichment; FACE). Effects of elevated atmospheric CO_2 on unmanipulated forests have been difficult to detect (Aber and Driscoll 1997) due to the challenge of evaluating effects of relatively small (albeit sustained) flows of C from the atmosphere through trees to soil, and the complex interactions between C and N in the soil (Zak et al. 2011).

Analyses of climate change effects on forest C and N dynamics have largely focused on temperature and precipitation during the growing season. However, processes during the dormant season have been shown to be a key driver of N oligotrophication (Durán et al. 2014, 2016; Elmore et al. 2016). Subtle and indirect effects of climate change on snow depth and soil frost and changes in plant-microbial interactions during seasonal transitions may have more pronounced effects on ecosystem C and N cycles than changes associated with mean annual temperature or precipitation (Campbell et al. 2005; Groffman et al. 2012). Changes during winter can be particularly important as warmer temperatures decrease the depth and duration of snowpack, potentially increasing soil freezing severity, which in turn affects microbial, soil and plant ecosystem processes (Brooks et al. 2011; Martz et al. 2016), not only during the winter, but also in the following growing season (Durán et al. 2014, 2016; Liu et al. 2016; Sorensen et al. 2016b). However, the complex nature of snowpack and soil freezing and the varied responses of ecosystem processes and organisms to climatic change and other stresses have challenged our ability to project how winter climate change will influence nutrient cycles (Henry 2007).

Ongoing research at the Hubbard Brook Experimental Forest (HBR), including through the Long Term Ecological Research (LTER) program, has been addressing N oligotrophication and winter climate change effects on northern hardwood forests. Long-term (50+ year) watershed studies, have shown marked declines in N exports that began well before atmospheric N deposition began to decline (Bernal et al. 2012; Likens 2013). More recent analyses have shown long-term (40 year) declines in available N production via microbial mineralization (Durán et al. 2016). A series of snow manipulation and elevation gradient studies of the effects of winter climate change have found that reductions in snow cover have likely contributed to the decrease in soil N mineralization both overwinter as well as in the subsequent growing season (Durán et al. 2014; Groffman et al. 2001). Other recent studies have shown that gaseous losses of N via denitrification are higher than previously thought, and may be increasing due to changes in soil conditions during winter-to-spring transitions and increases in intense rainfall events (Morse et al. 2014, 2015a, b; Wexler et al. 2014). Finally, new analyses suggest that changes in soil C fluxes may be linked to declines in N availability and export. Specifically, long-term increases in forest floor C:N ratio (Yanai et al. 2013), labile C, and dissolved organic carbon (DOC) flux all suggest that increases in atmospheric CO_2 and/or deacidification effects on decomposition and plant mycorrhizal status (Battles et al. 2014; Juice et al. 2006) are increasing C flow from the atmosphere through plants into the soil, which should reduce N mineralization and availability (Hart et al. 1994).

In this paper, we synthesize data from multiple sources to advance the idea that multiple components of environmental change are driving the northern hardwood forests at HBR toward a condition of N oligotrophication by two mechanisms (Fig. 1). First, we argue that increased C flow (caused by both increased atmospheric CO_2 and recovery from acid rain) stimulates microbial immobilization and decreases available N production via mineralization. This reduction in available N leads to reduced litterfall N input to soils. This decline in soil N inputs causes trees to resorb more N, further exacerbating low N availability in soils and decelerating the ecosystem N cycle. Second, we argue that climate change exacerbates N oligotrophication through longer winter-to-spring transitions, longer growing seasons, and increasingly frozen soil conditions in winter due to loss of snowpack that together lead to decreased production of available N via mineralization in winter and greater N uptake by plants in the longer, warmer, and wetter growing seasons. It is important to note that these are internal mechanisms that would reduce N availability to plants even if atmospheric N deposition were not declining. To develop our new conceptual model, we present a mixture of published and unpublished data that illustrate the dynamics depicted in Fig. 1 and highlight areas of uncertainty that need to be explored in future research.

Methods

Site

The HBR is located in the White Mountain National Forest, New Hampshire USA (43°56′N, 71°45′W) and

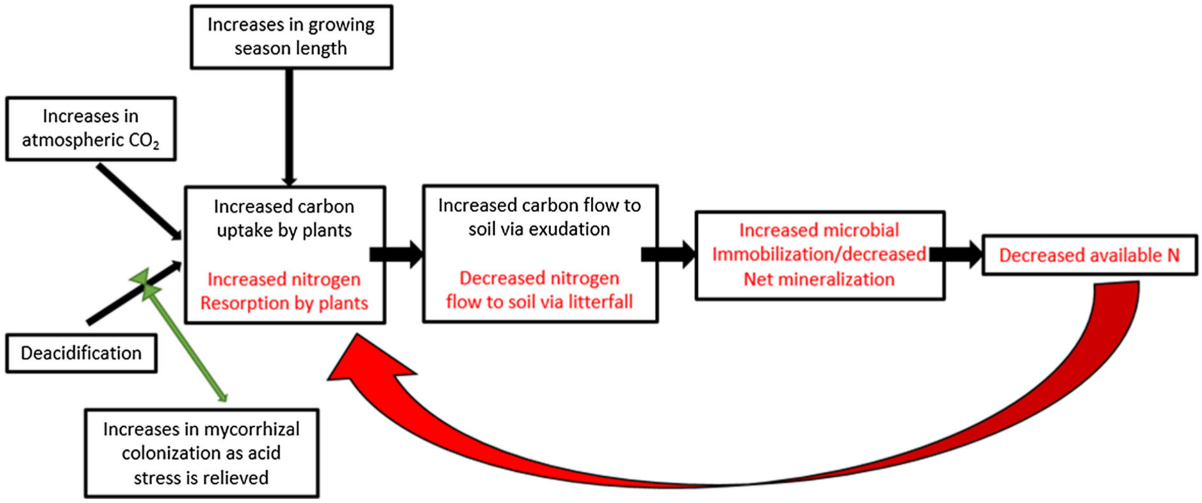


Fig. 1 Conceptual diagram showing mechanisms driving N oligotrophication in the northern hardwood forest

is dominated by northern hardwood forest vegetation (Schwarz et al. 2003). Soils are mostly shallow (75–100 cm), Spodosols (pH 3.9) developed from unsorted basal tills, with occasional deeper profiles.

To develop our conceptual model, we analysed published and unpublished data from multiple sources on HBR watershed N export, soil solution chemistry, soil microbial carbon and nitrogen cycle process, forest floor C and N content, and soil to atmosphere fluxes of nitrous oxide (N_2O). We note that many of the data cover different time periods as many new monitoring efforts arose in response to variation in the long-term watershed N export record.

Watershed nitrate export

Nitrate and ammonium concentrations in the stream draining the *reference* (unmanipulated) watershed (watershed 6) at HBR have been monitored weekly since the mid-1960s (Likens 2013). Monitoring of dissolved organic N (DON) began in 1995. The forest in this watershed was last disturbed by cutting early in the twentieth century and by a hurricane in 1938.

Soil solution chemistry

Nitrate and dissolved organic carbon (DOC) concentrations in soil solution samplers (zero tension lysimeters) of the design described by Johnson et al. (2000) have been monitored monthly at four sites along an elevation gradient in the *reference* watershed at HBR since 1983 (Dittman et al. 2007; Fuss et al. 2015). Nitrate and DOC have been measured on these samples by ion chromatography and detection of CO_2 following persulfate digestion and ultraviolet enhanced oxidation (McDowell et al. 1987) respectively.

Soil microbial carbon and nitrogen cycle process

In situ net N mineralization and nitrification have been measured in various locations at HBR since 1977 using “buried bag” methods (Durán et al. 2016; Groffman et al. 2009; Robertson et al. 1999). Systematic measurements of microbial respiration and potential net N mineralization and nitrification have been made along an elevation transect adjacent to the *reference* watershed since 1994 (Bohlen et al. 2001; Fiorentino et al. 2003; Groffman et al. 2006a). Samples have been collected in mid-summer and rates have been quantified by measuring CO_2 and inorganic N production during 10 day incubations in the laboratory as described in Durán et al. (2016).

Forest floor C and N content

Forest floor mass and C and N content along the elevation gradient in the reference watershed have been sampled every 5 years since 1977 (Yanai et al. 2013). Fixed-area samplers were used to quantify mass and C and N content were analyzed with a combustion-based elemental analyser.

Soil to atmosphere fluxes of nitrous oxide (N_2O)

Soil to atmosphere fluxes of N_2O have been measured along the elevation gradient west of the *reference* watershed since 2001 (Groffman et al. 2009) using the in situ chamber design described by Bowden et al. (1991). Fluxes were also measured in a series of small plots used for snow manipulation studies from 1998 to 2000 and 2003 to 2004 that varied in dominant tree canopy species and/or elevation (Groffman et al. 2006b, 2010).

Results and discussion

Long-term data from HBR show significant declines in watershed stream N export (Fig. 2) since the early 1960s (Bernal et al. 2012; Likens 2013; Yanai et al. 2013). These declines are surprising because the forests at HBR are mature (i.e., neither aggrading nor sequestering increasing amounts of N in biomass) (Battles et al. 2014; Bormann and Likens 1979; Yanai et al. 2013). Moreover, the declines in stream N began while atmospheric N deposition was still high and relatively constant (i.e., N deposition has significantly declined only since the early 2000s). Recent analyses have found coincident decreases in soil mineralization and nitrification rates (Fig. 3a, b, respectively) and soil inorganic N concentrations since the early 1970s (Durán et al. 2016). More intensive soil sampling reinforces the observation of rapid declines in potential mineralization and nitrification since the mid-1990s (Fig. 3c). The declines do not appear to be driven by changes in in-stream sinks for N, which can increase as forests mature or after extreme events such as ice storms or windfall that add organic matter to streams (Bernhardt et al. 2005), although this is a topic of active research at HBR.

Fig. 2 Nitrate and ammonium concentrations (**a**) and inorganic N flux (**b**) in precipitation and streamwater for the reference watershed at HBR from 1964 to 2014

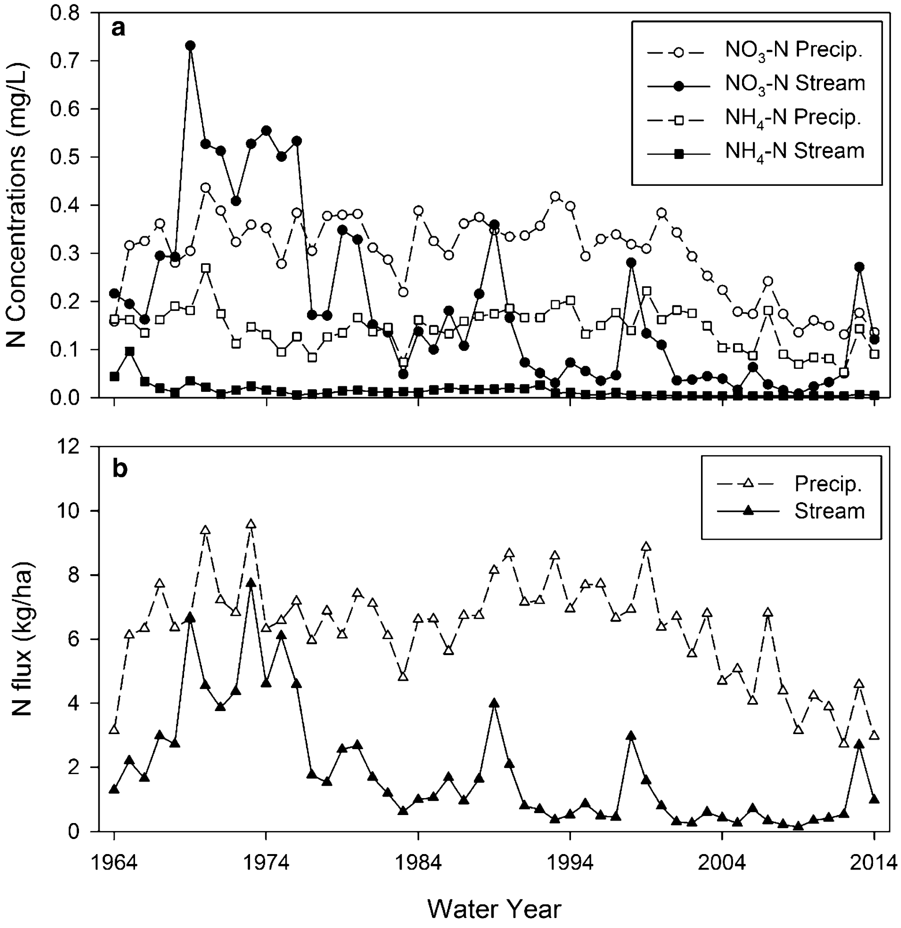
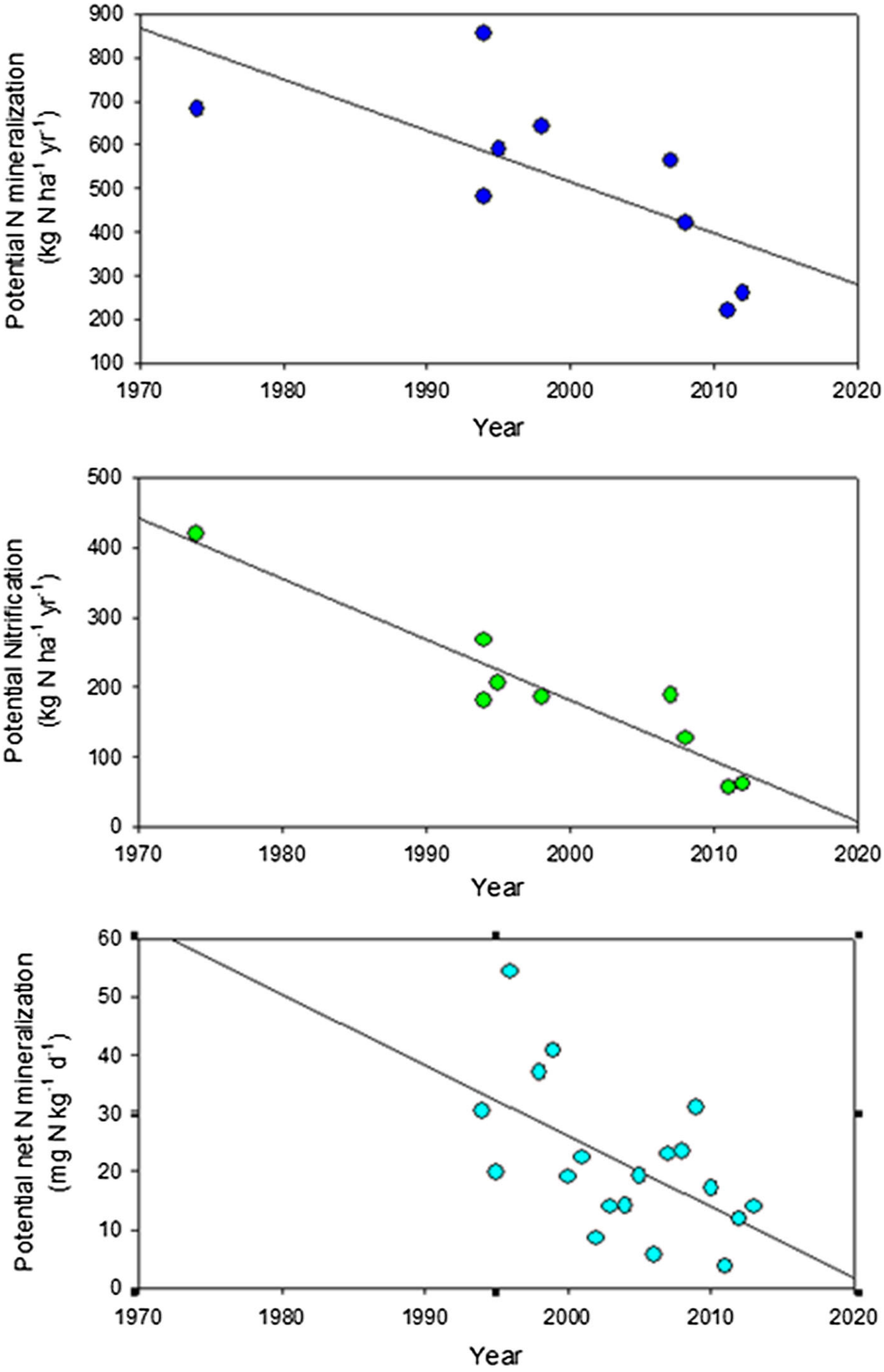


Fig. 3 Changes in potential net N mineralization (top) and nitrification (middle) since the 1970s and more detailed sampling showing changes in potential net N mineralization since the 1990s (bottom) at HBR. The top two panels are from Durán et al. (2016) and use data from the 1970s collected using somewhat different methods than in subsequent years. All relationships significant at $p < 0.05$



It is important to note that the relatively high loss rates of N from watershed 6 in the 1960s and 1970s may have resulted from a combination of the extreme drought in the mid-1960s followed by severe defoliation in the early 1970s (Aber and Driscoll 1997) and that those high N loss rates may be the exception in the record, which otherwise would appear relatively flat and low. However we note that the most intensive soil microbial measurements began in the mid to late 1990s and have shown marked declines in N availability since that time, indeed much more marked than the declines in stream N export. We also note that the climatic disturbances that caused high losses in 1988 and 1998 and in the 1960s and 1970s no longer produce high losses in the 2000s (Judd et al. 2011; Groffman et al. 2012), a further symptom of oligotrophication. It is also important to note that monitoring of DON at Hubbard Brook began only in 1995 and thus our assessment of long-term trends is incomplete. However, we note that DON has declined along with nitrate since 1995 and that total watershed export N flux is dominated by nitrate (Bernal et al. 2012; Rosi-Marshall et al. 2016). Finally, it is important to note that many of our explanatory variable records (e.g., Figs. 5 and 6) originated in mid-1990s when N deposition peaked at HBR and began a 20-year long monotonically-decreasing trend. Thus the trends in microbial respiration (Fig. 5) and N_2O flux (Fig. 6) may be partially or dominantly controlled by changes in deposition as well as changes in internal processes.

Many environmental factors have changed over the last 50 years at HBR, including climate. There has been an increase in mean annual temperature, a decrease in annual snow accumulation, and an increase in the number of winter thawing degree days (Durán et al. 2016; Holmes and Likens 2016). Precipitation has also increased by nearly 15%, with a decrease in the proportion of precipitation occurring as snow and an increase in the proportion of rainfall occurring in large events (Campbell et al. 2007a). Coincidently, acid deposition first increased (in the 1960s) and then markedly decreased, resulting in an increase in the pH of soils and streams in recent years (Driscoll et al. 2001; Fuss et al. 2015; Holmes and Likens 2016; Likens 2013; Likens and Buso 2012). Atmospheric concentrations of CO_2 have also increased steadily over this same period (Keenan et al. 2016). Below, we discuss how these diverse changes have contributed to N oligotrophication, with a focus on how increases in C flow from the atmosphere to plants and soils is driving declines in N availability and loss.

C flows from the atmosphere to plants to soils

It is challenging to evaluate the effects of enhanced flows of CO_2 from the atmosphere into plants and then into soils. While FACE experiments have shown that forest trees take up more CO_2 when exposed to elevated atmospheric levels of this gas, and that much of this additional C is ultimately transported to soils (Drake et al. 2011; Hofmockel et al. 2011), it has been much more difficult to evaluate these effects and flows in mature forests experiencing chronic, gradual increases in ambient CO_2.

At HBR, we see evidence of changes in the C cycle that could well be driving N oligotrophication. While direct measurement of increased C flux from trees to soil in mature forests is not possible, we can however examine evidence for effects of increased C transfer from plants to soil. For example, while the pool of N in the forest floor (organic surface soil horizons) has not changed since the mid-1970s, the C:N ratio of the forest floor has increased significantly over this period (Fig. 4), suggesting changes in C input and processing of organic matter in soils, a key site of N cycling in the ecosystem (Yanai et al. 2013). Further evidence that changes in the C cycle are driving N oligotrophication include increases in microbial respiration (Fig. 5), decreases in soil to atmosphere fluxes of nitrous oxide (N_2O) (Fig. 6), and increases in the C:N ratio of waters draining from soils (Fig. 7). Microbial respiration (measured in 10 day incubations in the laboratory) is an index of soil “respirable” or “labile” C and the observed increases in recent decades could result from either an increase in the production or a decrease in the consumption of this C. These trends all point to an increase in the transfer of labile C into soils that could be driving N oligotrophication at HBR.

While increases in atmospheric CO_2 are a likely cause of the increases in C flow to soils at HBR, an additional contributing factor could be ecosystem “deacidification” (Driscoll et al. 2007; Likens and Buso 2012; Likens et al. 1996). Recent results suggest that decreases in acid deposition over the past 40 years are catalyzing increases in decomposition of forest soil organic horizons (forest floor) and in the flow of C to soil microbial populations responsible for production and consumption of reactive N (Johnson et al. 2014; Oulehle et al. 2011, 2017). At HBR, these mechanisms have been studied in a watershed experimentally treated with a calcium silicate mineral to replace the calcium lost to 50 years of acid deposition and accelerate the deacidification process (Cho et al. 2012; Shao et al. 2016). This addition has increased forest growth and aboveground litterfall (Battles et al. 2014), increased late-stage litter decomposition

Fig. 4 C:N ratio of the whole forest floor (closed squares) and the Oie horizon alone (open squares) at the HBR from 1977 to 2002 ($p < 0.05$). From Yanai et al. (2013)

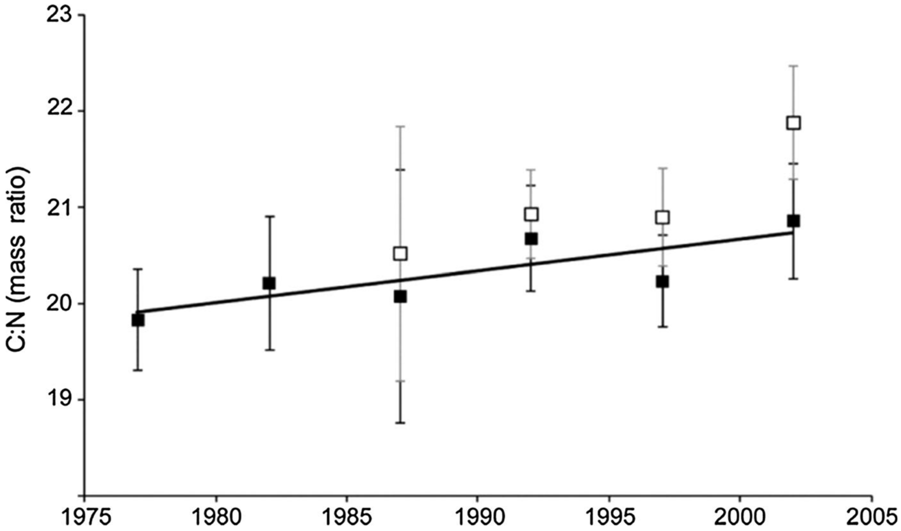
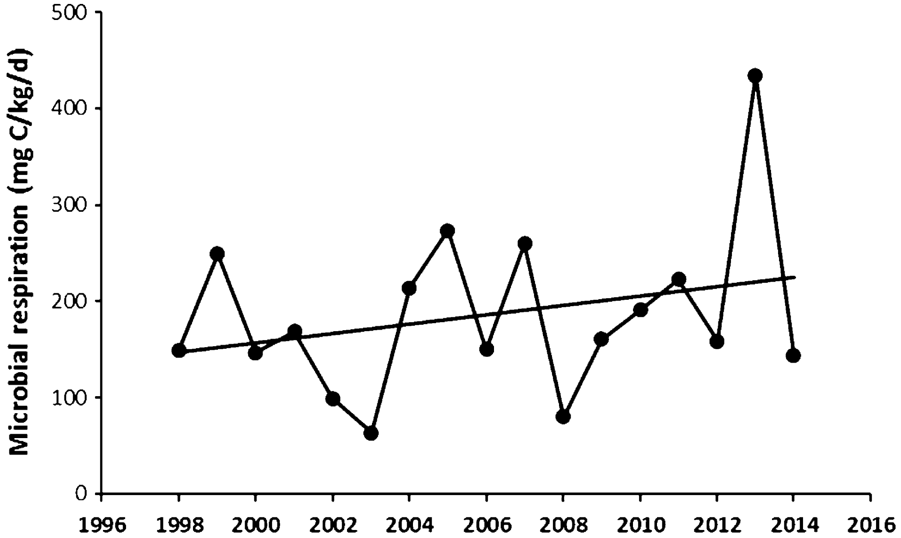


Fig. 5 Soil microbial respiration (an index of labile C availability) measured at multiple sites at HBR from 1997 through 2012. Groffman (unpublished data). Trend is not statistically significant ($r = 0.28$, $p < 0.27$)



(Lovett et al. 2016), stimulated decomposition of soil organic matter (Johnson et al. 2014), and increased mycorrhizal colonization of forest trees (Juice et al. 2006). All these factors increase the flow of C from vegetation into soil microbial communities. The responses on WS1 are complex however. While we assume that increased decomposition of the forest floor increases C flow to soil via DOC, this has not yet been shown empirically. Analysis of this flow is complicated by effects of pH on the solubility of DOC (Dawson et al. 2009). We have also observed declines in fine root biomass on WS1 (Fahey et al. 2016), which represents a decrease in C supply to soil.

Carbon–nitrogen interactions in the soil

Increases in the flow of C into soil are well known to shift the balance between production of available N (by microbial mineralization) and consumption of this N (by microbial immobilization) towards net N immobilization (Hart et al. 1994; Robertson and Groffman 2007). Certainly the declines in mineralization (Fig. 3), the C:N increases in the forest floor (Fig. 4) and soil solutions (Fig. 7), and the declines in soil to atmosphere N_2O fluxes (Fig. 6) all suggest that this pattern is occurring at HBR. We suggest that these trends are driven both by increases in atmospheric CO_2 and by deacidification. In the HBR calcium-

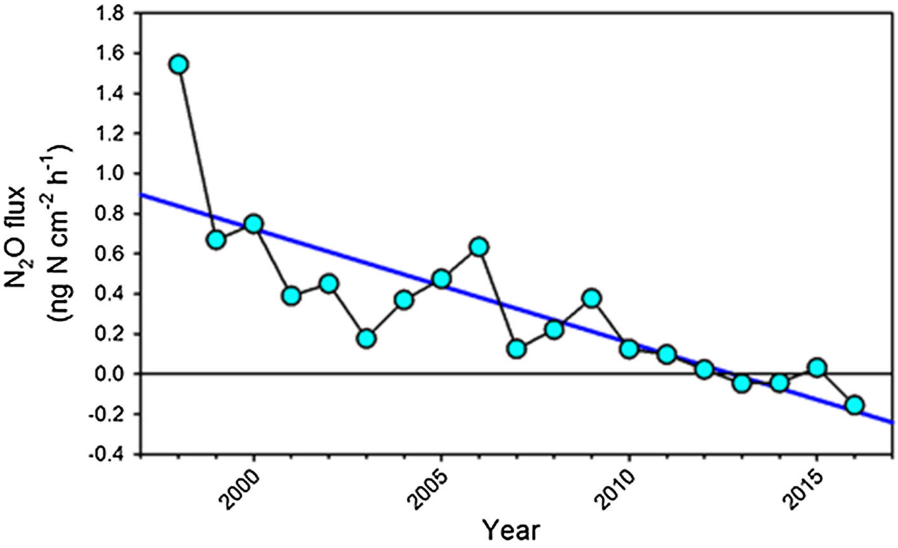


Fig. 6 Soil to atmosphere flux of N_2O flux at HBR from 1998 to 2016. Values are means of variable numbers of sites, sampled at variable frequency in different years along elevation gradients. Trend is statistically significant ($r = -0.90$, $p < 0.001$)

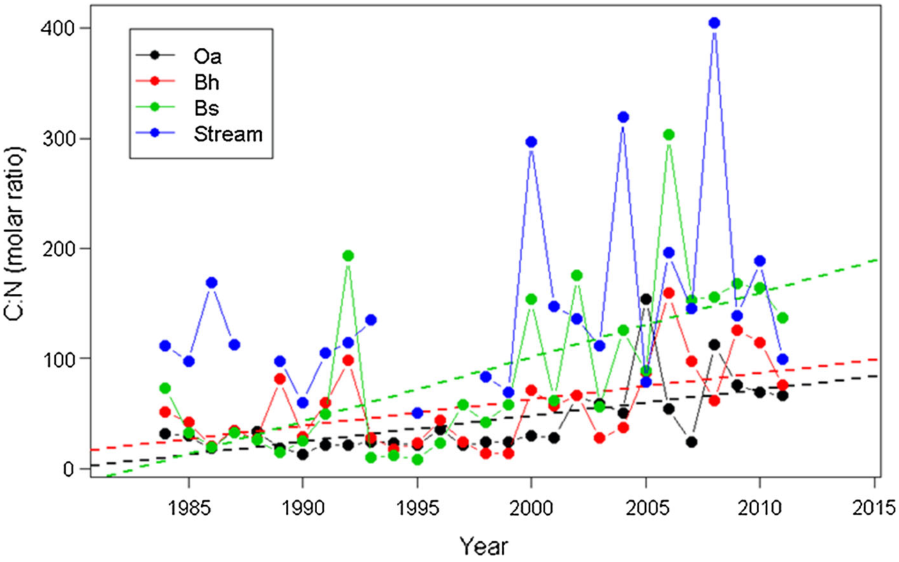


Fig. 7 C:N ratio of soil solutions (dissolved organic carbon:dissolved inorganic nitrogen) of soil solutions at the Hubbard Brook Experimental Forest from 1983 to 2012. Driscoll et al. (unpublished). Trend is statistically significant ($p < 0.05$) for the Bs horizon only

treated watershed, increases in plant productivity and mycorrhizal colonization have increased plant demand for N, and increases in decomposition of soil organic matter indicate greater availability of labile C. Both of these changes are consistent with observed reductions in N mineralization and availability in this watershed (Groffman and Fisk 2011), especially in the early years following the calcium addition. Overall, it appears that increases in C flow to soils due to both increases in atmospheric CO_2 and deacidification have the potential to drive N oligotrophication at HBR.

Plant-soil feedbacks

As shown in our conceptual diagram (Fig. 1), the development of N oligotrophication involves complex interactions between plant and soil processes. Much of the N in living plant foliage is translocated from leaves prior to abscission (resorption) thereby conserving this limiting nutrient within the plant (Chapin et al. 1990; Ryan and Bormann 1982). Resorption efficiency is the proportion of leaf N resorbed and resorption proficiency is the average N concentration in leaf litterfall (Killingbeck 1996). Although it is anticipated that resorption would increase as soil N availability declines, this pattern has not always been observed in gradient or fertilization studies. However, studies in northern hardwood forests in and around HBR have reported significant decreases in resorption efficiency with increased soil N availability (Fahey et al. 1998; See et al. 2015) (Fig. 8). In related work, Gonzalez (unpublished) observed that N fertilization of these forests resulted in increased foliar N and decreased N resorption efficiency, but no change in N resorption proficiency—that is, trees reduced N concentration in litter to roughly constant levels. Finally, it has been observed that N resorption at HBR varies considerably from year to year. For example, Hughes and Fahey (1994) reported two-fold variation across 3 years in resorption proficiency in mature northern hardwoods. The causes of this variability are unknown.

Resorption could hypothetically influence the N oligotrophication process in two ways. First, high resorption efficiency results in lower root N demand in the following year to supply new leaf growth (Ryan and Bormann 1982). Second, high resorption proficiency results in litter with high C:N ratio potentially stimulating higher microbial immobilization of N (Gosz et al. 1973; Li and Fahey 2013). To test this idea, soil C availability, N mineralization and nitrification, resorption, plant N uptake and litterfall N input measurements should be conducted at plots along a spatial gradient in C and N availability. These measurements would provide valuable, hitherto unavailable data for modeling how variation in C and N flows influences coupled soil plant dynamics in the ecosystem.

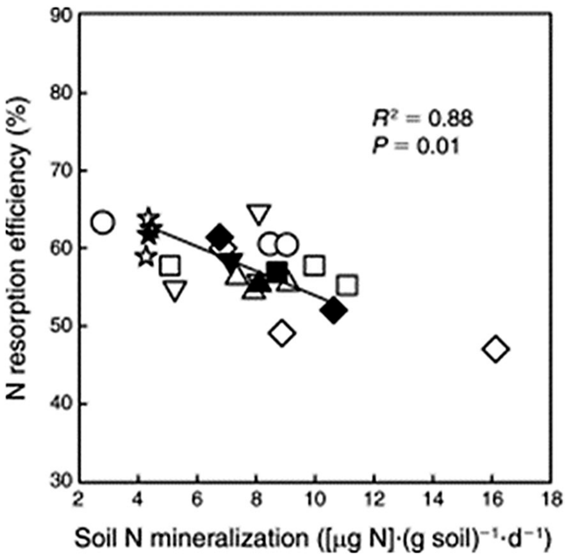


Fig. 8 Community-level N resorption efficiency as a function of soil N mineralization rate in the Oa horizon. Solid shapes depict stand means. Individual plots are shown as open shapes. Lines and fit statistics reflect simple linear regression of stand means (n = 6 replicates). From See et al. (2015)

Carbon–nitrogen–climate interactions

Relationships between climate and N cycling have been a major theme of the research at HBR over the past several decades. Some of the increase in C flow from the atmosphere to plants and into soil, discussed above, has likely been driven by increases in growing season length (Keenan et al. 2014; Richardson et al. 2010). However, other research suggests that changes during the winter and at the transition between winter and spring are also important drivers of N oligotrophication. For instance, previous research has shown that climate warming that reduces snow cover and increases soil freezing leads to decreased N mineralization and nitrification rates during winter (Groffman et al. 2001, 2009; Reinmann et al. 2012; Sorensen et al. 2016a, b). Although N cycling rates are much lower in winter than in summer at HBR, significant amounts of reactive N are generated in winter and then are available for hydrologic or gaseous loss during the winter/spring transition period (Judd et al. 2007) or for plant uptake during the subsequent growing season.

Experiments at HBR involving snowpack manipulation have shown different responses of soil solution N loss over time. In the late 1990s–early 2000s, snowpack removal experiments exhibited marked release of NO_3^- with limited change in DOC (Fitzhugh et al. 2001; Tierney et al. 2001). This NO_3^- response, which appeared to be driven by damage to fine roots, was diminished in later snowpack removal experiments in the 2000s, while greater release of DOC was noted (Campbell et al. 2014; Groffman et al. 2010). More recently, over the period 2010–2012, Fuss et al. (2016b) used a climate gradient approach to examine spatial variation in soil freezing, and observed marked release of DOC to soil water in response to soil freezing with no release of NO_3^-. Whole-watershed response to natural freeze events has also become more muted in recent years (Judd et al. 2011). We speculate that the varying soil response to soil freezing over time may be a manifestation of long-term changes in N oligotrophication in temperate forests. As N availability declines in soils over recent decades, the response to a shrinking snowpack appears to have become more muted.

In addition to changes in snow and soil freezing overwinter, there has been interest in changes in "vernal asynchrony" during the winter/spring transition period and the role that these changes play in N oligotrophication. The winter/spring transition is a critical period for forest ecosystem biogeochemistry, representing a time when soil microbial mineralization, N leaching and denitrification processes are active, but plants have not yet transitioned to being a dominant sink for water or nutrients (Muller and Bormann 1976; Zak et al. 1990). This period of "vernal asynchrony" is lengthening as snow melts and soils warm earlier under a warming climate, while tree canopy expansion is occurring earlier but has not kept pace with this advance (Groffman et al. 2012; Fig. 9). Of particular note is the rapid increase in soil temperature, just as snow melts, resulting in an abrupt increase in soil microbial activity; a "spring trigger" and the "opening" of the vernal window.

The balance among soil microbial production, uptake, and dissimilation of N during the spring vernal period, and how this balance is altered by changing conditions during this period are poorly understood. These processes can affect N retention both by mediating transfer to organic N pools via microbial growth and turnover, and by influencing the growth and activity of nitrifying and denitrifying organisms (Groffman et al. 1993; Morse et al. 2015b; Sorensen et al. 2017; Zak et al. 1990). Hence, we expect interactions among microbial N mineralization, NH_4^+ oxidation, and plant N uptake to be sensitive to the timing and duration of the vernal transition period in hardwood forests (Fig. 9).

Mobilization of DOC by soil freezing could interact with increases in atmospheric CO_2 and the flow of labile C from plants to soils to contribute to changes in soil N dynamics and loss (Fitzhugh et al. 2001; Fuss et al. 2016b; Groffman et al. 2010). Indeed, DOC dynamics are changing at HBR with a pattern of increased mobilization in recent decades (Driscoll et al. 2007; Fakhraei and Driscoll 2015; Fuss et al. 2015). As discussed above, such an increase has been suggested to decrease NO_3^- losses following freezing disturbance by increasing microbial immobilization. Increased DOC concentrations in soil solution can also increase denitrification (Goodale et al. 2005). Either process could contribute to long-term trends in N oligotrophication.

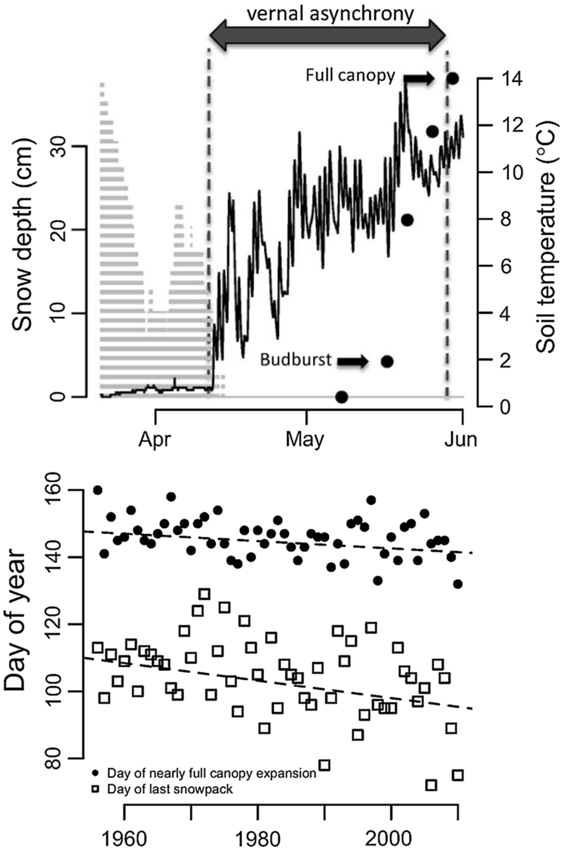


Fig. 9 The relationship between snowmelt, soil temperature, and leaf phenology (above) and changes in the modeled day of nearly complete canopy expansion and last snowpack at a middle elevation at HBR, 1960–2010 (below). In the upper figure, disappearance of snowpack (horizontal shading) coincides with an abrupt increase in soil temperature at 4 cm depth (solid line). Closed circles represent spring leaf development and the arrow denotes the period of 'vernal asynchrony' that has increased over recent decades. Below, spring leaf out (closed circles) is occurring earlier at a rate of $-$ 1.40 ± 0.53 days decade^{-1} ($p < 0.01$), while the day of last snowpack (open squares) is occurring earlier at a rate of $-$ 3.58 ± 1.05 days decade^{-1} ($p < 0.002$); thus the length of the period between snowmelt and full canopy development has increased by approximately 11 days in 55 years. From Groffman et al. (2012)

There is particular uncertainty about plant uptake during the winter to spring transition period. It is possible that lower growing season rates of soil mineralization and nitrification caused by a smaller winter snowpack and greater depth and duration of soil freezing lead to lower N uptake by trees in spring as well. Alternately, warmer spring temperatures and earlier snowmelt may stimulate plant N uptake, even before the trees leaf out. Multiple studies have demonstrated that plants take up N in the dormant season prior to leaf out, (Andresen and Michelsen 2005; Weih 2000; Weih et al. 1998), including measurements on sugar maple trees at Hubbard Brook (Campbell et al. 2014). Because mycorrhizal uptake of N is temperature sensitive, presumably increasing rapidly following the spring trigger, N uptake by trees could increase as the spring vernal period increases in duration. Increased plant uptake in spring is consistent with the observation that N losses from HBR watersheds have declined primarily during spring (Bernhardt et al. 2005).

Snow-removal experiments at HBR demonstrate that a shallower and shorter duration of winter snowpack results in fine root damage and mortaliy (Cleavitt et al. 2008; Comerford et al. 2013; Tierney et al. 2001) which leads to diminished rates of N uptake during the early growing season (Campbell et al. 2014). In another study at HBR, root ingrowth (with 2 mm mesh) and exclusion (with 50 μm mesh) cores were buried at six plots varying in winter snow and soil freezing depth and duration (Sorensen et al. 2016a). Root ingrowth over 2 years was positively related to winter soil frost depth and duration, likely due to the compensatory effect of belowground growth following damage induced by soil freezing. Interestingly, both greater winter soil freezing and the presence of roots resulted in significant reductions in soil net nitrification rates, suggesting that the contribution of climate change to N oligotrophication can be attributed to both direct effects of winter climate change on microbial activity and indirect effects mediated by plant roots.

Changes in hydrology and hydrologic flowpaths could also influence the retention of N overwinter and during spring to summer transitions. Greater precipitation as rain and less as snow in the winter and diminished snowpack likely result in greater infiltration of water and deeper flowpaths, allowing for greater N retention and decreases in hydrologic N losses (Fuss et al. 2016a). Alternatively, deeper flow paths, particularly those below the root zone, could actually enhance nitrate concentrations in streams by bypassing the active uptake zone (Gold et al. 2001).

Isotopic tracers provide a means for sorting out N dynamics during the winter/spring transition period. Two studies at HBR used enriched (99 at.% ^{15}N) tracer additions to better understand N cycling during winter and spring snowmelt periods. In the first study, ^{15}N-NO$_3$ was added to the surface of the snow in late winter (as $NH_4^{15}NO_3$), along with a conservative tracer (LiBr), to evaluate N retention processes in the snowpack and forest floor (Campbell et al. 2007b). Results indicate that approximately 50% of the $^{15}NO_3^-$ tracer that was lost from the snowpack after melt was recovered in soil leachate, suggesting that much of this N was retained in the forest floor during snowmelt.

In the second study, Campbell et al. (unpublished data), applied $^{15}NH_4Cl$ to the forest floor on low elevation (less snow, more frost) and high elevation (more snow, less frost) plots immediately before snowpack development. The purpose of this isotopic tracer addition was to improve understanding of the influence of changing climate on subnivean N cycling. The added ^{15}N-NH$_4$ was nitrified in the forest floor beneath the snowpack during winter in both high elevation and low elevation plots. However, lower rates of nitrification occurred in the low elevation plots in this experiment, demonstrating reduced nitrification in colder soils that occur in lower elevation soils with less snowpack accumulation. Other studies also demonstrate lower rates of N cycling in soils experiencing less snow and greater soil freezing in winter and in the following growing season as well (Durán et al. 2014, 2016; Sorensen et al. 2016a). The isotope studies confirm that soil N cycling processes during the early spring are significant, dynamic and sensitive to environmental conditions.

Conclusions

While much research over the past 30 years has focused on the deleterious effects of excess N on forests, recent observed declines in atmospheric N deposition in many areas around the world, and our analysis here, raise new concerns about N oligotrophication and limitation of forest productivity. While the advent of N oligotrophication will reduce concerns about the effects of excess N on air and water quality and forest health, it raises new concerns about forest productivity and capacity to dynamically respond to disturbance and environmental change. With less N, forests may grow more slowly than they would have under more N-rich conditions, they may be less able to exploit increases in atmospheric CO_2, and they may recover more slowly from disturbances such as soil freezing events.

Our analysis suggests that N oligotrophication in northern hardwood forests is driven by increased C flow from the atmosphere through plants and into soils that decreases available N production by mineralization by stimulating microbial immobilization, increasing N resorption by trees, and reducing litterfall N input to soils. Analysis of the flow of C from the atmosphere to plants and into soil in intact, mature forest ecosystems, and how this changes with increases in atmospheric CO_2, remains extremely challenging and will need to be addressed in future research.

Our analysis also suggests that N oligotrophication has been exacerbated by changes in climate that increase the length of the growing season and that alter conditions during the winter to spring transition period. Still, the balance between N loss (leaching, runoff, denitrification) and N retention (immobilization, plant uptake) processes during the early spring remains highly uncertain. There is a strong need for further research on N dynamics during this inherently dynamic, and now changing period.

Altogether, these results suggest that there is a need to re-evaluate the nature and extent of temperate forest N cycling and for a better understanding of how N oligotrophication will influence forest ecosystem response to multiple, dynamic components of global environmental change.

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